# SPATIAL ASSOCIATIVE MEMORY IN PIGEONS

by

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#### ABSTRACT

A series of six experiments was conducted examining spatial memory in pigeons. Spatial memory in this species has traditionally been characterized as poor in relation to other avian species, and this has led to speculations about adaptive specializations in spatial memory systems. The results from the experiments conducted in the present thesis in which novel procedures were used to study pigeons' spatial memory suggest that this characterization has been a result of the experimental procedures used to assess spatial memory, rather than an inherent lack of ability. The procedures that were employed in the current research are also novel in that they are consistent with a theoretical memory distinction proposed by Gaffan (1974) between recognition and associative memory. Recognition memory tasks are procedures in which only the to-be-remembered stimulus is presented during the study phase of a trial. The subject must subsequently discriminate between that stimulus and novel or unfamiliar stimuli during the retention test. Associative memory tasks are procedures in which all stimuli to be presented during the retention test are also presented during the study phase of the trial. In these tasks the subject must identify the target from among the presented set of stimuli and remember its identity when subsequently reexposed to the same stimulus set during the retention test.

In the current research, pigeons performed well with extended retention intervals when tested on an associative memory task but not

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when tested on a recognition memory task. The birds exposed to four spatial locations and given a brief interval to ascertain which one of the four locations was rewarded showed excellent retention for the rewarded location, for periods of up to 72 hr. This level of retention is far greater than that observed in previous spatial memory tasks with this species. The procedures that were employed here are somewhat similar to procedures that have been used to study spatial memory in food-storing birds (Brodbeck, Burack & Shettleworth, in press).

Although comparisons across experiments and procedures must be viewed with caution, the present results suggest that under some conditions, pigeons apparently perform better than food-storers on this type of task. As such the findings from the current research program have important implications in relation to the issue of adaptive specializations in memory systems and for the comparative study of spatial memory.

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#### INTRODUCTION

This thesis is about spatial memory in pigeons. This species has typically been characterized as having inferior spatial memory abilities in relation to other animals. The results from the current series of experiments suggest that this poor characterization is unjustified and that the level of performance obtained depends upon the nature of the test used to assess performance. Pigeons are apparently very sensitive to task variables and this dissertation identifies certain task variables that are important in mediating performance on spatial memory tasks. A theoretical memory distinction previously unexplored in pigeons, between recognition memory and associative memory (Gaffan, 1974) provides a useful framework for classifying the procedures used here. It also provides a potential bridge between the current work and work done with food-storing birds (i.e., Brodbeck, Burack & Shettleworth, in press) and has important implications for the issue of adaptive specializations in memory. As such, the approach adopted here is to paint a fairly broad picture of where the current research fits into the previously existing framework on the comparative study of spatial memory. It begins with a brief discussion of what comparative cognition is, how the study of comparative cognition has been approached, potential problems associated with the study of comparative cognition and how the procedures and findings from the current work help to alleviate those problems.

The working-associative-reference memory distinction first elaborated by Honig (1978) has been the dominant theoretical framework for the study of spatial memory in animals. However, this framework does not apply well to the procedures employed in the current research. An alternative framework, the recognition-associative memory distinction of Gaffan (1974), mentioned previously, is presented and the results from the current work are interpreted within that framework.

This is followed by a brief review of spatial memory research, in general, and a fairly detailed review of spatial memory research in pigeons. This information is presented to show that the spatial memory abilities of pigeons and other species are, when examined closely, more similar than is typically presented in the literature.

The procedures and theoretical positions adopted here have grown out of previous work conducted in this laboratory and that work is reviewed in detail below (Willson, 1988; Willson & Wilkie, 1991). In that work it was discovered that discrimination training between sample and distractor locations enhanced spatial memory performance. The first three experiments of this thesis are primarily concerned with examining the mechanisms by which this effect is mediated. It was suggested that the discrimination training enhanced attention to the location of the sample and the distractor, an effect that has been observed previously in delayed matching to sample with colour and shape stimuli (Urcuioli & Callender, 1989). The findings from the current research are not entirely consistent with that theoretical position and a reevaluation of

those results in terms of a distinction between recognition and associative memory is presented.

The final three experiments employ a novel associative memory procedure for examining spatial memory in pigeons. The main strength of the procedure is that it is conceptually simple and offers the subject flexibility in terms of how to solve the task. In brief, the pigeon is exposed to four illuminated pecking keys and must determine each day which key provides reinforcement. Memory for the location of the previously rewarded key is assessed during an initial unrewarded period at the start of each session. The birds show a strong tendency to begin responding each day at the location that had been rewarded during the previous session, even when that session occurred 72 hr previously. This level of performance is far beyond that previously seen with this species and may be comparable or better than the performance of foodstoring birds on a similar task (cf., Brodbeck *et al*, in press).

The findings, presented briefly above, are discussed in relation to previous work on spatial memory in pigeons as well as in relation to the issue of adaptive specializations.

### Some general comments on the study of comparative cognition

In a general sense, this thesis concerns aspects of comparative cognition. Comparative cognition has been defined as "...the study of the minds of organisms. Mind is the set of cognitive structures, processes, skills, and representations that intervene between experience

and behavior." (Roitblat, 1987 pp. 1-2). Mind in this instance implies nothing about consciousness, nor does it refer to any non-physical entity. It is intended only as a convenient term for summarizing a group of biological structures and processes that are not directly observable and must therefore be inferred from the behavior of the organism.

Comparative cognition occupies a somewhat unique position in the biological sciences because it arose out of very diverse parent disciplines. The roots of comparative cognition can be found in comparative psychology, ethology and behavioral ecology, cognitive science, and neuroscience. Scientific endeavors within comparative cognition have often served more than one master. Recent work with food-storing birds, corvids (i.e., crows, Clark's Nutcrackers) and parids (i.e., chickadees, tits) nicely illustrates this point (see Krebs, 1990, for an excellent review of this work).

Food-storing birds collect food (generally seeds and/or insects) during times of abundance, cache these food-items and subsequently recover these caches hours, days, weeks, even months later. Cache recovery is mediated by spatial memory. From the perspective of comparative psychology this phenomenal memory performance is of interest because it contrasts sharply with the observed performance of traditional laboratory species such as the rat. Efforts have centered on examining the similarities and differences between food-storing birds and other animals (see Sherry, 1984; Shettleworth, 1990). From the

perspective of ethology and behavioral ecology, food-storing birds have been studied in relation to Optimal Foraging Theory (Krebs, Ryan & Charnov, 1974) and in relation to the issue of adaptive specializations (Krebs, 1990). From the perspective of cognitive science, food-storing birds have been studied in relation to the theoretical issue of multiple versus unitary memory systems and attempts to generate criteria for distinguishing between those alternatives (see Sherry & Schacter, 1987). From the perspective of neuroscience, food-storing birds offer a unique opportunity for examining correlations between brain structure and behavior. Members of the corvidae and paridae families differ in the degree to which they depend on stored food and these differences in degree have been found to correlate well with differences in the size of the avian hippocampus in those species. The more reliant the species on stored food the larger the hippocampus (relative to brain and body size, reviewed in Krebs, 1990).

Two distinct but related approaches to the study of comparative cognition exist. One, the synthetic approach (Domjan & Galef, 1983; Kamil, 1987), advocates combining the methodology and theory of psychology with the insights of behavioral ecologists and ethologists into how animals use learning and memory in nature. Closely related species differing in some aspect of ecology are compared on tasks thought to reflect the abilities that they use in nature, and differences are attributed to the differences in ecology. In reality, this approach has been rather difficult to apply, given that it is

probably impossible to find closely related species that differ in only one or a limited number of aspects of their ecologies. Any inferences drawn must be interpreted cautiously. Nonetheless, work comparing storing and non-storing corvids (Balda & Kamil, 1989; Olson, 1991) and comparing storing and non-storing parids (Krebs, Healy & Shettleworth, 1990; Shettleworth, Krebs, Healy & Thomas, 1990) has provided promising, if somewhat complex, results at both the behavioural and anatomical level.

The more traditional approach to comparative work (Bitterman, 1975) advocates comparing very different species on traditional learning tasks. This is the most dominant approach adopted within comparative cognition but its utility has been questioned (Macphail, 1982) on the grounds that it has, thus far, shed very little light on the issue of species differences in cognitive abilities. Although Macphail does not advocate rejecting the traditional approach, he suggests that any differences that have been detected are probably attributable to differences in sensory or motor ability (Macphail, 1987).

One reason for this failure to detect cognitive differences is that the comparisons needed to make inferences about species differences within this approach has generally not been made. Comparisons between the performance of different species on a single task severely limit the types of conclusions that can be drawn, usually to the extent of concluding that species A is better than species B on task C. Comparisons across several related tasks fare no better, unless the

differences between species vary systematically as a function of task. If variation exists, a comparison of task demands can provide insight into the cognitive processes underlying behavior. An especially strong case can be built by comparing species on related tasks on which the differences in performance are reversed (i.e., species A is better on task C, species B is better on task D). This approach, called systematic variation, (Macphail, 1987) has been underutilized within comparative cognition.

Work on pigeon spatial memory, reviewed below, has not adopted the systematic variation approach, although more recent work has progressed in this direction (i.e., Spetch & Edwards, 1986; Willson & Wilkie, 1991). The conclusions advanced to date concerning pigeon spatial memory have been limited to the form "pigeons are apparently inferior to many other species on spatial memory tasks". Reasons for their apparent inferiority have often been couched in terms of an appeal to some aspect of pigeons' foraging ecology (see Bond, Cook & Lamb, 1981). An alternative explanation, initially proposed by Macphail (1982, 1987), is that procedural variables and/or sensory-motor ability differences account for all apparent differences in cognitive ability between species. In the specific case of pigeon spatial memory the weakness of this explanation is that attempts to design procedures on which pigeons perform at levels comparable to other species have, thus far, met with only limited success.

The position adopted in this thesis is not as extreme as the position adopted by Macphail (1982, 1987). Specialized cognitive abilities do exist (i.e., song learning). However, there are also cognitive abilities that are general. Spatial memory falls into the latter category. This hypothesis is at odds with the recent suggestion that spatial memory in food-storing birds is an example of an adaptive specialization (i.e., Krebs, 1990) but the findings from the current work showing levels of performance in pigeons far better than their performance on more traditional spatial memory tasks suggest that spatial memory as a general process is tenable.

The first section of this thesis builds upon previous work from our laboratory (Willson, 1988; Willson & Wilkie, 1991) examining spatial memory in the pigeon. In that work we demonstrated that pigeons' were much more proficient on some spatial memory tasks than previously believed. These experiments will be reviewed in detail below. Several questions remained unanswered in that research program and one of the goals of the experiments described here is to address these unresolved issues. Specifically, the issue of the mechanism by which the improved performance (relative to previous work) observed was mediated is explored. It is concluded that the abilities tested by the procedures employed here mostly closely resemble recognition and associative memory tasks. It is also concluded that the improved performance observed following discrimination training is partially the result of enhanced attention to the relevant sample dimension (i.e., spatial location) but

that this effect works in conjunction with the formation of associations between particular locations and the presence or absence of food.

This initial section begins with a a brief, general review of the study of spatial memory. The study of spatial memory in pigeons is then discussed in some detail, as are the results of our previous work. The six experiments that compose this thesis are then presented. The first three focus on the mechanisms that mediate the enhanced performance observed previously. The latter three experiments focus on a novel procedure for studying spatial memory and data are presented that suggest that the spatial memory abilities of pigeons are far better than previously thought. The thesis concludes with a discussion of the results and their implications for the comparative study of spatial memory and the issue of adaptive specializations in learning and memory.

### A Brief Review of Spatial Memory Research

The use of mazes to assess animal intelligence dates back to Small (1901) who used a miniature version of the Hampton Court maze to examine mental processes in the rat. Small used a maze because of its apparent similarity to the rat's natural environment (i.e., a series of interconnected burrows). He believed that one could accurately assess an animal's intelligence only through the use of apparatuses and procedures resembling the natural environment and the problems that an animal might encounter there. This idea, supported by many researchers

today, temporarily disappeared under the onslaught of the behaviorists' search for general principles of learning through the use of arbitrarily chosen stimuli, responses and testing environments, so that today the main contribution made by Small's research was the introduction of the use of mazes into comparative psychology, as well as the use of the comparative psychologists' favorite subject, the albino rat.

The use of mazes (and rats) in the study of learning quickly proliferated. Researchers, such as E.C. Tolman, who favoured a molar view of behavior as flexible and purposive, used mazes of various configurations to attack the molecular, reflex-based behaviorism of Hull and his associates. Tolman and his colleagues demonstrated such diverse phenomena as latent learning (Tolman & Honzik, 1930a,b), place learning (Tolman, Ritchie, & Kalish, 1946b) and short cut learning (Tolman, Ritchie & Kalish, 1946a), phenomena that were hard to reconcile with a strict S-R view of behavior. Tolman (1932) also introduced the idea of the "cognitive map", an idea that will be discussed in some detail below.

Researchers who supported the molecular S-R view of behavior also used mazes but their emphasis was on the automatic nature of maze running in well trained rats. For example, in one experiment rats were trained to run a maze by making a series of left-hand turns. One of the left-hand arms was subsequently blocked and the opposite arm made correct. Every subject initially failed to notice the change and "every one of the rats banged his nose into the end of the blind alley with

considerable violence" (Gingerelli, 1929, p. 255). Similarly, well trained rats ran over a pile of food placed in the middle of an alley, seemingly oblivious to its existence (Stoltz & Lott, 1964). These findings were hard to reconcile with the flexible view of behavior advocated by Tolman, and the molecular S-R view of Hull and his contemporaries (Hull, 1943) came to dominate until well into the 1960's. With the advent of the automated operant chamber, mazes and spatial learning tasks fell out of general use.

However, in the last 15 years the use of mazes and spatial learning tasks has once again come to the fore in animal learning and ideas first expressed by Tolman, such as the cognitive map, have received considerable attention. This reorientation was the result of a variety of factors. One such factor was the recognition of the distinction between "knowing" and "doing"; for example animals often have knowledge that is not manifested in overt behavior (e.g., Wilkie & Masson, 1976). A second factor was the introduction of tasks such as delayed matching to sample (DMTS - Blough, 1959) that could be solved only by responding on the basis of information that was not longer physically present and thus could be explained only by reference to some type of representation. A final factor was the rise of a more cognitive orientation in the study of human learning and this influence slowly spread to the study of animal learning. Many of the tasks devised to examine learning in animals during the 60's and 70's were meant as analogs of tasks used to study learning and memory in humans.

An example of this was the radial maze introduced by Olton and Samuelson (1976). The wagon-wheel shaped, eight-armed apparatus that they used to study short-term memory in the rat was initially viewed as a spatial analog to the learning of word lists in human cognitive psychology. In their procedure a rat was allowed to explore the maze freely until it had found all of the food hidden at the distal end of each arm. All arms were baited with a piece of food at the beginning of a trial. Olton and Samuelson's subjects proved to be very proficient at the task, quickly learning to visit each arm once without repetition. Various control manipulations ensured that the rats' performance was based on memory, not non-memorial strategies such as response algorithms or odor trails.

Since that seminal paper, work on spatial memory has concentrated on specifying its characteristics both within and between species. Considerable debate has arisen from both of these approaches and each will be discussed in turn.

Much of the debate about the characteristics of spatial memory has centered on how spatial information is represented in memory. Olton (1978, 1979) proposed that spatial memory was best conceptualized as a working memory with the following characteristics: 1) the capacity is large but limited, 2) accuracy declines as a function of memory load, 3) information does not decay over time, or at least very slowly, 4) there are no primacy or recency effects, 5) spatial memory can be reset at the

end of a test, and finally 6) storage is in the form of a list in which each place is individually represented.

However, several of these assumptions have been questioned, specifically the idea that spatial memory can be reset and that the nature of the representation is list-like. Evidence against the idea of resetting come from experiments showing proactive interference (Wright, Urcuioli & Sands, 1986) which will be examined first.

Spatial memory has proven highly resistant to interference, but recent experiments by Roberts and Dale (1981) have demonstrated that proactive interference can occur under some conditions. Their subjects received five trials per day on an eight arm radial maze. Roberts and Dale examined error patterns within the five trials. The rats never made errors on their first or second choices of any trial. However, the probability of making errors on the third through fifth choices clearly differed between the second and subsequent trials. On the first trial performance remained error free until after the fifth choice. On subsequent trials performance started to decline after the second choice, a finding consistent with the presence of proactive interference and incompatible with the notion of a resetting mechanism.

In an additional experiment Roberts and Dale showed that imposing a retention interval between a forced and free choice had differential effects depending upon whether the rats were being given their first, second, or third trial of the day. Accuracy was much lower following a retention interval on the second or third trial of the day relative to

accuracy on the first trial, a finding consistent with the presence of proactive interference and inconsistent with the notion of a resetting mechanism.

As a final bit of evidence against the notion of a resettable working memory, Dale and Roberts noted that their subjects tended to avoid alleys chosen during the latter part of trial N-1 when making their initial choices on trial N. If the rats were resetting working memory at the end of each trial initial choices on trial n should have been uncorrelated with choices on trial N-1. Clearly the rats were remembering their final choices on trial N-1 and avoiding those arms at the beginning of trial N (see also Roitblat & Harley, 1988).

The list-like nature of spatial memory has also been questioned. The notion of a cognitive map, an idea first proposed by Tolman (1948), has received considerable support. This evidence will be reviewed below but some initial comments about what constitutes a cognitive map are in order. A detailed examination of this issue is beyond the scope of the present discussion but a clarification of the terminology is warranted.

Tolman's choice of the term "cognitive map" was somewhat unfortunate because it implied the existence of a map per se. Tolman was using the concept as an analogy but it nonetheless led to images of cartographic maps located in the brain and also to images of homunculi poring over these maps. A better terminology would have been to refer to the process of cognitive mapping, a process rather than a structure. In essence, mapping refers to the application of a lawful system for

representing information. In the cartographic sense, mapping refers to the process of transforming an object set (physical space) into a representational set via a mapping function. The set definition establishes relations between places and the function specifies the relationships in physical space that will be maintained in the representational space (Downs, 1979). Note that mapping does not refer to the medium in which the representation is expressed. Maps are the end product of mapping but the physical medium of the map is largely independent of the mapping process. For example, one could use the same mapping system to draw a map on a piece of paper, a blackboard or on the beach. Of course the physical characteristic of the map can influence the accuracy and durability of the representation but this is independent of the rules by which the representation is constructed.

For the most part investigations of cognitive mapping have focussed on trying to specify the mapping function rather than the medium in which the mapping is expressed (see O'Keefe & Nadel, 1978 for a notable exception) and the term cognitive map has been used as a shorthand for how animals represent their physical world. As noted earlier the idea of a cognitive map was first introduced by Tolman and he and his associates conducted several experiments aimed at demonstrating that animals possessed far richer representations of physical space than suggested by the strict S-R theorists. The phenomena of shortcut learning (Tolman, Ritchie & Kalish, 1946a) and place learning (Tolman, Ritchie & Kalish, 1946b) were hard to reconcile

with S-R accounts of maze learning. They are also hard to reconcile with the list-like nature of spatial memory proposed by Olton (1978). However, these experiments proved to be hard to replicate (Gentry, Brown & Kaplan, 1947; Gentry, Brown & Lee, 1948) and have been justifiably criticized on logical grounds (Olton, 1979) so will not be described here. However, as is sometimes the case in science, ideas initially rejected as untenable later turn out to be well founded. Such was the case for the idea of cognitive mapping. More recent work has provided convincing demonstrations of shortcut learning and place learning (for an excellent review of these issues see Gallistel 1990, especially Chapter 5).

Menzel (1973, 1978), working with chimpanzees, demonstrated the phenomenon of shortcut learning in the following way. In one experiment a handler carried a chimp around a large enclosure and allowed the chimp to watch from close range while an experimenter hid food in 18 locations. The route taken on this food hiding expedition was convoluted and often recrossed paths already taken. Once all the food was hidden, the chimp was returned to its home cage and then released. The questions of interest were: 1) would the chimp remember where the food had been hidden and 2) if so, how would the chimp go about harvesting the hidden food? The answer to both questions was clear. The chimps remembered about 2/3rds of the hiding places and furthermore did not follow paths similar to those used during food-hiding, but minimized the distance travelled in collecting the food from the

remembered locations (see MacDonald & Wilkie, 1990 for a similar experiment with New World monkeys). These results are consistent with the notion of a cognitive mapping process in which the relationships between important locations are preserved (the nature of the relationships that are preserved will be addressed briefly below) and are hard to reconcile with a list-like representation of important locations as proposed by Olton (1978).

Place learning was demonstrated in an ingenious experiment by Morris (1981). His apparatus, the "water maze", consisted of a circular swimming pool filled with cool, opaque water. A single location in the pool contained a small, submerged platform and his subjects, rats, were released into the pool and allowed to swim around until they located this hidden platform. Swimming, especially in cool water, is mildly aversive to rats and the platform provided a means of escaping the water. After a few trials the rats swam directly to the position of the platform regardless of whether they were released from the original training position or, as was demonstrated in subsequent transfer tests, from a novel position; even if the platform was moved to a new location. When they failed to find the platform in its expected location they spent some time searching near that location before expanding the search area. Clearly, the rats learned a place rather than a response and that place was defined in terms of the relationships between environmental cues outside of the pool (since there were no local cues present).

Work by Gould (1984, 1986, 1987) with bees and by Suzucki, Augerinos and Black (1980) with rats also supports the notion of cognitive mapping. Previous work with bees has shown that bees captured as they leave the hive and transported in darkness to a feeding site hundreds of yards away and out of sight of the hive can, when released, fly straight back to the hive (Gould, 1984). In an additional experiment, foragers were transported to a feeding site that was either in the middle of a lake or on the far shore. After feeding they were allowed to return to the hive and dance. Dancers that had been fed on the far shore of the lake successfully recruited other bees. Dancers that had been fed in the middle of the lake did not, suggesting that the potential recruits extract some information about location from the dance and make judgements on it about the suitability of the advertised site (Gould, 1984). Although suggestive of cognitive mapping, these findings can also be explained by reference to "route-specific memory" (Wehner, 1981).

A more convincing demonstration of cognitive mapping comes from an experiment in which Gould (1986) trained individual bees to forage at a feeding station (A). The bees quickly learned to fly straight from the hive to the feeding station. Gould subsequently captured these foragers as they left the hive and transported them, in darkness, to another site (B). When released, the bees headed directly towards Site A, their original destination, even though it was not visible and the bees had never flown between Sites A and B before. Various control conditions

were run that insured that the observed performance could not be explained by anything other than cognitive mapping.

In a series of experiments, Suzuki, Augerinos and Black (1980) examined the role of extramaze cues in spatial memory. They trained rats on an eight-arm radial maze that was enclosed in a large cylindrical chamber on whose walls extramaze cues could be mounted. Extramaze cues facilitated performance. Rats trained without extramaze cues tended to respond in stereotyped response chains. Transposition of the extramaze cues disrupted performance but rotation of the entire extramaze cue array did not. Suzuki *et al* concluded that their subjects used a map-like representation of the extramaze cues to remember the arms on the maze that they had previously visited.

More recent work has focussed on the mapping function (i.e., Cheng & Gallistel, 1984; Gallistel, 1990); the types of relationships in the physical environment that are maintained during cognitive mapping. Although it seems highly unlikely that animals would form incorrect representations of space, their representations could vary in completeness.

For example, Cheng and Gallistel (1984) have described a mapping function in which only a small subset of Euclidean properties are maintained. In this system important locations are assumed to lie at a point that is an intersection of several straight lines, each of which has two other distinct landmarks on it, one on each side of the important location. The animal represents the fact that the important

location lies at the intersection of lines between the pairs of landmarks. The animal arrives at the goal by attempting to position itself between the various pairs of landmarks. In this system order properties of space are represented, but metric properties of space such as distance and angular separation are not. Cheng and Gallistel have suggested that this might be the type of representation that digger wasps use to find their burrows (Thorpe, 1950).

Additional work by Cheng and Gallistel also demonstrated that rats represent metric properties of space. Rats were trained in an X-shaped maze in which the distal end of each arm was baited with food. One arm contained 18 food pellets, another six, another one and the last was empty. Each arm was associated with a unique landmark. The subjects quickly learned to visit the 18 pellet arm first followed by the six pellet arm, etc. Cheng and Gallistel then performed a series of affine transformations. Affine transformations are transformations that maintain all non-metric properties of space. This was accomplished by moving each landmark to a neighboring corner. This transformation severely disrupted performance suggesting that the rats were representing metric properties of space.

In summary, current conceptions of spatial memory suggest that spatial information is represented in "map-like form" and that many animals represent metric as well as relational properties of space. Locations are encoded in terms of nearby landmarks. Spatial memory is

highly resistant to interference effects and has a large, but probably limited capacity.

### Comparative Spatial Cognition

The vast majority of spatial memory research has been conducted with rats. However, examining spatial memory in other species is important. If we assume, reasonably, that some form of spatial memory developed early on in evolutionary history, its evolutionary history is likely to have been highly convoluted with many false starts, divergences and convergences. We can learn much from studying the variations. An example should help clarify this point.

Consider birds and bats. Both can fly. However, the means by which they accomplish flight are very different. This is a clear example of convergent evolution; different mechanisms for solving the same problem. From a structural point of view comparing the two is like comparing apples and oranges. The wing structures are very different. However, from a functional point of view comparing the two can be very useful because both mechanisms accomplish the same goal. They get the animal off the ground and keep it aloft. If we are interested in flight per se we can learn a lot by comparing the similarities and differences. We can learn what aspects of the ability are general and what aspects are specific to the particular structures involved. The same can be said of any cognitive ability, including spatial memory.

Research on spatial memory has focussed on examining differences and similarities between species (these comparisons have until recently been accomplished by examining a series of single species experiments). Even a brief survey of the range and number of species tested would be beyond the scope of the present thesis. People (Aadland, Beatty & Maki, 1985), birds (Balda, 1980), fish (Roitblat, Tham & Golub, 1982), other rodents (Wilkie & Slobin, 1981) and even insects (Gould, 1984) have all been tested on a variety of different spatial memory tasks and the list continues to grow. To summarize briefly, these various experiments have revealed that animals form representations of space and that the strength or completeness of those representations vary (see Gallistel, 1990, ch. 1-6, for a good overview of much of this research). In addition, these comparisons have revealed striking differences in the capacity and durability with which spatial information is represented.

On the one hand, we have the rather remarkable spatial memory of the food-storing birds mentioned previously. Their ability to remember hundreds of cache sites for extended periods of time has frequently been contrasted with the abilities of other species (Sherry, 1984; Sherry & Schacter, 1987; Shettleworth, 1985) and has led to speculation that this ability may be an adaptive specialization. As mentioned previously, the existence of adaptive specializations has proved to be rather difficult to pin down at the behavioral level and to date the sparse experimental evidence that does exist has been messy (see Krebs, 1990).

On the other hand, we have another favorite laboratory species, the pigeon. The spatial memory abilities of pigeons, when tested with laboratory procedures, are apparently rather limited (see Bond, Cook & Lamb, 1981). This contrasts sharply with the remarkable spatial abilities demonstrated by this species outside the laboratory (i.e., homing). Since this paradox is likely an artifact of the testing procedures in the laboratory, these procedures will be examined in some detail in the next section.

## SPATIAL MEMORY RESEARCH IN PIGEONS

The approach adopted in this section is to examine the major experiments on spatial memory in pigeons, individually and in some detail, in a roughly chronological order. This previous work can be broadly classified as maze studies and delayed matching of key location studies (DMKL, see Wilkie & Summers, 1982). Both lines of research are relevant to the present thesis and will be examined separately. There are many apparent contradictions in the data but in a later section the major findings are summarized and some tentative reasons for these apparent differences in pigeons' spatial memory abilities are discussed. Readers interested in only the main themes of the research can safely proceed to this later section (p. 51). Work from our own laboratory on pigeon spatial memory, upon which the current research is based is examined separately in a later section.

BOND, COOK AND LAMB (1981)

One of the first systematic examinations of spatial memory in pigeons was conducted by Bond, Cook and Lamb (1981). They compared the performance of pigeons and rats on a radial arm maze. An idea predominant at the time, and still predominant (see Roitblat, 1987), was that an animal's foraging ecology would influence the evolution of its cognitive abilities. One variation on this theme was what Bond et al termed the "resource-distribution hypothesis". Olton and Schlosberg (1978) had suggested that animals for whom food resources were diffusely distributed, irregularly available and easily depleted should systematically avoid recently exploited resources and that these animals should demonstrate proficient working memory for recently exploited locations (Bond et al called this event memory). The successful performance of rats on the radial maze reflected this "win-shift" tendency. Individuals for whom food resources were concentrated and dependable should tend to return to the same site, to use a "win-stay" strategy and poor working memory because the problem can be solved solely through the use of reference memory.

There was abundant evidence that some animals could use a "winshift" strategy (Gill & Wolf, 1977; Kamil, 1978; Olton & Schlosberg, 1978) and that this ability was mediated by memory. However, evidence for poor working memory in a species that exploited dependable and abundant food sources was lacking. Bond *et al* examined the foraging

ecology of the domestic pigeon and concluded that the pigeon seemed a likely candidate to exhibit this tendency.

Pigeons feed in locations that are not readily depleted in a single foraging bout, are gregarious foragers that use the presence of other birds as a signal for the occurrence of locally abundant food resources and use traditional feeding sites (Goodwin, 1967). Furthermore, field observations had suggested excellent reference memory for previously profitable sites even after absences of a year or more (Levi, 1974). Subsequent work by Vaughan and Green (1984), mentioned previously, has confirmed that pigeons have excellent reference memories. For these reasons, Bond *et al* decided to compare rats' and pigeons' performance on the radial arm maze.

The results of Bond *et al's* experiment at least partially confirmed their hypothesis. Pigeons were far inferior to rats. In fact, the performance of the pigeons was so poor that the authors were unable to rule out the possibility that the pigeons were using some nonmemorial strategy to solve the radial maze task. They recognized that their experimental design was weak and considered the possibility that task variables or other ecological variables could also have been responsible for the observed differences between rats and pigeons.

# WILKIE, SPETCH AND CHEW (1981)

At about this time, Wilkie, Spetch and Chew (1981) published a report on short-term memory for location in the ring-dove, a species

closely related to the pigeon. Their apparatus was a modified radial maze, consisting of two parallel levels of seven arms. The levels were separated by a vertical distance of 30 cm and the entrances to adjacent arms on a given level were also 30 cm apart. The arms of the maze consisted of tubes 8 cm in diameter and 14 cm long. There was a perch at the entrance to each arm but food was visible only once an arm was actually entered. At the beginning of each session all arms were baited with a small amount of food and sessions continued until a subject had made 14 choices. A choice was defined as landing on a perch in front of a tube.

Although initial training was extensive (approximately 100 sessions), at asymptote the bird performed at levels far above chance. On average, the birds were correct on 80% of their 14 choices (chance was 64.5%). Interestingly, Wilkie *et al* also considered the role of foraging ecology in the evolution of spatial abilities and concluded that the conditions were quite conducive to the evolution of a proficient spatial working memory.

### OLSON AND MAKI (1983)

An additional experiment questioning the generality of Bond *et al's* findings was presented by Olson and Maki (1983), who demonstrated that pigeons could perform well on a delayed alternation task. This type of task requires both an accurate working memory and the use of a "win-shift" strategy. Olson and Maki trained pigeons to perform a
delayed alternation task on a T-maze. Each trial began with a forced choice in which the subjects were allowed to enter the unblocked arm of the maze and consume a small amount of grain. They were then removed from the maze, returned to the start box and then given a free choice between the two arms. Choice of the novel arm was reinforced but choice of the familiar arm was not.

Pigeons acquired this task quickly, and their accurate responding depended upon the use of extramaze cues. Furthermore, they could tolerate delays between the forced and free choices of up to 16 min. Also of interest was the fact that the pigeons readily learned a "winshift" version of the task but not a "win-stay". These same authors failed to find good performance by pigeons on a radial arm maze (unpublished observations described in Olson & Maki, 1983).

## ROBERTS AND VAN VELDHUIZEN (1985)

Roberts and Van Veldhuizen's (1985) experiment was motivated in large part by the contradiction between the results of the three experiments described previously. They reasoned that pigeons' performance on the radial maze might be improved if initial training took the form of a gradual introduction to the requirements of the task. Their subjects were initially trained with only two arms of the maze available. The number of available arms was gradually increased until the birds were choosing freely amongst all eight arms (only four arms were used in some experiments).

The results of a series of seven experiments were reported. In the first experiment it was demonstrated that pigeons could remember visits to four arms, a level of performance better than that suggested by the research of Bond *et al.* In the second experiment, pigeons were allowed to choose freely amongst all eight arms and Roberts & Van Veldhuizen concluded that the pigeons performed at a level comparable to that seen in rats. The third experiment demonstrated the phenomenon of proactive interference (PI). When tested with massed trials, the birds accuracy on later trials was inferior to their accuracy on earlier trials. Roberts and Dale (1981) had previously demonstrated this phenomenon in rats.

In their fourth experiment, Roberts and Van Veldhuizen investigated the effects of imposing a retention interval between four forced choices and an opportunity to choose freely between all eight arms. Performance declined following a delay but was still above chance at the longest retention interval tested (5 min). In the fifth experiment, the question of whether the observed radial maze performance was based on the use of intramaze or extramaze cues was investigated. Performance dropped when intramaze cues were removed but still remained well above chance. The authors concluded that the pigeons were using both intramaze and extramaze cues. The final two experiments examined reference memory. In one experiment only four of the arms of the maze were baited but the same arms were baited each day. The pigeons quickly learned to visit only the baited arms and rarely re-visited an arm

during a trial once it had been visited. In the last experiment, four arms were again baited each day but the arms differed in terms of how much grain they contained at the beginning of the session. One alley always contained 9 g of grain, another 3 g, another 0.5 g and the last was empty. The birds quickly learned to visit the alleys in a sequence corresponding to the amount of grain located there. Initial choices were most often directed to the 9-g alley, second choices were usually directed towards the 3-g alley, etc. The now unbaited alley was rarely visited. These results clearly indicated that the pigeons quickly formed a reference memory of which alleys did and did not contain food and, furthermore, that they could also learn associations between particular locations and particular amounts of food. Similar findings had been observed with rats (Hulse & O'Leary, 1982; Olton & Papas, 1979).

Roberts and Van Veldhuizen concluded that spatial memory was similar in pigeons and rats, differing only in capacity (perhaps) and durability. To explain the necessity of special training the authors appealed to the notion of "preparedness to learn" (Seligman, 1970). The "resource-distribution" hypothesis, mentioned above, is an example of this type of hypothesis (i.e., because of evolutionary pressure certain animals are predisposed to learn particular tasks). Roberts and Van Veldhuizen suggested that the confining nature of radial mazes and their strictly defined pathways might initially inhibit pigeons' performance,

given that pigeon foraging behavior has evolved to cope with foraging in open, unconfined spaces.

#### SPETCH AND COLLEAGUES

Spetch and her colleagues have conducted a number of studies examining spatial memory in pigeons using a modified version of the radial maze. The "walking maze" consists of a number of feeding stations in a large room. The pigeon's task is to visit each feeding station and collect the grain contained there. The path between feeding stations is not constrained in any way and the feeding stations can be set up in any configuration. This open-field type of arrangement was designed to be more similar to the pigeons' natural foraging environment.

### Spetch and Edwards (1986)

Spetch and Edwards' first attempt to study pigeons' spatial memory in an open-field type of environment was a qualified success. Their initial apparatus consisted of eight wall-mounted feeders and the birds' task was to visit each feeder by flying up to a perch mounted on the wall. The birds learned the task quickly and performed above chance levels of accuracy without special training but the procedure was problematic. The subjects often took considerable amounts of time between choices, in effect imposing their own retention intervals. Baseline performance, although above chance, was low. These factors

made it rather difficult to make some inferences about what the birds were doing and how they were doing it (i.e., how temporally persistent was their working memory?). Goodwin (1967, 1983) had noted that pigeons are predominantly ground feeders and that the tendency to go to the ground to feed might be innate (Goodwin, 1954). These observations suggested to Spetch and Edwards that a ground level open-field arrangement of feeders might be a better set-up for examining spatial memory in pigeons. This "walking maze" open-field arrangement also afforded the authors a greater degree of flexibility in terms of the spatial organization of the testing environment. Horner (1984) had previously shown that the structure of a maze can influence both accuracy and the tendency to use non-memorial strategies on spatial memory tasks. Spetch and Edwards wished to see if pigeons would show a similar tendency.

The results of their second experiment showed clearly that the birds were using spatial memory to solve the open-field task and that performance was largely controlled by extramaze cues. The configuration of the maze (they compared circular and linear arrangements of feeders) did influence the pigeons' patterns of responding: when the feeders were relatively far apart the birds showed a tendency to minimize travel distance (Menzel, 1973, 1978) but this tendency could not completely account for the observed level of performance.

#### Spetch and Edwards (1988)

Spetch and Edwards also used a version of the "walking maze" to examine pigeons' use of global and local cues in spatial memory. Global cues refer to those cues that are macroscopic or large-scale features of the environment (Gallistel, 1990). Local cues are cues particular to specific places within the environment. This distinction is similar to the extramaze-intramaze cue distinction used previously. The subjects were initially trained in a situation in which both global and local cues could be used to locate a baited feeder between two unbaited feeders. The middle feeder was always baited and the three feeders were always located in the same room position. In this arrangement, the two unbaited feeders served as local cues and the features of the testing room served as global cues.

In a series of subsequent unreinforced tests, the testing environment was manipulated in various ways to examine the birds' reliance on global and local cues. In one test, global and local cues were pitted against each other by shifting the complete array of feeders laterally. After the shift, one of the end feeders was in the correct room position (as defined by global cues) but the middle feeder was still in the correct location based on the configuration of the local cues. The pigeons showed a strong tendency to choose the middle feeder, suggesting that their choice behavior was controlled by the local cues. In another test, local cues were eliminated by removing one of the end feeders. Nonetheless the birds nearly always chose the feeder located

in the correct room position, a finding that suggests that the birds could also respond based on the configuration of global cues. In a final test, global cues were eliminated by moving the test array to a novel room position. The pigeons' strong tendency to visit the middle feeder on these tests could be explained only by the use of local cues. On the basis of these results, Spetch and Edwards concluded that pigeons encode both global and local cues but that the type of cue used to guide behavior is situation specific with redundant cues being hierarchically organized.

#### Spetch and Honig (1988)

Spetch and Honig also conducted a series of experiments using the "walking maze". Previous work with rats had suggested that maze performance was best under conditions in which the animal was allowed to form a cognitive map of the testing environment (Suzucki *et al*, 1980). Rearranging the positions of the available cues within the testing environment between trials inhibits (but does not eliminate) accurate performance of the radial maze task. Spetch and Honig examined whether a similar phenomenon would be observed with pigeons. They were also interested in how temporally persistent spatial information was in pigeons' working memory. Previous work (Olson & Maki, 1983; Roberts & Van Veldhuizen, 1985; Spetch & Edwards, 1986) had examined this issue with different apparatuses (Spetch and Edwards used the "flight" maze) but it had not been examined using the "walking maze".

In one experiment, they compared two groups of pigeons. For one group, the features of the testing environment remained constant from trial to trial (the Constant group). For the other group, the features of the environment were rearranged between trials (The Variable group). It was not possible to rearrange all features of the environment (i.e., walls, doors, windows, etc.), so only a subset of those features (i.e., those that were portable) was rearranged. The Constant group clearly performed better than the Variable group. Honig and Spetch concluded that an intact cognitive map facilitated performance on the working memory problem although it was not necessary for performance. They also considered the possibility that the observed differences might have been due to differences in the "richness" of the map. Because it was impossible to manipulate all features of the testing environment, it is possible that the performance of the Variable group was also mediated by an intact cognitive map of the environment, albeit one based on fewer cues.

In their second experiment, Spetch and Honig examined the temporal persistence of spatial information on the walking maze task. Trials began with four forced choices. Once a bird had visited all four available sites it was removed to a small holding cage. Following a delay of up to 2 hr, the pigeon was released into the testing environment and allowed to choose freely between all eight feeding sites. On average, the birds performed well with delays of up to 32 min but performed at chance levels when tested with a delay of 2 hr.

Spetch (1990)

Roberts and Van Veldhuizen (1985) suggested that pigeons' performance on spatial memory tasks might be influenced by memory load. Dale (1988, see below) has reiterated this point. Memory load refers to the number of items currently held in working memory. The suggestion is that temporal persistence and memory load are negatively correlated. The greater the memory load the lower the temporal persistence and vice versa. Roberts and Van Veldhuizen cited this as the main factor underlying the difference in temporal persistence observed in the work of Olson and Maki (1983) and their own research. In the former case the memory load was assumed to be one (i.e., one arm of a T-maze) and temporal persistence was at least 16 min. In the latter case, the memory load was assumed to be four (i.e., four forced choices on an eight arm radial maze) and performance dropped to chance levels after a delay of only 5 min. Spetch directly tested this hypothesis by varying the number of forced choices given to pigeons on the walking maze prior to a retention interval.

She found no effect of memory load. Memory for previously visited sites declined as a function of increasing retention interval (RI) but the forgetting function was similar under all memory load conditions (two, four, or six forced choices prior to the RI). In all conditions performance was still above chance levels with a 60-min RI. In an additional experiment she demonstrated that the observed performance was

due to spatial memory and that control of responding was based on the global cues inherent to the testing environment.

#### DALE (1988)

Dale has also examined spatial memory in pigeons using a four arm radial maze constructed of chicken wire. His choice of this particular apparatus was founded on an interest in four aspects of pigeons' performance on maze tasks.

The inferior performance of pigeons on the radial maze relative to their performance on the walking maze has often been attributed to the constrained nature of available response paths in the radial maze (i.e., subjects must return to the center platform between choices, Spetch & Edwards, 1986). Dale reasoned that another potentially confounding factor was the availability of extramaze cues. Radial mazes, at least those used with pigeons, restrict the view of the surrounding environment. By constructing his maze of chicken wire, Dale removed this restriction but left the response paths constrained.

Dale was also interested in the memory load hypothesis (see previous section). He reasoned that performance on a four arm maze should fall somewhere between that observed in a T-maze (Olson & Maki, 1983) and on an eight arm radial maze (Roberts & Van Veldhuizen, 1985) if this hypothesis had merit. His study preceded that of Spetch (1990) so he was unaware of her results.

Spetch and her colleagues had examined the importance of intramaze and extramaze cues in pigeon spatial memory in a variety of ways (Spetch & Edwards, 1986, 1988; Spetch & Honig, 1988; Spetch, 1990) but the nature of the possible transformations that they had examined was constrained by the nature of the apparatus that they used (i.e., it was difficult to manipulate extramaze cues). Dale used a rotation procedure to manipulate the relationship between intramaze and extramaze. In this procedure once the subjects have acquired the task, the maze is rotated in relation to the surround. This manipulation has been used successfully to investigate the relative importance of intramaze and extramaze cues in rats (Dale & Innis, 1986; Suzucki *et al*, 1980).

As a final manipulation, Dale examined whether pigeons could reexamine spatial memory following an error and then respond appropriately. Previous research had revealed that errors in memory paradigms are not always due to forgetting (Roitblat & Scopatz, 1983; Wilkie & Spetch, 1981).

The procedure that he used was fairly straightforward. Pigeons were given three forced choices, removed from the apparatus and, following a delay, given two opportunities to choose the remaining arm. In some conditions the maze was rotated by 90 degrees.

The subjects acquired the task quickly and performed well with delays of up to 5 min. Accuracy on second choices was above chance levels with RI's of up to 30 min. The results of the maze rotation manipulation suggested that the pigeons responded on the basis of room

(i.e., extramaze) cues. Following the rotation, the pigeons generally went to the arm that was "correct" relative to the room cues rather than the arm that was "correct" relative to the maze (i.e, the "correct" place rather than the "correct" arm).

Dale concluded that spatial memory in pigeons was similar to that of rats but that rats seemed better able to remember events in spatial memory in the face of extended delays. Furthermore, he concluded that memory load could influence performance (recall that he was unaware of Spetch's (1990) results). In addition, he concluded that pigeons could reexamine spatial memory and respond appropriately based on that reexamination.

#### ROBERTS (1988)

Roberts (1988), using a modified version of the walking maze, has examined pigeon spatial memory in a simulated patchy environment. He discussed his results in relation to Optimal Foraging Theory (OFT) as well as memory, but the aspects of his data relating to OFT are irrelevant to the present thesis and are therefore not discussed. He set up four "patches" within a large room and allowed his subjects to explore freely. Patches consisted of circular arrangements of eight feeding stations and were differentiated both by their location within the room and by the amount of food that they contained at the beginning of a session. The amount of food available per patch was varied by manipulating either the amount of food contained per feeder or by

varying the proportion of feeders within a patch that were baited. The locations of the patches was held constant from session to session, as was the amount of food that they contained at the beginning of the session.

Roberts found good evidence of memory for patch characteristics under some conditions but not others. When food density per patch was manipulated by varying the amount of food contained in each feeder, the pigeons tended to visit the richer patches first and to spend more time there. They also tended to visit all patches before making repeat visits. When food density was varied by manipulating the proportion of baited feeders per patch, the birds responded similarly but without visiting the richest patch first. Initial patch choice was unrelated to food density.

Even under conditions in which the pigeons demonstrated accurate memory for patch characteristics, they showed little evidence for memory of visits to feeders within patches. When re-visiting a patch, the birds were as likely to visit depleted feeders as to visit full ones.

Roberts concluded that the birds exhibited excellent reference and working memory for patches but little working memory for visits within patches. He suggested that this poor within-patch working memory may have been a result of the similarity between patches. Although the patches were spatially distinct, each feeder within a patch was physically identical (in fact, all 32 feeders were physically identical). Thus the discrimination between feeders within a patch was

probably extremely difficult, and visits to other patches may have interfered with the ability to recall visits within a particular patch (proactive interference). Although Spetch and Edwards (1986) had demonstrated that pigeons could perform well on the walking maze with eight physically identical feeders, Roberts concluded that the combination of physical similarity and proactive interference was probably responsible for the pigeons poor memory performance within patches.

# ZENTALL, STEIRN AND JACKSON-SMITH (1990)

Zentall and his colleagues have developed an operant analog to the radial maze. In their task pigeons are confronted with an array of five illuminated pecking keys. For some birds, this array was linear (L), for others it was a two-dimensional matrix (M). For some birds all five keys were illuminated with white light (W) and for other birds each key was illuminated with a distinctive hue (H). To receive reinforcement, a pigeon had to peck five times consecutively at the same key. These five pecks constituted a "choice". Only the first choice of a particular key was reinforced. The birds were allowed to go through the sequence of keys in a self-determined sequence. Once they had chosen all five keys, the chamber was darkened and after a brief intertrial interval (ITI), another trial began. Zentall *et al* interpolated delays at various points in the choice sequence and manipulated the number of responses that constituted a choice.

All subjects learned the task but birds in the M group and the H groups learned faster. Somewhat surprisingly, birds for whom the keys were in a matrix and distinctively coloured did not learn faster than birds for whom either space or colour were distinct. The number of responses that constituted a choice did not affect the speed at which the birds acquired the task. It did, however, affect how well the pigeons remembered their previous choices. When 20 responses constituted a choice, there was little evidence of forgetting, even with delays of up to an 1 hr. The point at which the delay was interpolated into the response sequence also affected performance. Delays interpolated between the second and third choice or between the third and fourth choice were more detrimental than delays interpolated between the first and second choice or between the fourth and fifth choice. Zentall et al interpreted this result in terms of flexible coding. If the delay occurred before the mid-point of the trial the pigeon encoded previous choices (a retrospective strategy), after the mid-point the pigeon encoded choices yet to be made (prospective coding).

### WILKIE AND COLLEAGUES

Up to this point the discussion of pigeon spatial memory has primarily focussed on maze or maze analog studies of various types. Memory for non-spatial stimuli in pigeons has typically been studied using operant procedures such as delayed matching to sample (DMTS). Wilkie and his colleagues have conducted an extensive series of

experiments examining pigeon spatial memory using an operant procedure delayed matching of key location (DMKL, Wilkie & Summers, 1982; see also, Smith, Attwood, & Nieorowski, 1982) that is a spatial version of DMTS. In this procedure, the pigeon faces a small, 3 X 3 matrix of pecking keys. At the start of a trial one of these keys (the sample) is illuminated briefly, usually for about 2 sec. The key is then extinguished and following a delay it is re-illuminated together with another randomly chosen key from the array (the distractor). These keys remain lit until the subject responds. If the pigeon chooses the sample, the keys extinguish and the bird is rewarded with a brief access to grain. If the bird chooses the distractor, both keys extinguish and an intertrial interval (ITI) begins.

## Wilkie and Summers (1982), Wilkie (1983a)

In their initial study of DMKL, Wilkie and Summers examined acquisition, sample duration, retention and memory load. Acquisition was rapid. Most of their subjects reached asymptotic levels of performance (80-90% correct) within 30 sessions (36 trials per session). However, levels of performance were better than chance (50%) much sooner than this, in some cases during the very first session. There was no effect of sample location. All positions in the nine key array were matched with equal accuracy. There was, however, an effect of distractor location. Trials on which distractors appeared close to the sample location resulted in lower levels of performance than trials on

which the distractor was distant from the sample. Performance was above chance on both trial types. Accuracy was also effected by the number of distractors illuminated during the test phase of a trial.

In one experiment, sample presentation was followed by illumination of the sample plus one randomly chosen distractor or by the illumination of the entire nine key array. Accuracy on the latter trial type was significantly lower than on the former, although still above chance. As in the previous experiment, distractors close to the sample location were more likely to be chosen than distractors far from the sample location.

In another experiment, Wilkie and Summers systematically varied sample and delay duration. Grant (1976) had previously demonstrated that longer sample durations improved retention in delayed matching with colour stimuli. The same effect was found in DMKL. Longer samples (maximum = 2 sec.) were remembered better than short (minimum = 0.2 sec.). With 1 sec samples, performance dropped to chance levels following a delay of only 8 sec between sample presentation and sample/distractor presentation. In a final experiment, Wilkie and Summers varied the number of sample locations presented at the start of each trial. On some trials, only one sample location was presented. On other trials, three sample locations were presented in either a linear (row, column or diagonal) or random relationship. Following a 1 sec delay, a sample and one distractor were illuminated. On three sample trials, the test sample was chosen randomly from the set of three

presented initially. Accuracy was better on one sample trials relative to three sample trials but above chance on both. Performance on linear three sample trials was better than on random three sample trials. Within the range of linear three sample trials, row and column samples were remembered better than diagonal samples.

In an additional experiment, Wilkie (1983a) demonstrated that the observed level of matching performance in DMKL generalized to matching of locations that the pigeons had never encountered previously. He trained pigeons on the DMKL task using only a subset of the nine possible location sample stimuli. He then ran a series of transfer tests in which all nine sample locations served as samples. Four of his five subjects performed as well with novel locations as sample stimuli as they did with familiar sample stimuli, a result suggesting that the birds had learned a generalized rule of the form "choose the location that matches the sample".

#### Wilkie (1983b)

Wilkie next turned his attention to the issue of retroactive interference. Retroactive interference refers to the potentially disrupting effects of behaviors or stimuli that occur between the to-beremembered stimulus and tests for memory of that stimulus. DMTS can be disrupted when events intervene between sample presentation and testing (Cook, 1980), but radial maze performance in rats is quite insensitive to such interference, occurring only when the intervening stimuli are

highly similar to the to-be-remembered stimuli (Roberts, 1981). Wilkie found a similar effect in DMKL. Changes in illumination during a retention interval did not affect matching accuracy. However, presenting an additional spatial stimulus did. If the interpolated stimulus matched the sample location, accuracy was enhanced relative to trials in which no interpolated stimulus was presented. If the interpolated stimulus matched the (as yet unseen) distractor stimulus, accuracy declined sharply to chance levels. An irrelevant stimulus presented during the retention interval also disrupted performance but not as severely as presenting the distractor. Additional manipulations ensured that the subjects were not simply remembering the last location seen.

### Wilkie (1984, 1986)

Wilkie has also addressed the issue of proactive interference (PI). The presence of proactive interference in spatial memory argues against the notion of a resettable memory (see the discussion of spatial memory above). Robert and Dale (1981) had demonstrated that PI occurs on spatial tasks under some conditions with rats. Roberts and Van Veldhuizen (1985) had also demonstrated PI in pigeons on the radial maze. Wilkie conducted a series of experiments to see if PI also occurred in DMKL.

In one series of experiments, Wilkie (1984) manipulated ITI and RI length. He found that matching accuracy declined as a function of

decreasing ITI and as a function of increasing RI. Although this finding was consistent with the presence of PI, Wilkie was cautious in his interpretation because these data were also explicable by an appeal to differential expectancies of reward during trials and intertrial intervals. Shortening the ITI and lengthening the RI both reduce the difference in expectations. In other words, the pigeons have a high expectation of reward during a trial and a low expectation of reward during the ITI. Increasing the RI decreases the expectation of reward during the trial. Decreasing the ITI increases the expectation of reward during the ITI. Wilkie favoured this latter interpretation of his results.

In two additional experiments he demonstrated that presenting noncontingent reinforcement during the ITI resulted in a decrease in matching accuracy (cf., Gamzu & Williams, 1971) but that presenting response contingent reinforcement facilitated performance irrespective of the reinforced locations' relationship to the trial stimuli. Reinforced sample presentations (the sample from the next scheduled trial), distractor presentations (the distractor from the next scheduled trial) or an irrelevant location all facilitated performance. Nonreinforced sample presentations during the ITI disrupted matching performance but non-reinforced distractor or irrelevant location presentations had no consistent effects. Wilkie interpreted these results as being more consistent with the differential reward

expectancies explanation and concluded that in some respects DMKL resembled classical conditioning.

In another series of experiments, Wilkie (1986) again examined the issue of PI. One manifestation of PI is that performance on later trials within a session should be poorer than performance on earlier trials. Wilkie found no evidence for this type of deterioration within sessions. Another characteristic of PI is that it exerts stronger effects when a small potential set of sample stimuli is used (see Wright et al, 1986) and when the potentially interfering event is recent. Wilkie systematically varied the size of the sample set and found no evidence of stronger PI with smaller sample sets. In fact, his subjects performed better with smaller sample sets, a finding opposite to what would be expected if PI was exerting an influence. He also examined the effects of sample recency on matching accuracy. On some trials, the sample location from trial N-l served as the distractor on trial N. On other trials, the distractor was chosen from trials other than N-1. There was no difference in performance between these two types of trials. The pigeons performed equally well whether the distractor had been the sample on trial N-1 or from an earlier trial. Wilkie concluded that DMKL performance might be immune to PI and that the main reason for this immunity is probably the speed at which location information is forgotten in this paradigm.

Wilkie and Kennedy, 1987; Wilkie, Willson and Lee ( 1990)

Wilkie and Kennedy (1987) developed a computer simulation of pigeons' performance on the DMKL task. The model was based on six assumptions: 1) The key matrix is stored in a stable, map-like representation. 2) Working memory is assumed to involve an attention focus or "pointer" that moves ("drifts") over the surface of the map matrix. 3) This pointer migrates towards the representation of the sample location while the sample key is illuminated. 4) The pointer wanders randomly when the sample is not illuminated. 5) During acquisition, the pigeon learns the rule "choose the key location whose representation is closest to the location of the pointer" and 6) Between trials the pointer is positioned randomly on the key matrix representation.

Wilkie and Kennedy's computer simulation of this "drift" model of pigeon short-term memory for spatial location (see also, Roitblat, 1984a,b, 1987) yielded results that were in accord with the majority of previous results obtained with the DMKL procedure. Furthermore, several predictions were derived from the simulation. Wilkie, Willson and Lee (1990) tested some of these predictions.

The "drift" model predicts that accuracy on trials during which two sample locations are presented simultaneously should vary as a function of the distance between the two samples. Accuracy should be higher on trials with adjacent samples relative to trials with nonadjacent trials. In the former case, the pointer will stop close to the

boundary of the two keys. In the latter case, the pointer should stop somewhere between the two sample keys. It follows from this that pigeons should make more errors when an incorrect key falls between two correct keys than when it is adjacent to a correct key. This prediction was confirmed. Pigeons were much more likely to respond incorrectly to a distractor key located between two sample keys. Matching accuracy on this type of trial was actually below chance, a finding that was also predicted by the "drift" model. On linear three-sample trials (i.e., the sample defines a row, column or diagonal), the "drift" model predicts enhanced accuracy when the middle sample is presented as the test sample relative to trials on which one of the end samples is presented. This prediction was also confirmed.

### Wilkie (1989)

The "drift" model assumes that pigeons represent the DMKL key matrix in a map-like form. A recent experiment by Wilkie (1989) supports this idea. Cheng and Gallistel (1984), mentioned previously, have suggested that rats represent Euclidean properties of space such as distance and direction. Their conclusions were based on several studies in which space was transformed in various ways. In DMKL these physical transformations are difficult to achieve so Wilkie used multidimensional scaling techniques (MDS) to make inferences about the structure of this map-like representation. MDS refers to a set of related computational

techniques capable of constructing a map strictly from distance information.

Wilkie assumed that confusions between locations were a good index of psychological distance. Easily confused locations are psychologically close. He used confusion scores as "distances" in an MDS program and recovered a reasonable approximation of the key matrix as output. He tested several different geometries (e.g., city-block) but discovered that a two-dimensional Euclidean geometry produced the best fit to the data.

## CHENG (1988, 1989, IN PRESS)

Cheng conducted a series of experiments examining pigeons' use of landmarks to find a hidden goal. His task is similar to the Morris Water maze (Morris, 1981) described previously. He trained pigeons to search for a hidden food-well in a small rectangular arena. The arena contained one or more distinct landmarks. To ensure that the withinarena landmarks came to control the pigeons' search behavior rather than the features of the surrounding room, Cheng shifted the arena within the room each trial. Once the pigeons had acquired the task various transformations of the within-arena landmark were performed. Displacing the landmark(s) in the horizontal plane caused the pigeons to shift their searching behavior by a distance comparable to the size of the shift. Vertical displacements or changing the size of the landmark(s) did not disrupt searching. When two landmarks were present, the pigeons

relied more heavily on landmarks closer to the hidden food-well (i.e., shifting a near landmark caused a greater shift in searching behavior than moving a far landmark.

Cheng proposed a vector sum model to account for his results. According to this hypothesis, the pigeon encodes a number of landmarkto-goal vectors. When searching for the hidden food-well again, the pigeon adds to each landmark-goal vector the corresponding vector from its present location to the landmark in question to generate navigation vectors. The pigeon then moves to a location determined by a weighted average of the navigation vectors. Near landmarks are weighted more heavily than far landmarks.

Similar models have been proposed for bees (Cartwright & Collett, 1983, 1987), rats (Cheng, 1986; Cheng & Gallistel, 1984) and gerbils (Collett, Cartwright & Smith, 1986). Rats, pigeons and gerbils all encode metric properties of space. Bees apparently do not. Landmark displacement experiments have also been conducted with Clark's Nutcrackers with similar results but no formal model of landmark use has yet been offered for this species (Vander Wall, 1982).

## PIGEON SPATIAL MEMORY: A SUMMARY

Although initial work on spatial memory in pigeons led to the suggestion that their spatial memory abilities were limited or even nonexistent (Bond *et al*, 1981) more recent work has painted a somewhat brighter picture (Spetch & Edwards, 1986, 1988; Spetch & Honig, 1988;

Spetch, 1990). Spatial memory in pigeons appears to be very similar to that observed in other species such as the rat, differing only in terms of temporal persistence and, perhaps, capacity.

Pigeons' performance on spatial tasks is very sensitive to procedural variables. They perform best on tasks that provide a wealth of landmarks and relatively unconstrained pathways between goals. The spatial distinctiveness of the to-be-remembered locations is also important. Spatially distinct locations are easily recalled, even in the face of extended delays (Spetch & Honig, 1988). Locations that are not spatially distinct (Wilkie & Summers, 1982) can be remembered only for brief periods of time. Space is represented in a map-like form in which Euclidean properties of space are maintained (Cheng, 1988, 1989, in press; Wilkie, 1989). "Richer" maps, that is, maps in which more features and relationships between features are represented, support higher levels of performance, both in terms of accuracy and temporal persistence, than impoverished maps (Spetch & Honig, 1988; Wilkie & Summers, 1982).

The data bearing on the capacity issue are equivocal. Studies purporting to show capacity constraints have typically confounded memory load with other factors (Dale, 1988; Roberts & Van Veldhuizen, 1985) or tested subjects under suboptimal conditions (Roberts, 1988). Studies failing to show capacity constraints have probably not employed procedures that come close to straining pigeons' capacity (Spetch, 1990).

It has been suggested that animals such as the rat and foodstoring birds learn associations between locations and the presence or absence of food (Shettleworth, 1985; Staddon, 1983). The same is apparently true of pigeons. However, the sensitivity of pigeons to procedural variables on spatial tasks makes comparisons between tasks problematic so it is unclear how readily one can generalize across tasks. This is especially true of comparisons between maze studies and DMKL studies. Willson and Wilkie (1991) have addressed this issue by modifying the DMKL procedure in various ways to produce levels of performance that are comparable to that observed in maze procedures.

#### WILLSON & WILKIE (1991)

Attempts to answer the question "How should radial maze procedures, as used to study spatial memory in rats, be modified for the study of spatial memory in pigeons?" have led to a much greater understanding of spatial memory in pigeons. In a recent series of experiments, Willson and Wilkie (1991) asked a similar question in regards to DMKL. They asked: Is it possible to modify the DMKL procedure in such a way as to attain levels of retention comparable to that seen with other spatial memory tasks?

One potentially limiting factor in the DMKL procedure was the apparatus. Sample locations are presented within a small matrix of keys on an opaque, vertical surface, in a dimly lit room. Willson and Wilkie

reasoned that making the potential sample locations more spatially distinct, both by increasing the distance between potential samples and by providing prominent landmarks, would improve retention. The apparatus that they developed is pictured in Figure 1. It was constructed of Plexiglas and a single key was mounted on each of 10 sides of the apparatus. A feeder was mounted on the eleventh side.

Although proactive interference has not been conclusively demonstrated in the DMKL procedure Willson and Wilkie sought to reduce the possibility that it might manifest if the retention of spatial information in this paradigm was improved. The best way to avoid PI is to employ trial-unique stimuli or at least not repeat stimuli within a session. Because the potential number of possible sample locations was limited (10) the authors conducted only one trial per day. Within a block of 10 sessions each key served as the sample once and as the distractor once. The same key was never used on consecutive days. On a given trial, the sample and distractor were always equidistant from the feeder to prevent key biases. Willson and Wilkie also modified the DMKL procedure in four other ways.

Increasing sample duration has been shown to improve matching accuracy on the DMKL procedure (Wilkie & Summers, 1982). Matching accuracy also improves when responding to the sample is reinforced (Wilkie, 1983c). Both of these features were incorporated into the procedure. Willson and Wilkie used a 15-min sample presentation and

Figure 1. A schematic diagram of the apparatus used in Willson and Wilkie (1991). Numbers indicate pecking key positions.



reinforced responding to the sample on a variable interval (VI) 30-sec schedule.

A third procedural change was made in light of the fact that errors on memory tasks are not always due to forgetting (Brown & Cook, 1986; Dale, 1988; Devenport, 1989; Roitblat & Harley, 1988; Wilkie & Spetch, 1981). Because single incorrect responses may or may not reflect forgetting, the authors allowed the pigeons to make several choices on a trial. During retention tests, both the sample and a distractor were illuminated for 1 min. If a subject made more responses to the sample during this period, the distractor extinguished and responding to the sample was reinforced on a VI 30-sec schedule for 5 min. If the subject made more responses to the distractor, both keys extinguished and the trial ended. If a subject made an equal number of responses to the sample and distractor during the test, the next response determined the trial outcome.

The final modification was made in light of a finding by Urcuioli and Callender (1989). These investigators gave their pigeons offbaseline training to discriminate between the stimuli that served as samples in a DMTS task. Pigeons that received discrimination training acquired DMTS faster than pigeons who did not. Urcuioli and Callender interpreted this finding as stemming from enhanced attention to the sample stimuli produced by differential reinforcement. Previous work from our laboratory (Willson, unpublished data) had suggested that the modifications described previously were not always sufficient to enhance

retention of the sample location. Thus we incorporated discrimination training into some conditions in the hope that it would enhance attention to the sample location.

In their first experiment, Willson and Wilkie tested six pigeons in two conditions. In one condition, the Sample Alone condition, a key was lit and responding to that key was reinforced on a VI 30-sec schedule for 15 min. This was followed by a delay and then the illumination of the sample and a distractor. In the other condition, the Sample/Distractor condition, two keys were lit. Responding to one, the sample, but not the other, the distractor, was reinforced. Following the delay both of these keys were re-illuminated. Subjects received 30 daily trials on each condition and the delay was always 30 sec. The order in which the subjects received the conditions was counterbalanced.

Somewhat surprisingly, performance on the Sample Alone condition was near chance and did not improve over the course of training. However, performance on the Sample/Distractor condition was excellent, better than 80% for all subjects. Furthermore, this excellent performance was present from the first day of training. Willson and Wilkie observed that performance on the Sample Alone condition was subject to PI. Performance tended to be better as the number of days between key repetitions increased. A regression equation fit computed for the data intersected chance at 2.53 days. Thus it seemed that the subjects in the Sample Alone condition could remember the location of

the sample stimulus but found it difficult to discriminate between current and previous presentations of that stimulus. No evidence for PI was found on the Sample/Distractor condition. Willson and Wilkie concluded that the improved performance observed following Sample/Distractor training was likely due to enhanced attention to the Sample (and Distractor) stimuli produced by differential reinforcement.

In a second experiment, Willson and Wilkie varied the length of the retention interval (RI) between Sample/Distractor training and the retention test. All six subjects performed well with RI's of up to 30 min but most subjects did much better than this, and one subject demonstrated above chance performance following an RI of 24 hr. These data are presented in Figure 2.

Thus the answer to the question "Is it possible to modify the DMKL procedure in such a way as to attain levels of retention comparable to that seen with other spatial memory tasks?" is apparently "yes". However, it remains unclear exactly what modifications mediated this improved performance. The discrimination training between sample and distractor is apparently critical, but the degree to which the other factors (i.e., the physical layout of the apparatus, only a single trial per day, etc.) contributed is unclear. The purpose of the present research was to examine pigeons' performance on a modified version of the DMKL procedure using the original DMKL apparatus in a multiple trial per day procedure.

Figure 2. The retention interval data from Willson and Wilkie (1991), Experiment 2. All data points, except the final one for each subject, represent blocks in which criterion was met (DR > 0.70).



### EXPERIMENT 1

The purpose of the first experiment was to replicate the findings from our previous work using the traditional DMKL apparatus and more than one trial per day. An additional aim was to compare the effects of Sample/Distractor training vs Sample Alone training within sessions. Each bird received four daily trials. Two trials began with the illumination of a randomly selected key. On the other two trials both a sample and a distractor were illuminated. Only responses to the sample were reinforced. This initial portion of the trial lasted 10 min. The keys were then turned off and a retention interval began that lasted either 5 or 30 sec. Thus the four trial types were: Sample Alone-5 sec, Sample Alone-30 sec, Sample/Distractor-5 sec, and Sample/Distractor-30 sec. The order in which the trial types occurred was randomized.

#### METHOD

#### Subjects

Four King pigeons who had varied experimental histories in standard operant chambers were used. All subjects were maintained at approximately 90% of their free feeding weight by mixed grain obtained during the experimental session and from occasional post-session supplements when necessary. Vitamin enriched water, health grit and crushed oyster shell were available *ad libitum* in the large, plastic
coated, wire mesh home cages. Subjects were tested 5 days per week during the middle portion of the light cycle that was matched to natural sunrise and sunset times.

## Apparatus

The apparatus consisted of a panel that could be attached to the side of a subjects' home cage. A subject was transported, in its home cage, to the small dark testing room and the panel was attached to the side of the cage. Each cage was equipped with a door that could be opened to allow the subject access to the panel. Each panel was composed of a standard grain feeder, a houselight, and a square 3 X 3 matrix of pecking keys. Behind each key was a microswitch, which detected pecks having a force greater than .15 N, and a red lightemitting diode. The keys were about 3 cm in diameter and were mounted about 5 cm apart, center to center. Data collection and experimental control were carried out by a Data General NOVA 3 computer operating under RDOS and the MANX programing language (Gilbert & Rice, 1979).

### Procedure

Preliminary Training. Because all subjects had previously been trained to respond to illuminated pecking keys, relatively little preliminary training was necessary. All birds were shaped until they were responding at a steady rate on all nine keys on a VI 30-sec schedule. The experiment proper began on the following day. Trials. There were four daily trials. On each trial, a pair of pecking keys was chosen at random. One key was designated as the sample, the

other as the distractor. Subjects received two trials on which both keys were illuminated throughout the trial (the Sample/Distractor condition) and two trials on which only the sample was illuminated during the initial phase (the Sample Alone condition). Each of these trial types was paired with a short retention interval (5 sec) and a long retention interval (30 sec). There was a 2-min ITI between trials. The houselight was illuminated during trials but the ITI was spent in darkness.

Initial Phase. In the Sample/Distractor condition both keys were illuminated and remained lit for 10 min. Pecks to the sample were reinforced on a VI 30-sec schedule with 4 sec of access to mixed grain. Pecks to the distractor had no scheduled consequences. Following 10 min of exposure, the next peck to the sample produced a final reinforcement (to ensure that the sample was the last key responded to prior to the The pecking keys extinguished after this final reinforcement and RI). remained dark for the duration of the retention interval (RI), that lasted for either 5 sec or 30 sec. The RI was timed from the end of the hopper presentation. The Sample Alone condition was identical in all respects except that the distractor key was not illuminated. All subjects were tested on these conditions for 30 days. Test Phase. Following the RI, the sample and distractor were illuminated and remained lit for 1 min. Pecks during this period were recorded, as was the location of the pigeon's initial choice. If the subject had made more responses to the sample by the end of the 1-min period, the distractor was turned off and pecks to the sample produced 4 sec of access to mixed grain on a VI 30-sec schedule for 5 min. This was followed by an ITI of 2 min. If the pigeon made more responses to

the distractor, both keys were turned off and 5 min were added to the ITI. [If a subject happened to make an equal number of responses to both keys, the first response following the end of the 1-min test period determined whether or not the trial continued.]

Data Analysis. Two performance measures were computed for each subject. A discrimination ratio (DR) based on responding during the 1-min test period was calculated for each trial type and averaged over blocks of 10 sessions. A DR is a ratio of correct responses to total responses. Thus if the subject responds only to the sample, the DR will be 1.0. If the subject responds to the sample and distractor equally often, the DR will be 0.50, and so forth. The proportion of correct first responses was also computed for each trial type and averaged over blocks of 10 days. To increase statistical power, two factors, each containing two levels, (Sample Alone vs Sample/Distractor and Short RI vs Long RI) were combined to form one factor (Trial Type) with four levels.

### RESULTS

Figure 3 shows the DRs for each subject. All subjects exhibited a similar pattern of results. Performance was much higher on the Sample/Distractor trials (M = .751) than on the Sample Alone trials (M = .517). Three out of four subjects remained at chance level on the Sample Alone trials and the performance of the one subject that was above chance dropped on the long retention interval trials. There was no effect of retention interval on the Sample/Distractor trials; all subjects were well above chance levels of performance at both the long and short retention interval (M = .748 vs M = .755, respectively).

The percent correct first choices data from each subject are depicted in Figure 4. Although the pattern of results is similar to that of the DRs, there is clearly much more variability and the overall level of performance is lower. The only trials on which all subjects were clearly above chance were the Sample/Distractor trials with a short retention interval (M = .71).

The mean performance on each trial type and retention interval for both the DR measure and percent correct measure are shown in Figure 5. The differences discussed above can be seen clearly and were confirmed through statistical analyses. A 3 (Blocks of 10 sessions) by 4 (Trial Types) by 2 (Measures) analysis of variance revealed both a significant effect of trial type and measure [F(3,27) = 16.43, p < .001, and F(1,9) = 34.200, p < .0004, respectively]. Post-hoc Newman-Keuls comparisons revealed that performance on the two Sample Alone trials did not differ nor did performance on the two Sample/Distractor trials, thus there was no effect of retention interval. However, performance on Sample Alone trials was significantly lower than performance on Sample/Distractor

trials. Performance as measured by the DR measure was significantly higher than as measured by the percent correct 1st choice measure. (All Newman-Keuls comparisons were conducted with alpha = .05).

There was no effect of block [F(2,9) = 0.1293, p > .87]; performance during the initial block of sessions was the same as in later blocks of sessions, nor were any of the interactions significant [ all p's > .38].

Figure 3. Average discrimination ratio for each subject on Sample/Distractor (DR\_SD) vs Sample Alone (DR\_S) trials in Experiment 1.

e.





Bird 2







Bird 4



**69** 

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Figure 4. Average percent correct first choices for each subject on Sample/Distractor (PC\_SD) vs Sample Alone (PC\_S) trials in Experiment 1.





Bird 2











4

Figure 5. A comparison of the group means for each trial type and each measure of performance from Experiment 1. Symbols are the same as in Fig. 3 and 4.



Average

## DISCUSSION

These findings clearly replicate the findings of Willson and Wilkie (1991). The facilitative effect of the Sample/Distractor trials is clearly evident on both short and long RI trials. It is also clear that the DR provided a higher, more stable measure of performance relative to the percentage of correct first choices. In comparison to performance on the traditional DMKL task (where performance typically drops to chance at an 8-sec RI, Wilkie & Summers, 1882), the subjects performed better on Sample/Distractor trials at the 30-sec RI based on the DRs (M = .666), but not on the percentage of correct first responses (M = .436).

Also of interest is the fact that performance on Sample Alone trials remained at approximately chance levels during the experiment. One possibility is that the subjects failed to acquire the Sample Alone task; they received only 30 Sample Alone trials during the experiment. However, pigeons typically acquire the DMKL task quickly, sometimes within the very first session (Wilkie & Summers, 1982). Furthermore, in related research, pigeons have been tested on the Sample Alone condition for hundreds of trials with no improvement in performance (Willson, unpublished data). Clearly, extending the sample presentation and reinforcing the sample stimulus do not necessarily lead to improved matching performance.

The fact that pigeons fail to perform well on Sample Alone trials in the present protocol is also relevant to the issue of what mechanism

facilitates performance on Sample/Distractor trials. Willson and Wilkie (1991) suggested that the observed levels of performance were due to enhanced attention to the location of the sample. The present findings suggest that attentional enhancement, if it occurs, is fairly transitory, operating only within trials, a finding not completely in accord with the findings of Urcuioli and Callender (1989) who demonstrated that off-baseline discrimination training facilitates the acquisition of matching and concluded that the mechanism underlying the effect was attentional. Discrimination training enhances attention to the stimulus dimensions relevant to the matching task and thus facilitates acquisition. Willson and Wilkie hypothesized that a similar mechanism mediated performance on Sample/Distractor trials in their research.

However, an important difference between the two experiments is how the discrimination training was conducted. In Urcuioli & Callender's research, discrimination training occurred off-baseline (i.e., independent of the matching procedure). Such was not the case in Willson and Wilkie's experiment. Discrimination training was an integral part of the matching procedure, in effect, on-baseline. In the present research, discrimination training occurred in both contexts. On Sample/Distractor trials discrimination training was an integral part of the trial. However, the discrimination training inherent to Sample/Distractor trials was in essence off-baseline discrimination training on the Sample Alone trials. Therefore, performance on Sample

Alone trials should have been better than the levels of performance obtained in Willson and Wilkie (1991), if the discrimination training was enhancing attention to the relevant sample dimension, location. It clearly was not facilitating attention to location in general but may have enhanced attention to the particular locations used within a trial. If discrimination training had been enhancing attention to location in a general sense, performance on the Sample Alone task following training on the Sample/Distractor task in Willson and Wilkie's original experiment should have been better than performance on the Sample Alone task prior to Sample/Distractor training. There was no such effect.

A more plausible explanation is that the excellent performance observed following Sample/Distractor training resulted from differential conditioning to the stimuli presented during the initial part of the trial. The pigeons learned that one stimulus was associated with reinforcement, the other with extinction. Following the RI, the subjects continued to approach the S+ and avoid the S-. On Sample Alone trials, the pigeon also learned that one stimulus was associated with reinforcement but made errors during the test because the distractor stimulus had also been associated with reinforcement in the relatively recent past. This explanation is consistent with the PI data from Willson and Wilkie (1991). Recall that their subjects performed better on the Sample Alone task when the number of days between repetitions of the trial stimuli increased.

Although this explanation is plausible, the data upon which it is based are weak because the order in which the trial types occurred was randomized. Sample Alone training did not consistently follow Sample/Distractor training and any effect of Sample/Distractor training on Sample Alone trials would have been attenuated as a result. The purpose of the second experiment was to test the attentional and differential conditioning hypotheses more directly.

# EXPERIMENT 2

One approach to testing the attentional vs differential conditioning hypotheses would be to train the subjects on the Sample/Distractor condition first, then test them on Sample Alone trials. This procedure was implicit in the training received by some of the subjects in Willson and Wilkie's (1991) first experiment. Recall that half of the subjects received Sample/Distractor training prior to Sample Alone training. It follows from the attentional hypothesis that these subjects should have performed better on Sample Alone trials than subjects that had not received Sample/Distractor training. As mentioned above, no difference was apparent and this lack of an order effect argues against the Attentional hypothesis.

However, another possibility is that this procedure was not sensitive enough to differentiate between these two hypotheses. If the effects of Sample/Distractor are not long-lasting and its enhancing

effects therefore deteriorate, performance on Sample Alone trials would decrease during the course of the 30 days of testing. Two of the three subjects that received Sample/Distractor training prior to Sample Alone training performed best during the first block of 10 Sample Alone trials. Although far from conclusive, this result does suggest that a more sensitive test might be required to differentiate between the Attentional and Differential Conditioning hypotheses.

Therefore the approach taken in the present experiment was to test these two hypotheses using a within-trials procedure. Subjects received four daily trials. One trial was identical to the Sample Alone condition in the previous experiment. The other three trials began with Sample/Distractor training but differed in terms of the stimuli presented during the retention test. One trial was identical to the Sample/Distractor condition in the previous experiment. On the critical trials, one of the stimuli presented during Sample/Distractor training was replaced with another stimulus during the test portion of the trial. On one trial, the distractor was replaced (Novel S-), on the other, the sample was replaced (Novel S+). Although these stimuli were not strictly novel (having potentially been used on previous trials) they were novel with respect to the trial in progress. The differential conditioning and attentional hypotheses make clearly different predictions on these trials.

The differential conditioning hypothesis predicts that performance on Novel S- trials will be identical to that observed on Sample Alone

trials. The testing conditions are identical in the two cases. Therefore, the pigeons should confuse the S+ from the current trial with a stimulus that had (potentially) served as an S+ on a previous trial but now served as the distractor. Performance on Novel S+ is a bit harder to predict but should also be similar to performance on Sample Alone trials for reasons similar to those outlined above. Presumably the attenuated performance would arise as a result of confusion between two stimuli recently associated with extinction.

The enhanced attention hypothesis predicts that performance on the Novel S- and Novel S+ trials will be similar to performance on Sample/Distractor trials. The discrimination training enhances attention to the location of the sample stimulus (and presumably to the location of the distractor). Thus on Novel S- trials, the pigeon should continue to approach the S+ and on Novel S+ trials should avoid the S-.

## METHOD

## Subjects and Apparatus

Three of the four subjects from Exp. 1 and one new subject participated in the present study. Although naive with respect to the present procedures, this new subject had participated in previous DMKL research and required no preliminary training. All housing conditions were identical to those of the previous experiment. The same apparatus was also used.

#### Procedure

Because all birds responded to illuminated pecking keys preliminary training was unnecessary. There were four daily trials. On one trial (Sample Alone), a randomly selected key was illuminated and remained lit for 10 min. Responses to this key were reinforced on a VI 30-sec schedule with 4 sec of access to mixed grain. On the other three trials a pair of randomly selected keys was illuminated and remained lit for 10 min. Responses to one key (S+) but not the other (S-) were reinforced on a VI 30-sec schedule. On all four trials, the 10-min sample exposure ended with a final reinforcement (response contingent) and a brief, 30-sec RI began.

Following the RI a pair of keys was illuminated and remained lit for one min. On Sample Alone trials this pair consisted of the sample (S+) and a randomly selected distractor (S-). On Sample/Distractor trials, this pair consisted of the sample (S+) and distractor (S-) from the initial portion of the trial. On Novel S+ trials, the pair consisted of the distractor (S-) from the initial phase of the trial and a randomly selected key (S+) and on Novel S- trials, the pair consisted of the sample (S+) from the initial phase and a randomly selected key (S-). Responses to each member of the pair were recorded separately during the 1-min test. If the subject made more responses to S+ during the test, S- was extinguished and responses to S+ were reinforced on a VI 30-sec schedule for an additional 5-min period followed by a 2-min ITI that was spent in darkness. If the subject made more responses to

S-, both keys were extinguished and 5 min were added to the ITI. If a subject made an equal number of responses to S+ and S- during the test period the next response determined the trial outcome. The order in which the four trial types occurred was random. The measures of performance computed in Exp. 1 were also computed for this experiment.

## RESULTS AND DISCUSSION

The data from the present experiment are shown in Figure 6. Performance as measured by the DRs was again better, on average, than the percentage of correct first choices (PC), but the pattern of results was similar in both cases. All subjects performed best on the Sample/Distractor trials relative to the other three trial types (DR =.727, PC = .642). Performance on the Novel S+ and Novel S- trials was better than on the Sample Alone trials but did not differ from each other (DR = .60, PC = .59 and DR = .57, PC = .57, respectively) . Performance on the Sample Alone trials was at chance (DR = .50, PC =.44).

A 12 (Blocks of 5 sessions) by 4 (Trial Types) by 2 (Measures) analysis of variance revealed a significant effect of measure [F(1,36)= 8.1157, p = .008] and a significant effect of trial type [F(3,108) = 16.7686, p = 0]. There was no significant effect of block [F(11,36) = 0.8429, p = .60], nor were any of the interactions significant.Post hoc Newman-Keuls comparisons revealed that performance on Sample/Distractor trials was better than on the other three trial types. Performance on

Figure 6. A comparison of the mean performance on the four trial types from Experiment 2 for each subject. Both the DR and PC data are presented. The group average is also shown.





Bird 2













Average

the Novel S+ trials and Novel S- trials was better than on Sample Alone trials but didn't differ from each other. (All comparisons were conducted with alpha = .05)

The results of the present experiment are not entirely consistent with either the differential conditioning hypothesis or the enhanced attention hypothesis. Although performance on Novel S- and Novel S+ trials was better than that observed on Sample Alone trials (as would be predicted by the enhanced attention hypothesis) it was not as good as performance on Sample/Distractor trials (as predicted by the differential conditioning hypothesis). Thus neither account, by itself, can explain the present findings. However, aspects of both can account for the results. An example will be used to illustrate.

Assume that the total amount of associative value available in a conditioning situation can vary between -1 and 1. All potentially predictive stimuli compete for this total value. Pairings with reinforcement increase the value of a particular stimulus and pairings with non-reinforcement decrease its value (cf., Rescorla & Wagner, 1972). In the absence of conditioning this value "drifts" towards 0. The total amount of associative value that accrues to a particular stimulus will depend on not only its own predictive value but also the predictive value of other stimuli present in the conditioning situation. As conditioning progresses the subject learns that some stimuli are more predictive of reinforcement than others and learns to direct its attention towards those stimuli.

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For example, during the initial part of a Sample Alone trial, attention is directed towards both the illuminated stimulus and its location. Both of the cues predict reinforcement to an equal extent so the associative value of both increase towards a maximum of 0.5 (half of the total associative value available). On Sample/Distractor trials, one location exclusively predicts reinforcement and its associative value increases towards 1. The other location predicts nonreinforcement and its associative value decreases towards -1. The illuminated stimuli on Sample/Distractor trials are associated equally with reinforcement and non-reinforcement and their associative value remains near 0. Stimuli from previous trials have an associative value of close to 0 because they have been associated in the past with both reinforcement and non-reinforcement, and because associative value tends to drift towards 0 in the absence of further conditioning.

If we assume that the 10-min sample period is sufficient time for the associative values to attain their maxima and that the associative value do not decrease much during the RI, the following conditions prevail during the test portion of the trial:

# STIMULUS TYPE

	TRAINING				TEST	
TRIAL TYPE	PS+	VS+	PS-	VS-	С	D
SA	0.5	0.5	N/A	N/A	0.5	0.0
SD	1.0	0.0	-1.0	0.0	1.0	-1.0
NS	1.0	0.0	-1.0	0.0	0.0	-1,0
ND	1.0	0.0	-1.0	0.0	1.0	0.0

where:

P = location stimulus
V – visual stimulus
S+ = rewarded
S- = non-rewarded
C = correct
D = distractor
SA - Sample Alone
SD = Sample/Distractor
NS - Novel Sample
ND - Novel Distractor

Thus performance on Sample/Distractor trials should be best because the choice involves a discrimination between two stimuli with extreme and opposite associative values. Performance on Sample Alone trials should be poor because the choice involves a discrimination between two stimuli with intermediate associative values. Performance on Novel S- and Novel S+ trials should fall somewhere between because

the choice is between a stimulus with an extreme associative value and one with an intermediate associative value.

That this model can explain the pattern of results obtained in the present experiment is no surprise since it was designed with that purpose in mind. However, it can also explain the data from Willson and Wilkie (1991). This issue will be addressed in the General Discussion below.

In the next experiment, the issue of temporal persistence is addressed. Specifically, the question asked is: How long can pigeons remember the location of the rewarded sample on this modified DMKL procedure?

### EXPERIMENT 3

The matching accuracy of the subjects on the Sample/Distractor trials in Experiments 1 and 2 did not decrease following an RI. The purpose of this third experiment was to explore the degree to which pigeons could retain spatial information at even longer delays. It seemed unlikely that performance would equal that observed in Willson and Wilkie (1991) due to the lack of visible landmarks and the close proximity of the response alternatives in the traditional DMKL procedure. Nonetheless, performance should be superior to that typically observed in DMKL procedures.

### METHOD

### Subjects and Apparatus

The three subjects from Experiment 1 who had also been used in Experiment 2 were used in the present study. The apparatus was identical to that used in the previous experiments. All aspects of the pigeons care and housing were identical to those in the previous experiments.

## Procedure

All subjects were tested on the Sample/Distractor condition for three daily trials. At the beginning of a trial, two stimuli were randomly selected and illuminated, as in the previous experiment, and all other conditions were identical to those of the previous experiment, except as indicated below. The interval between initial training and subsequent testing assumed one of three values at random. The shortest interval, which occurred in each session, was 5 sec. The initial values of the two other RI's were 30 sec and 60 sec, respectively. Subjects were tested on this distribution of retention intervals for 30 sessions to establish a baseline. The longest retention interval was then increased to 5 min, and the middle RI to 60 sec. This distribution remained in effect for 20 sessions at which time the middle RI was increased to 5 min, and the longest RI to 10 min. The duration of the middle and longest RI's was doubled every 20 sessions until the value of

the longest RI was 40 min and the middle RI was 20 min. The experiment ended after 20 sessions with the RI's at these values. Matching accuracy was measured by calculating a DR based on responding during the first minute of the test phase, as in the previous experiment.

# RESULTS AND DISCUSSION

Figure 7 shows the retention interval data for each of the three subjects and the mean. The forgetting functions for all three subjects are fairly flat. Only Subject #2 showed a substantial decrease in performance as the RI was lengthened and the decay assumed an inverted U-shape rather than a linear decrease. Subject #3 actually performed better at the longest RI (i.e., 40 min). Two of the three subjects were still performing at .70 or better when testing was terminated and all subjects were still performing at levels well above chance. An analysis of variance performed on the DRs at each of the seven delays used in the present experiment revealed no significant drop in performance [ F(6,12)= 1.0280, p > .45 ]. A one-sample t-test on the DR values from the 40min RI confirmed that performance was still significantly better than chance [ t(2) = 7.28, p < .02 ].

The data from each of the memory interval distributions tested are depicted in Figure 8. Although the data are quite variable, it is clear that the memory functions based on the three RI's tested in each block of sessions are fairly flat. Recall that each subject received three daily trials and that the RI for one of those trials was always 5 sec.

Figure 7. Mean performance at each retention interval for each subject in Experiment 3. The group average is also shown. Note that the x-axis is a log scale.





Bird 2







Average



Figure 8. Mean performance on each of the memory interval distributions used in Experiment 3 for each subject. The group average is also shown. The first block of intervals is called DR1, the second block, DR2, and so forth.



Bird 1

Bird 2










Performance on the 5-sec RI trials was highly variable and tended to decrease as the length of the other RI's increased. For all three subjects, performance was lowest on the 5-sec RI trials when the middle and longest RIs were 20 and 40 min, respectively, although this difference was not significant [F(4,8) = 3.3665, p < .07]. Honig (1987) found a similar effect in a delayed matching to sample paradigm with color stimuli. In his experiments, performance on a common RI decreased as the average length of the RI's increased (e.g., performance on a 5-sec RI was worse when the 5-sec interval was embedded in a distribution including 5- and 10-sec RI's relative to a distribution in which the 5-sec RI was embedded in a distribution including 1- and 5-sec RI's). He attributed the effect to an expectancy of the average duration of the RI. Such an explanation could also account for the findings from the present research.

## **EXPERIMENT** 4

The results from the previous three experiments clearly indicate that discrimination training facilitates performance on a modified delayed matching of key location task. However, it is also clear that the observed level of performance is unlikely to reflect the full extent of pigeons' ability to remember the location of the previously rewarded key in this type of paradigm. The close proximity of the response alternatives and the lack of visible landmarks are almost certainly

factors inhibiting performance. Recall that Willson and Wilkie (1991) observed retention of up to 24 hr under some conditions when they used similar procedures but a larger Plexiglas apparatus from which room cues were visible.

One potential problem with the procedure that they used was the fact that the to-be-remembered location was not the location at which the birds actually received food (see Figure 1). Remembering where to respond to get food may be more difficult than remembering a location at which food is actually available.

Another potential problem with Willson and Wilkie's procedure was that correct responding depended on the use of a win-stay strategy. Bond *et al* (1981) have suggested that win-stay may be the type of strategy that pigeons use when foraging because they typically forage in locations that are not depleted in a single foraging bout. However, Olson and Maki (1983) demonstrated that pigeons readily learn a winshift strategy and learn win-shift faster than win-stay. Plowright and Shettleworth (1990) make a similar point based on pigeons' performance on a two-armed bandit problem (TAB). TAB procedures require that the subject discover which of two response alternatives provides the highest payoff (food is typically dispensed on a random ratio schedule). The values of the alternatives (i.e., the number of responses required, on average, to receive a reinforcement) typically change either within or between sessions and the subject must track the changes to maximize their rate of food intake. In Plowright and Shettleworth's experiment

the values of the response alternatives changed between sessions so the pigeons' task was to figure out each day which of the two alternatives had the highest payoff. Plowright and Shettleworth tested a particular mathematical model of choice behavior in this situation and found a reasonably good fit to their data. Any deviations from the model depended on a strong tendency to shift away from the most recently reinforced alternative. Subsequent experiments clearly showed that shifting was learned more readily than staying and that this tendency to shift depended upon the proximity of the response alternatives. The pigeons showed a strong tendency to shift when the response alternatives were widely separated but not when they were close together.

However, Shettleworth and Plowright (1989), using a similar TAB problem, found that pigeons exhibited a strong tendency to return to previously rewarded locations. It seems, then, that pigeons are capable of both staying and shifting. Their strategy depends upon procedural variables and the method by which the tendency to stay or shift is assessed. At the molecular level, the level of individual responses, pigeons show a strong tendency to shift away from previously rewarded locations. At the molar level, the level of overall preferences, they show a strong tendency to return to previously rewarded locations.

The procedure presented below addresses these potential problems by assessing spatial memory in a large Plexiglas operant chamber. A pecking key and food hopper are mounted on each wall so the to-beremembered location is also the location at which the pigeons receive

food and it can be encoded in terms of the landmarks external to the The pigeons' task is to discover, each day, which one of the four box. pecking keys provides grain. Retention for the location of the previously rewarded key is assessed during an initial 1-min period at the start of the session. Reinforcement is not available during this assessment. In essence, the task, in terms of memory, has no correct answer. What the birds do during the initial portion of the trial is independent of what happens during the later part of the trial (i.e., there is no contingency between responding during the "test" and responding later in the trial). This flexibility should allow the birds to exhibit their natural tendency. If they remember the location of the previously rewarded site they should either return to that location at the start of the next session (a win-stay strategy) or avoid that location (a win-shift strategy). Either outcome would indicate that the birds remembered the previously rewarded site. If the birds cannot remember the location of the previously rewarded key their responses during the assessment phase should be distributed randomly or they should exhibit some systematic searching strategy (i.e., always start searching at key 1).

#### METHOD

## Subjects

The subjects were four King pigeons who had previously served in a variety of different behavioral experiments but who were naive with respect to the procedures used in the present study. Housing conditions were identical to those employed in the previous experiments.

### Apparatus

A 3.5 cm-diameter key was mounted on the center of each wall in each of two large square Plexiglas chambers. Each key was mounted 20 cm above the floor. Behind each key was a microswitch, which sensed pecks having a force greater than .15 N, and a 28 VDC #313 lamp covered by a red gelatin filter (about  $1.5 \text{ cd/m}^2$ ). A standard grain feeder was mounted directly below each key. Each chamber was located in a small (about 2 m x 2 m x 3 m), well lit testing room. Subjects could see a variety of room cues (window, door, wall posters, etc) through the transparent Plexiglas walls of the boxes. The floor area of the boxes were  $3600 \text{ cm}^2$  and  $2025 \text{ cm}^2$ . Data collection and experimental control were carried out by the MANX language (Gilbert & Rice, 1979) running on a minicomputer.

## Procedure

Because each subject had previous key peck training, no preliminary training was required. Each subject received 51 sessions of training during this experiment. Sessions occurred at approximately the same time (a few hours after light onset) each day, 5 days a week. Sessions began with the illumination of the four identical red pecking keys and lasted for 17 min following the first response. During all sessions food reward for key pecking was unavailable during an initial period that lasted 1 min. This unreinforced interval is represented in black in Figure 9, which shows a schematic of two consecutive sessions.

After this initial non-rewarded period, food for keypecking was available according to a VI 30-sec schedule on one of the four keys. The key that provided food, represented by the crosshatched bar in Figure 9, was selected randomly in each session by a computer program. Thus, during each daily session the probability was 0.25 that a particular key would produce food. The probability that the same key would produce food on two consecutive sessions was 0.0625. In summary, the key feature of the procedure was that the location of the profitable key varied in an unpredictable way from session to session. The basic requirements of the task were that subjects had to first locate the key that provided food intermittently and then respond on that key to obtain as many as 32, on average, 5-sec food reinforcements per session.

In each session a record was kept of how many times the subjects pecked each of the four keys, during both the initial 1-min nonrewarded

Figure 9. Two consecutive sessions are shown schematically. The black bar represents a period (1 min in length), initiated by the first keypeck, during which food was unavailable. The crosshatched bar represent the key on which food was available on a VI 30-sec schedule for the last 16 min of the session (key 3 in the Day N-1 session and key 1 in the Day N session). During this period food was not available on the keys represented by grey bars.



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period, and the subsequent 16-min period in which food was available on one of the four keys. Frequencies of pecking the four keys were used to form two discrimination ratios (DR). The first was based on the last 16 min of the session and was the ratio of pecks on the rewarded key to the total number of pecks to all keys. For example, in Figure 9, which shows two consecutive sessions, this DR would be the ratio of pecks on key 3 to the total pecks on all keys during the session labelled "Day N-1". In the session labelled "Day N" this DR would be the ratio of pecks to key 1 to the total pecks on the other keys. This DR, referred to as the "terminal" DR, is a measure of the subjects' ability to locate, and then exploit, the profitable key within a session.

The second DR was calculated from the pecks made during the initial unrewarded period and was the ratio of pecks made on Day N to the key that had been rewarded on Day N-1 to the total number of pecks made to all keys on Day N. For example, in Figure 9 this DR for Day N would be the ratio of pecks on key 3 (the rewarded key on Day N-1) to the total number of pecks made in the initial nonrewarded period. This DR, referred to as the "initial" DR, is a measure of perseveration of responding, from Day N-1 to the beginning of Day N, to the location that had previously provided food. Response perseveration implies that subjects remember the location of food from the previous day (avoiding the previously reinforced key would imply the same thing). Random responding would yield DRs of 0.25 in both the initial nonrewarded period and in the subsequent rewarded period because there are four

possible response alternatives. We also calculated a DR based on the number of responses made on Day N to the key that had been rewarded on Day N-2. This DR was a ratio of the pecks to the key that had been rewarded on Day N-2 to the total responses minus responses to the key that had been rewarded on Day N-1. This DR was calculated this way because it became clear that responses during the initial unrewarded period were not randomly distributed, but were biased towards the key that had been rewarded on the previous day. Under this protocol, random responding would yield a DR of .333. Days on which the same key was rewarded in consecutive sessions were not included in the N-2 analysis.

## RESULTS AND DISCUSSION

Figure 10 shows initial and terminal DRs for each subject, based on the last 50 sessions in the experiment. The first, crosshatched, bar is the terminal DR (i.e., relative responding on the rewarded key during the final 16 min of a session). This DR is an index of subjects' ability to find, and respond to, the rewarded key. This DR is much higher than chance (0.25) for all subjects.

The grey and black bars in Figure 10 show the initial DRs (i.e., relative responding to the key that had been rewarded on the previous day during the initial unrewarded period of each session). The grey bars show sessions separated by 24 hr (i.e., Tuesday through Friday sessions). The black bars show Monday sessions that occurred 72 hr after the previous session. All subjects responded primarily to the key

Figure 10. DRs for subjects in Experiment 4. The first, crosshatched bar is the DR for the final 16 min of each session. This terminal DR is a measure of how well subjects located and exploited the profitable key. The DRs represented by the grey and black bars are DRs from the first 1 min of each session. These initial DRs measure subjects' tendency to respond on a key that was rewarded during the previous session. The grey bars represent sessions separated by 24 hours, the black bar, sessions separated by 72 hours.



that had been rewarded during the previous session, even after 72 hours. Both the 24- and 72-hr DRs were significantly above chance [one-sample t-test of t(3) = 14.0, p = .008 and t(3) = 14.26, p = .007, respectively].

The results shown in Figure 10 show that subjects learned the location of food, remembered that information over periods of many hours, and used that information when deciding where to begin searching for the profitable key during the next session. This experiment lasted 51 sessions and the above results were based on the final 50 sessions. Initial DRs averaged over blocks of 10 sessions were also calculated. In examining these data only one interesting trend was observed - the initial DRs tended to get smaller over blocks. Figure 11 shows averaged data over the five blocks of 10 sessions. These data suggest that subjects were less likely to perseverate from day to day with increasing exposure to the conditions of the experiment. This decrease could be a consequence of several processes: the subjects' unlearning of a "winstay" strategy, subjects' learning that food location varies randomly from day-to-day, or a cumulative proactive memory interference effect. However, caution must be used in interpreting this trend because the decrease over blocks was not statistically significant when analyzed by a one-factor repeated measures analysis of variance [ F(4,12) = 2.01, p**-** .156].

Figure 11. Initial DRs for the five blocks of 10 sessions that composed Experiment 4.



An initial DR based on the number of pecks made during Day N to the key that had been rewarded 2 days before (i.e., on Day N-2) was also calculated. These DRs are shown in Figure 12. Again, subjects responded more on this key than would be expected by simple random responding to three keys, which would lead to a DR of 0.333. The DRs shown in Figure 12 are significantly larger than 0.333 [ one sample t (3) = 5.54, p =.012 ].

The results of this experiment show that pigeons tend to begin each session by responding primarily to the key that had been rewarded during the previous session. They also respond to the key that had been rewarded two sessions earlier. Such response perseveration implies that pigeons remember the location of a previously rewarded key over many hours, in some cases for as long as 96 hr. This level of retention is far greater than that previously seen with pigeons on any other spatial memory task.

### **EXPERIMENT 5**

The main purpose of Experiment 4 was to examine what pigeons would do on a spatial task in which the location of a profitable pecking key varied randomly from session to session. The results of that experiment unequivocally demonstrated that the birds remembered the location of the profitable key from previous sessions and used that information in deciding where to begin searching at the beginning of the next session.

Figure 12. Initial DRs calculated for the key that was profitable 2 days earlier in Experiment 4.



They clearly adopted a win-stay strategy and used that strategy to return to locations that they had not been exposed to for as long as 72 hr. This is far better performance than has been demonstrated in other spatial memory procedures with this species. In the present experiment the same procedure was used but a more detailed recording of within session responding was obtained. By examining the patterns of responding within sessions it should be possible to gain some insight into the relationship between discovering the profitable key, how quickly the pigeons learn about the location of the profitable key and how memory for that location is influenced by the speed of discovery and the degree to which that location is learned. The duration of the experiment was also increased from 51 to 81 sessions to see if additional exposure to the conditions of the experiment would modify the strength of the pigeons' tendency to use a win-stay strategy.

### METHOD

# Subjects and Apparatus

The subjects were four King pigeons maintained under conditions identical to those in the previous experiments. As in Experiment 4, all subjects had previously been trained to peck keys for food reinforcement but were naive with respect to the present procedures. The apparatus used in Experiment 4 was also used for the present experiment.

### Procedure

Because the subjects had previous key peck training, no preliminary training was required. The subjects received 81 sessions identical to those in Experiment 4. One procedural difference in this experiment was that pecking during the final 16 min was recorded in eight 2-min blocks during the final 25 sessions of the experiment. This was done in order to examine how quickly subjects were able to find the rewarded key during each session.

As in Experiment 4, subjects were tested at about the same time each day, 5 days per week. Testing was done a few hours after light onset.

### RESULTS

Figure 13 shows the initial DRs for each subject, averaged over all sessions in the experiment. As in Experiment 4 this DR, which measures subjects' perseveration at the key that was rewarded during the previous session, was considerably above chance, one sample t (3) = 10.07, p = .0021. Thus at the start of each session subjects responded more to the key that had been rewarded during the previous session.

In this experiment pecking during the final 16 min of the last 25 sessions was recorded in eight 2-min blocks. Figure 14 shows averaged DRs for each of these blocks. These data show that subjects quickly discovered the rewarded key. Subjects responded to the rewarded key

Figure 13. Initial DRs, averaged over 80 sessions in Experiment 5.



Figure 14. Terminal DRs for each of the eight 2-min blocks that composed a session. The data are from the last 25 sessions of Experiment 5.



significantly above chance levels even at the end of the first 2 min of a session [ one sample t (3) = 5.94, p = .0095 ].

The gradualness of the learning curves shown in Figure 14 mask occasions in which learning seemed to be "all or none". Figure 15 shows three selected sessions for each subject in which there was "all or nothing" responding to the rewarded key.

There was a moderate but significant, positive correlation between the terminal DR from session N-1 (the measure of learning) and the initial DR from session N (the measure of retention), calculated from the data from the last 25 sessions of the experiment (one sample t (3) = 4.27, p = .024 ). The Pearson r values for subjects 1 through 4 were: 0.602, 0.489, 0.259, and 0.229, respectively. Thus between 36 and 5% of the variance in the initial DRs was accounted for statistically by the terminal DRs from the previous session. The subjects that showed the strongest tendency to exploit the profitable key almost exclusively after finding it (as indexed by the terminal DRs) also showed the strongest tendency to begin responding on day N at the key that had been rewarded on day N-1. The mean terminal DRs from the last 25 sessions for subjects 1-4 were: 0.582, 0.675, 0.849, and 0.876, respectively. The mean initial DRs were: 0.420, 0.429, 0.525, and 0.615.

In Experiment 4 there was a trend for the initial DRs to decrease over the 50 sessions that composed that experiment. Figure 16 shows comparable data for the present experiment. Again, there was a tendency for initial DRs to decline over sessions. As in Experiment 4,

Figure 15. Terminal DRs for three selected sessions from the 25 sessions in Experiment 5 in which responding was recorded in eight 2-min blocks.







Figure 16. Initial DRs for the eight blocks of 10 sessions that composed Experiment 5.

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however, this decrease was not statistically significant when analyzed with a repeated measures analysis of variance, [ F(1,21) = 1.89, p = .1211 ].

The results of both Experiment 4 and 5 show that Day N-1 learning carries over to the early part of the Day N session. As in Experiment 4 we looked for evidence that learning on Day N-2 also affects responding on Day N. Figure 17 shows these initial DRs. These DRs are significantly above chance (.333) [ one sample t (3) = 3.90, p = .03 ].

## DISCUSSION

The results from the present study replicate and extend the findings from Experiment 4. The subjects clearly remembered the location of the rewarded key from trial N-1 and used that information in in deciding where to begin responding on Day N. The decreasing trend in the magnitude of this effect observed in Experiment 4 was also evident here but was, once again, not significant. The all-or-none pattern of responding observed once the birds had discovered the rewarded key suggests that they had learned that only one key provided access to food each session, but it seems unlikely that the birds were learning that the location of the rewarded key varied randomly from day-to-day. The subjects' continued use of a win-stay strategy supports this assertion. The decreasing, but non-significant trend in the magnitude of the initial DRs is most likely due to a build up of proactive interference

Figure 17. Initial DRs calculated for the key that was profitable 2 days earlier in Experiment 5.



up of proactive interference (PI). The data showing that subjects also remember the location of the rewarded key from session N-2 are consistent with the presence of PI.

The fact that the subjects in the present experiment were responding to the profitable key at above chance levels even during the first 2 min of the session suggests that the 16 min sessions used in the first two experiments provided more than sufficient time for the subjects to locate and subsequently remember the profitable key. In Experiment 6 the duration of the sessions was systematically manipulated in an attempt to discover the relationship between session length and memory for the location of the profitable key.

#### **EXPERIMENT 6**

The within-session data from the previous experiment showed that birds quickly discovered the location of the profitable key. This suggests that the birds may have been forming strong associations between particular locations and the presence or absence of food at an early point in the session. In this experiment the duration of the sessions was systematically shortened in order to examine how much exposure the birds required to form associations that would persist for 24 hr.

## METHOD

## Subjects and Apparatus

The same subjects and apparatus as used in Experiment 5 were used in this experiment.

## Procedure

After the completion of Experiment 5 the subjects were given an additional 20, 16-min sessions. These sessions were similar to those in Experiments 4 and 5: The first peck each day to one of the four illuminated pecking keys initiated a 1-min period in which food was unavailable and pecking was measured; this was followed by a 16-min period in which food was available intermittently on one key, the identity of which was chosen at random each day. The subjects were subsequently given 20 sessions in which the rewarded, second part of each session was shortened from 16 min to 12 min. After these sessions, the subjects received 20 sessions with each of the following durations: 8 min, 4 min, and finally, 1 min. These durations were timed from when the subject actually discovered the profitable key (i.e,. following the first reinforcement).

#### RESULTS

Figure 18 shows the initial DRs for each subject, averaged over all sessions of a particular duration. As in Experiments 4 and 5 this DR, which measures subjects' perseveration to the key that was rewarded during the previous session, was considerably above chance (.25) for 16min sessions, one sample t (3) = 8.21, p = .0038. All of the subjects' DRs were above chance during the 12-min sessions, but because of the large variance produced by subject 5's strong tendency to perseverate to the key that was rewarded on the previous day during the session, the one sample t-test of performance against chance was not significant, [t(3) =2.22, p =.11]. A t-test of performance versus chance with subject 5 excluded was significant for these sessions, [t (2) = 11.00, p = .0082].

The initial DRs remained above chance during both 8- and 4-min sessions, t(3) = 3.57, p = .038, and t(3) = 3.52, p = .039, respectively. Although the group mean DR was apparently above chance during the 1-min sessions (M = .36), the t-test was not significant, [t(3) = 1.90, p = .15].

The session duration variable was also analyzed by a repeated measures analysis of variance. This analysis showed no effect of duration, F(4,12) = 1.103, p = .3999.
Figure 18. Initial DRs for each session duration employed in Experiment

6.





Subject 6





Subject 7

Subject 8



## DISCUSSION

The basic finding of Experiment 6 was that pigeons require only a short exposure to the location of a rewarded pecking key in order to remember it for 24 hr. Two of the four subjects continued to show strong preferences for the N-1 key even with sessions of only 1 min in which they received, on average, only 2 reinforcements. The analysis of variance conducted on the session length variable did not detect any significant differences in performance in the different session lengths. However, a one-sample t-test showed that performance was indistinguishable from chance at the shortest session length (i.e., l min). However, it should be noted that there was considerable individual differences in performance during the 1-min sessions; subjects 6 and 8 were considerably above chance during these very short sessions. Although there was a non-significant trend for the magnitude of the initial DRs to decrease over the course of Experiments 4 and 5, this trend was nonetheless confounded with decreases in session length in the present experiment. It is possible, therefore, that the nonsignificant t-test on the 1-min session data was at least partially due to this confound. Although speculative, this suggestion does seem plausible.

## GENERAL DISCUSSION

Taken together, the experiments reported here clearly indicate that pigeons can retain spatial information for periods of time much

longer than previously demonstrated. The spatial distinctiveness of the to-be-remembered locations and the presence of visible landmarks was clearly important. Performance was much better in the last three experiments, in which spatially distinct locations were used and landmarks were available, than in the first three experiments, in which they were not. Discrimination training between profitable and nonprofitable sites was also very important. The results from the first two experiments clearly showed that performance in the absence of discrimination training remained at approximately chance levels. It was suggested that pigeons in the present task learn associations between locations and the presence or absence of food. The poor performance on Sample Alone trials was explained in terms of the pigeons' inability to discriminate between locations recently associated with food and locations associated with food in the more remote past. The results from Experiments 4 and 5 showing that pigeons remember profitable locations from previous sessions support this assertion, albeit indirectly.

Another possibility, one that has not been considered up to this point, is that Sample Alone trials and Sample/Distractor trials (and, by extension the trials in Experiments 4-6) are distinctly different tasks that test different aspects of memory. Gaffan (1974) has distinguished between recognition memory and associative memory tasks. Recognition memory tasks entail presentation of only the to-be-remembered stimuli in the study phase of a trial. During the test phase of the trial a

subject must discriminate between a familiar stimulus and a novel stimulus. Delayed matching and non-matching to sample are examples of a recognition memory task (as is Sample Alone training in the present context). In contrast, on associative memory tasks all of the stimuli to be discriminated later are present during the study phase of the trial. The subject must remember which of the previously viewed stimuli is important. Shettleworth and her colleagues (Brodbeck, Burack & Shettleworth, in press; Shettleworth, 1985) have argued that foodstoring is an associative memory task because birds often visit potential storage sites without storing food. They do, however, preferential return to sites where food was stored. The Sample/Distractor training employed in Experiments 1-3 and the procedure used in Experiments 4-6 in the present research also fit the definition of an associative memory task because the pigeon "visits" (i.e., responds to) locations that do and do not provide food but preferentially return to the sites associated with food. The parallels between associative memory tasks that have been used with food-storing birds and the present procedures will be explored in more depth below.

Several results in addition to the excellent retention observed in the current series of experiments also deserve comment. It is clear from the results of Experiments 4-6 that the birds were adopting a winstay strategy. In other words, they were returning to locations that had provided food in the past. Taken at face value, this finding contrasts with the findings of Plowright and Shettleworth (1990) who

observed that pigeons are predisposed to shift (win-shift or loseshift). As mentioned above, these findings are not contradictory when considered in their appropriate context. The tendency to stay was considered in terms of an overall preference. Single responses were not considered. Plowright and Shettleworth (1990) examined individual choices and observed a tendency to shift. Related research (Shettleworth & Plowright, 1989) that considered overall preferences found a tendency to return to previously profitable locations. The conclusion offered depends upon the level of analysis. Several naturalistic studies have observed a similar phenomenon (Gass & Sutherland, 1985; Smith & Sweatman, 1974; Zach & Falls, 1976).

For example, Gass and Sutherland observed hummingbirds foraging on patches of nectar-producing flowers. In some conditions, the authors enhanced patches by adding sugar water to the flowers. The hummingbirds quickly discovered and exploited these "enriched" patches and, at the start of foraging the next day, returned to the previously enriched patches.

An additional finding from the present research that deserves comment is the failure to observe enhanced performance following reinforced and extended sample presentation during Sample Alone training. This finding, when taken at face value, appears to contradict previous work showing that increasing the duration of the sample presentation and reinforcing the sample improve matching performance (Wilkie & Summers, 1982; Wilkie, 1983). If increasing sample duration

and reinforcing the sample are considered as techniques for increasing the informational value of the sample stimulus, the present results are not surprising. Presumably increasing the sample duration improves matching performance by providing the subject with ample opportunity to encode the identity of the sample. Reinforcing the sample presumably improves matching performance by identifying the sample as a stimulus associated with reinforcement. At some point, increasing the sample duration further and providing additional pairings of the sample with food does not add any further information. The session duration manipulations in Experiment 6 suggest that a 1 minute sample and two pairings (on average) of the sample with reinforcement are sufficient to reach this limit. However, this explanation must be viewed with caution since there were other factors in addition to extended sample presentation and reinforcement present during that experiment (i.e., discrimination training). An additional factor that suggests a cautious acceptance of this explanation is that sample duration and reinforcing the sample were not manipulated independently so it is unclear to what degree each of those manipulations contributed to the observed performance.

It has long been recognized that correct performance on memory tasks does not necessarily reflect intact memory. Animals can respond correctly through the use of non-memorial strategies or by chance (see Olton & Samuelson, 1976). An often overlooked but complementary point is that errors on memory tasks are not necessarily due to forgetting

(Dale, 1988; Devenport, 1989; Roitblat, 1980; Roitblat & Harley, 1989; Wilkie & Spetch, 1981; Willson & Wilkie, 1991). The findings from the present research add to that body of research. Performance on the present tasks, as measured by the percent correct first choices, was worse than performance as measured by the discrimination ratios. It was also much more variable. The processes that determine performance on memory tasks are complex and offering animals an opportunity to make several "choices" during memory tasks provides a far better measure of memory than single responses.

# THE ASSOCIATIVE MEMORY HYPOTHESIS REVISITED

The hypothesis that has been presented to explain the results from the current series of experiments rests on the idea that pigeons learn associations between locations and the presence or absence of food. Ignoring for the moment the possibility that Sample Alone trials test recognition memory whereas Sample/Distractor training trials test associative memory, the poor performance on Sample Alone trials is a result of a failure to discriminate between two stimuli that are weakly associated with food. On Sample/Distractor trials the excellent performance observed is based on a discrimination between a stimulus strongly associated with reinforcement and a stimulus strongly associated with non-reinforcement. The intermediate performance on Novel S+ and Novel S- trials implicate a possible attentional enhancement effect of discrimination training that strengthens the

association between particular locations and the presence or absence of food. Thus the level of performance on Novel S+ and Novel S- is the result of a discrimination between a stimulus strongly associated with reinforcement (or non-reinforcement) and a stimulus weakly associated with reinforcement (or non-reinforcement). The excellent performance of the subjects in Experiments 4-6 is based on a mechanism similar to that mediating performance on Sample/Distractor trials except that the discrimination is between a location that has recently been associated with reinforcement and three locations that have recently been associated with non-reinforcement.

If Sample Alone training is considered as a recognition memory task, the only conclusion that we can draw from the present research is that recognition memory is not as temporally persistent as associative memory but that discrimination training can sometimes improve performance on recognition memory tasks. For example, DMTS is a recognition task and Urcuioli & Callender (1989) have shown that discrimination training facillitates performance on DMTS tasks. Novel S+ and Novel S- trials also fit the definition of a recognition memory task. The stimuli presented during the study phase are not identical those presented during the test phase. The birds' task on the test is to discriminate between a familiar stimulus and a novel stimulus. In this case, however, there are two potential sample stimuli.

Wilkie and Summer (1982) showed that matching accuracy on DMKL tasks typically declines as the number of sample stimuli presented

during the study phase increases. The opposite result, an increase in performance, was obtained in the present work. Clearly, the discrimination training during the study phase of the trial had some enhancing effect. Based on previous research by Urcuioli and Callender (1989) the most likely explanation is enhanced attention to the location of the sample stimuli.

An important function of hypotheses is to organize an existing body of data and generate testable predictions from their synthesis. The associative memory hypothesis offered here adequately accounts for the present results and for the results from several previous experiments. The approach adopted in the next section is to apply the ideas developed here to our own previous work (Willson & Wilkie, 1991) and then extend the analysis to other paradigms that have been used to examine spatial memory in pigeons. The present work will then be compared to work on associative memory in food-storing birds. Comparisons across experiments and across species are somewhat problematic because of procedural differences but there are interesting parallels between previous work and the current work that deserve comment. There are interesting differences as well and these differences suggest several fruitful avenues for future comparative work. That issue will be addressed in a later section.

Willson and Wilkie (1991) revisited

Willson and Wilkie found results very similar to those reported here. This should not be surprising given that one of the main purposes of the current research program was to adapt the procedure that they developed for use with the traditional DMKL apparatus and multiple daily trials. An additional aim was to see if it was possible to improve upon the spatial memory performance that Wilkie and Summers (1982) observed. The current work replicates and extends the major findings from that previous research and these findings have been interpreted above as expressing associative memory. Several other aspects of their data are also consistent with the associative memory hypothesis.

Recall that Willson and Wilkie found evidence of proactive interference during the Sample Alone training. The associative memory hypothesis suggests that these PI effects were largely a result of the training protocol. The stimuli that they used were pairs of keys that were equidistant from the feeder. Each member of the pair served as the sample on one trial and the distractor on another within each block of 10 sessions. The same key pair was never used on consecutive days.

Consider the following hypothetical case during the first block of 10 trials. On trial N-2, key 1 serves as the sample and key 10 serves as the distractor (see Figure 1). Key 1 becomes associated with reinforcement. Key 10 remains fairly neutral because it has never been explicitly paired with reinforcement or non-reinforcement. During the test, the pigeon should correctly choose Key 1 because it has recently

been paired with reinforcement. On trial N, key 10 serves as the sample and becomes associated with reinforcement. Key 1 retains a fairly high associative value because it was recently paired with reinforcement and has not been explicitly paired with non-reinforcement. It will have lost some associative strength due to the tendency of associative value to "drift" towards zero but will remain quite high. During the test, the pigeon must decide between Key 10, which has most recently been associated with reinforcement, and Key 1, which has also been associated with reinforcement. This is a more difficult discrimination and errors are much more likely to occur. When more days intervene between the use and re-use of a particular key pair, the discrimination becomes easier because the associative value of the distractor has "drifted" further towards zero.

Two other predictions follow from this account. First, performance during the first 5 days of Sample Alone training should have been better than performance in subsequent blocks. Two out of three birds showed this trend. Second, performance on Sample Alone trials following Sample/Distractor training should have been worse than performance on Sample Alone trials prior to Sample/Distractor trials. This is a counterintuitive prediction in light of the hypothesized attentional enhancement function of discrimination training. However, it was also hypothesized that discrimination training results in a higher associative value for a particular location relative to Sample Alone training because of enhanced attention to the location of the

sample. Therefore, on Sample Alone trials following Sample/Distractor training the pigeon must choose between two stimuli of high associative value. This trend was apparent in Willson and Wilkie's data but was not significant, probably because of the small number of subjects in each condition.

## Zentall, Steirn and Jackson-Smith (1990) revisited

The associative memory hypothesis can also account for the findings of Zentall et al. They tested pigeons on an operant analog of the radial arm maze. Two of their findings seems especially important in relation to the hypothesis under consideration here. Recall that they found that a delay interpolated between the second and third choices or between the third and fourth choice was more detrimental to performance than a delay after the first choice or before the last choice. They interpreted their results in terms of flexible coding; early responses were controlled by retrospective strategy, and later responses were controlled by a prospective strategy. The associative memory hypothesis suggests a mechanism by which this change in choice criterion could be implemented. Early in the response sequence the pigeons respond by avoiding locations that have recently been associated with food. Later responses are controlled by avoiding locations that have not recently been associated with food.

In Zentall *et al's* procedure, the first choice was always correct (assuming that the bird fulfilled the response requirement before

switching) and the chosen stimulus was reinforced. Thus in order to respond correctly on the second choice the pigeon must simply avoid the location that has most recently been associated with food. On the third choice, assuming that the bird has responded correctly on the first two choices, the bird must avoid two locations that have recently been associated with reinforcement and the probability of making an error increases (due to the increased possibility of confusing visited and non-visited sites). Following the third choice, the bird's response criterion shifts from on avoiding locations recently associated with reinforcement to approaching locations that have not recently been associated with reinforcement. There are two such locations available and the probability of making an error remains high (due to potential confusions between visited and non-visited locations). On the fifth choice, correct responding depends on approaching the only location that has not been associated with reinforcement so the probability of making an error is low.

Zentall et al also found evidence of PI. Performance on later trails within a session was worse than on earlier trials. This PI likely results from the increasing similarity in the value of the to-bediscriminated locations on successive trials within the session. Associative value is assumed to drift towards zero during ITI's but nonetheless remains high for all of the stimuli at the beginning of a trial later in the session.

Comparisons with the study of associative memory in food-storing birds

Comparisons between experiments and across procedures are problematic because of differences in the conditions under which the experiments were run. Small details that are seemingly insignificant from the point of view of the experimenter can have profound influences on behaviour. Comparisons between species across experiments are especially prone to these problems. However, the procedure employed in Experiments 4-6 is functionally similar to one used by Brodbeck, Burak and Shettleworth (in press) to study one-trial associative memory in Black-Capped Chickadees, a food-storing member of the parid family.

In one of Brodbeck *et al*'s experiments (Experiment 1), chickadees released into a large indoor aviary encountered three feeders, one of which contained a peanut. Once the chickadee had discovered the baited feeder it was allowed to peck at the peanut for 30 sec. The lights were then turned out and the bird returned to its cage. During the retention interval, which lasted 5 min, the feeders were covered with Post-it notes to conceal the peanut and the bird was re-admitted to the aviary and allowed to search for the now hidden bait. Visits to feeders were recorded and the bird was allowed to search until it discovered and consumed the peanut. For one group of chickadees the locations of the feeders and the location of the peanut varied randomly from trial to trial (the unique group). For another group, the location of the feeders remained constant but the location of the peanut varied among the three feeders.

On being readmitted to the aviary, birds in the unique group relocated the hidden peanut in fewer responses than would be expected by chance and continued to do so throughout the course of the experiment. At the start of the experiment, the birds in the non-unique group also performed above chance but their performance deteriorated to chance levels with repeated testing. An examination of their response patterns revealed that they were systematically visiting the feeders during the recovery phase (i.e., used a response algorithm).

The procedure used in the present research is most similar to that experienced by the non-unique group in Brodbeck *et al*'s study. Ignoring for the moment the fact that the temporal parameters of the two studies were very different and that the method of assessing retention was also different, the pigeons in the present experiments performed better than the chickadees in Brodbeck *et al*'s experiment. The pigeons in the present research clearly remembered the location of the previously profitable key even after 72 hr and with initial exposure to the correct key of only 4 min (two birds performed above chance levels with exposure of only 1 min). The chickadees performed at chance levels with a delay of 5 min. It is possible, but unlikely, that the chickadees might have performed better with a longer retention interval. However, even if such were the case, unpublished research from our laboratory suggests that the preference for previously rewarded keys gets stronger with shorter retention intervals (Willson, Wilkie & Lee, unpublished data).

Of course, the differences between the the procedures used here and those used by Brodbeck *et al* (in press) makes these points extremely speculative at best. However, the data do suggest several promising avenues for further research. It is possible that the longer retention of pigeons on the non-unique task reflects a well developed ability to "relabel" potential feeding sites based on current experience that is absent or not so well developed in chickadees. If such were the case one would expect that spatial memory in chickadees would be more prone to PI than in pigeons. Another important issue is the speed with which associations between locations and the presence or absence of food are formed. Food-storing birds clearly form this type of association quickly, especially with unique locations. The results of the present experiments suggest that pigeons also form these associations quickly, but it remains unclear how they would perform with unique locations. These points are explored further in a later section.

## ECOLOGY AND COMPARATIVE COGNITION

The idea that an animal's cognitive capacities have been shaped by evolution and the demands of the natural environment is well accepted in comparative cognition. In the late 50's and early 60's researchers, in a sense, rediscovered Small's (1901) assertion that an animal's cognitive capacities can be understood only in relation to the problems that an it faces in the natural environment. This rediscovery was precipitated by a growing realization that animals were not the tabula

rasa that some behaviorists proposed. A growing body of evidence suggested that animals came into the laboratory with strong predispositions to behave in particular ways in response to particular problems (Bolles, 1970; Breland & Breland, 1961; Hinde & Stevenson-Hinde, 1973). The notion of biological constraints on learning is still an issue today (Rozin & Schull, 1988; Sherry & Schacter, 1987), although the phenomena are generally considered in terms of "adaptive specializations" in learning and memory rather than constraints.

Unfortunately, this approach has often been misapplied. Appeals to an animal's ecology have been used to justify the existence or lack of a particular skill as measured by a particular procedure (see Bond *et al*, 1981). However, statements such as "Species A can't do task B because its environment isn't conducive to the evolution of the necessary cognitive skills" add nothing to our knowledge about cognition. Functional accounts of behavior can be of use by defining the problems that an animal might face in the natural environment. Similarly, the knowledge about particular cognitive abilities that we gain in the laboratory can increase our understanding of how animals cope with the demands of the natural environment (Cheverton, Kacelnik & Krebs, 1985; Shettleworth, 1988).

A brief examination of the foraging behaviour of pigeons provides a good illustration of this approach. Pigeons are gregarious and forage in a limited number of traditional feeding sites that are not necessarily depleted in a single foraging bout (Goodwin, 1967; Levi,

1974). They also tend to revisit the same sites on a daily basis (Levi, 1974; Murton, Coombs & Thearle, 1972). They can, however, discover and exploit new sources of food when they become available and also seem to be sensitive to the availability of food resources as a function of time of day (Murton, Coombs & Thearle, 1972).

The above description suggests that the foraging behavior of pigeons should be influenced by the presence or absence of conspecifics (i.e., the presence of foraging conspecifics is a reliable cue for a profitable feeding site), the temporal availability of food and, perhaps, recent experience with particular foraging sites (and many other factors).

Lefebvre and Palameta (1988) have demonstrated that foraging behavior is influenced by social factors and recent work from our laboratory has demonstrated that pigeons can learn time-place associations (Wilkie & Willson, in press). The results of the present research suggest that recent experience with a profitable feeding site could potentially influence where a pigeon decides to begin foraging. At the present time, our knowledge of these potential determinants of foraging behavior is limited and the issues require additional attention. Our knowledge of how these factors interact is non-existent and this problem offers a productive area for further research, both in terms of understanding the mechanisms that determine foraging in the wild and in understanding the cognitive abilities of pigeons.

Taken at face value, the above analysis suggests that foraging in pigeons and foraging by food-storing birds such as chickadees represent different problems and therefore that the cognitive skills used by pigeons and food-storers during foraging are likely to be different. However, this interpretation must be viewed with caution. The idea that foraging is determined by different cognitive mechanisms is not really the issue (for example, social factors are unlikely to affect foraging by food-storers in the same ways that they influence pigeon foraging) nor is the potential existence of adaptive specializations in learning and memory at issue. At a functional level pigeons and food-storers face a similar problem while foraging, namely that of returning to locations where they expect to find food. For food-storers this is a location where the bird has created its own food source (i.e., a cache). For pigeons this is a location where they have encountered food in the past. However, previous research with food-storers has shown that memory for stored versus encountered food is similar in food-storing birds (Shettleworth, Krebs, Healy & Thomas, 1990), so the problems faced by pigeons and food-storers are in fact functionally similar.

The results of the present research suggest that pigeons can return to previously profitable locations in the face of extended delays and that the temporal persistence of their memory for that location is far more resilient than suggested by previous laboratory research. The mechanism by which they accomplish this feat is proposed to be the formation of an association between particular locations and the

presence or absence of food. A similar mechanism has been proposed for food-storing birds (Brodbeck et al, in press; Shettleworth, 1985). This tentative parallel between species suggests several promising avenues for further research. For example, do food-storing birds form associations between locations and the presence or absence of food more rapidly and effectively than pigeons? When trained under equivalent conditions are such associations better retained by food-storers? Are food-storers more prone to proactive interference than pigeons, and if so why? Are associative memory processes for spatial and non-spatial stimuli similar in these species? The number of potential questions is almost infinite but answers to any subset of those questions would greatly increase our understanding of cognition and would also bear on the issue of whether the memory performance of food-storing birds is an example of an adaptive specialization in learning and memory. Answers to these questions will depend upon direct comparisons between species on a variety of tasks. Devising appropriate procedures to do so will not be an easy task but a detailed analysis of the task demands of experimental procedures currently being used to study cognition would certainly provide a solid place to start.

#### CONCLUSIONS

The traditional approach to the study of comparative cognition, the approach that has been adopted here, has been justifiably criticized (Macphail, 1982) on the grounds that we have learned very little about

species differences using this approach. It was argued in the introduction that this lack of progress was largely a result of a misunderstanding about the types of information needed to make inferences about species differences within this approach. In order to make strong inferences about species differences it is necessary to compare performance on a variety of tasks in which the relative differences between species vary (systematic variation, Macphail, 1982, 1987). By analyzing differences in task demands it is possible to make inferences about differences in cognitive ability.

Comparisons between pigeons and other species on spatial memory tasks have consistently demonstrated that pigeons are apparently inferior to many other species. More recent work has painted a somewhat less bleak picture of pigeons' spatial memory abilities (see Spetch, 1990; Willson & Wilkie, 1991) but they still appear to be less proficient on spatial tasks. Spatial memory encompasses a vast range of potential processes. The range of spatial problems that animals face in the natural environment argue against the idea of an all-encompassing spatial memory.

Some spatial tasks performed by animals in the natural environment are unique to the ecology of the animal in question. Homing in pigeons and the food-storing behavior of some corvids and parids are obvious examples. However, it is possible, by analyzing the components of these apparently unique problems, to devise procedures for making valid comparisons. For example, the use of landmarks, an ability clearly

implicated in pigeon homing (Fuller, Kowalski & Wiltschko, 1983), has been studied in a variety of species. The results of the current series of experiments suggest that spatial associative memory, a cognitive ability thought to be critical in food-storing behavior, could also be a productive avenue for further comparative research.

The present research has been interpreted within the traditional comparative framework. This is a somewhat misleading interpretation, given that only one species was tested and the testing procedures were novel. There are clearly interesting parallels between the procedures used here and similar procedures used with food-storing birds (Brodbeck *et al*, in press). The possibility that pigeons may be better than foodstorers on spatial associative memory tasks under some conditions suggests it is probably premature to conclude that the phenomenal memory performance of food-storing birds represents an adaptive specialization in memory. However, any conclusions must remain speculative until the two species are compared under identical conditions.

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