

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

Papers in Behavior and Biological Sciences

Papers in the Biological Sciences

1989

Studies of Learning and Memory in Natural Contexts : Integrating Functional and Mechanistic Approaches to Behavior

Alan Kamil

University of Nebraska - Lincoln, akamil1@unl.edu

Follow this and additional works at: <https://digitalcommons.unl.edu/bioscibehavior>



Part of the [Behavior and Ethology Commons](#)

Kamil, Alan, "Studies of Learning and Memory in Natural Contexts : Integrating Functional and Mechanistic Approaches to Behavior" (1989). *Papers in Behavior and Biological Sciences*. 50. <https://digitalcommons.unl.edu/bioscibehavior/50>

This Article is brought to you for free and open access by the Papers in the Biological Sciences at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Papers in Behavior and Biological Sciences by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

Studies of Learning and Memory in Natural Contexts: Integrating Functional and Mechanistic Approaches to Behavior

Alan C. Kamil

Departments of Psychology and Zoology, Neuroscience and Behavior Program,
University of Massachusetts, Amherst MA 01003

Address Correspondence to: Alan C. Kamil, Middlesex House, University of
Massachusetts, Amherst MA 01003 USA

1. INTRODUCTION

My purpose in this paper is to describe two research projects that combine experimental psychology and behavioral ecology. The first employs the operant conditioning technology developed by psychologists to test hypotheses arising from ecological studies of foraging animals. The second uses concepts from natural history and ecology to explore the nature and evolution of spatial memory. These two projects demonstrate both the advantages and the challenges of interdisciplinary work.

There are many advantages to combining psychological and biological perspectives on the behavior of animals. But truly interdisciplinary work is rare, mostly because it is so difficult to achieve meaningful integration across the boundaries that define different approaches. The ideas of Lakatos (1) about the nature of science help illuminate this difficulty. According to Lakatos, scientists work within 'research programs'. A research program is characterized by a set of central assumptions which are not subjected to direct empirical test. This central core provides the overall framework within which specific hypotheses are generated. These hypotheses are then tested empirically. Different research programs, as well as different disciplines, differ in context and in which questions they consider most important. If these differences are not understood, appreciated and dealt with, truly interdisciplinary research is impossible. All too often, what passes for interdisciplinary research involves only superficial cross-disciplinary integration. Therefore, before discussing details of the research we have been doing, I will briefly outline the differences between the approaches of experimental psychology and behavioral ecology (more detailed discussions are available, see 2, 3). The particular branch of experimental psychology in which I am interested is the experimental analysis of animal learning. This area involves several traditions, particularly those of the Skinnerian (4) and of the associationist (5). Although these traditions differ in important ways, they do share a number of characteristics. They are both resolutely generalist in the sense that they assume that a relatively small set of principles will account for behavior in a wide variety of situations and a wide variety of species. They are also, as is most of psychology, heavily environmental and mechanistic. In terms of methodology, the emphasis is on automated, 'objective' laboratory studies of behavior under highly controlled laboratory conditions. Behavioral ecology is quite different in orientation (6). Where the psychologist's emphasis is on understanding behavior in the laboratory, the behavioral ecologist, even when engaged in laboratory studies of behavior, is primarily interested in

understanding behavior under natural conditions. Where the psychologist emphasizes a few general mechanistic principles (e.g., the law of effect or contiguity), the behavioral ecologist emphasizes functional principles, particularly the concept that behavior functions to maximize the representation of the individual's genes in succeeding generations. Where the psychologist tends to assume that principles are easily generalized across species, the behavioral ecologist tends to assume that species are different in many important ways.

Despite these differences, the integration of certain aspects of animal learning psychology and behavioral ecology are highly desirable, if not inevitable, because of convergent developments in the two disciplines over the past 20 years. In psychology, one of these developments has been the recognition of so-called 'biological constraints' on learning. Phenomena such as automaintenance, taste-aversion learning and the importance of species-specific defense reactions in avoidance learning have forced psychologists to recognize that the ecology and natural history of animals has important effects on what and how animals learn (3). Another factor has been the emergence of a more decision-making, cognitive view of animal behavior. This is consistent with the view of behavioral ecologists of the animal as a decision maker.

Behavioral ecology treats animals as decision makers. Most optimal foraging models regard the forager as being faced with several behavioral alternatives among which it chooses. The animal is assumed to possess considerable knowledge about these alternatives, knowledge which allows the animal to choose the option that will produce the best outcome. For example, even the earliest optimal foraging model of MacArthur & Pianka (7) assumed that animals know the energetic value of each prey type it encountered. Optimal foraging models generally do not consider how animals acquire or store information. But these psychological questions can often have important ecological implications (as discussed below, see 8).

One of the major tasks facing the scientist who attempts to combine experimental psychology and behavioral ecology is the task of integrating mechanistic and functional explanations of behavior. This issue has recently been addressed in several papers (e.g., 2, 3, 9). There are compelling reasons for believing that this integration will eventually be achieved. The most compelling is the simplest: there is a single set of phenomena that both mechanists and functionalists attempt to predict, the behavior of animals. Accomplishing integration between functional and mechanistic levels of explanation as well as across the disciplinary boundaries between psychology and organismic biology will be difficult, and will take time. The form of this integration is not clear. One of the crucial steps that must be taken is clear, however. We must begin to do research that pools the best from the different disciplines being brought together. The long-range goal of ethoexperimental analysis, combining psychology with ethology and behavioral ecology, must be to reconcile and integrate functional and mechanistic explanations of behavior. I believe that the value of research in this area should be judged by the extent to which it contributes towards reaching this goal.

When disciplinary boundaries are broken, many new lines of research suggest themselves. One of the most straightforward and simple approaches to interdisciplinary work takes the research techniques from one discipline and applies them to the test of theoretical ideas of another. The application of the operant conditioning procedures developed by psychology to questions about foraging behavior is an example of this possibility.

In the long run, such research will help us understand both the psychological mechanisms involved in the decisions of foraging behavior as well as their functional significance.

2. USING OPERANT CONDITIONING PROCEDURES TO STUDY FORAGING BEHAVIOR

During the last 25-30 years there has been a substantial change in the way in which ecologists think about and study foraging behavior (8, 10). A new body of theory, optimal foraging theory (OFT) has emerged as a powerful way of attempting to understand foraging behavior. Optimal foraging theory has been an important development, but the change that has taken place is actually much broader. As Schoener (10) points out, not only is OFT new, but the phenomena that OFT attempts to explain were largely ignored or unknown before about 1970. For example, in his survey of pre-1970 ecology textbooks, Schoener finds that feeding behavior was often not even mentioned, except perhaps in methodological or community structure contexts. Today, many ecologists are closely examining the behavior of individual animals while foraging, both in the field under natural conditions as well as in the laboratory under more controlled conditions (see 11 for many examples). The resulting data are changing the way ecologists think about foraging behavior, as well as raising many interesting psychological questions in an important ecological context.

2.1. Search Images

One of the earliest studies to closely examine the foraging behavior of individual animals was the extensive project during which L. Tinbergen (12) and his associates (13) measured two variables in great detail, insect populations and predation by birds bringing insects to their nest. The field data showed a sigmoidal relationship between relative prey density and predation. At low levels of availability, a particular insect type would be preyed upon less than would be expected by chance. At some moderate levels of availability, the insect was taken much more than expected by chance. Then, at very high levels of availability, the insect again would be taken less than expected. But in the middle range of availabilities, small increases in density were often associated with large increases in predation.

On the basis of these data, Tinbergen (12) proposed the search image hypothesis. According to this hypothesis, if a predator encounters the same prey type several times in a row, it then becomes more able to detect that prey type. Thus, Tinbergen argued, relatively small changes in density could result in the formation of a search image for that prey type, which in turn would produce a dramatic increase in predation on the type in question.

Tinbergen (12) was very specific about the search image being based upon a change in the ability of the predator to detect the prey. Many authors have taken any evidence that predators will continue to select the prey type they have been selecting in the past as evidence of the search image (9, 14). However interesting such evidence may be in its own right, it is irrelevant to Tinbergen's hypothesis.

Although Tinbergen postulated a particular mechanism, there are many alternative mechanistic explanations for the observed relationship between prey density and predation. The most important of these alternatives is based upon systematic patch exploitation. If different insect types are found in different areas, e.g., different microhabitats, then spatial learning could produce the sigmoidal prey density-predation relationship

observed. The birds could start each day by systematically sampling each microhabitat, then concentrating their predation in that microhabitat (and upon that prey type) that was most abundant that day. This could also produce a nonlinear density-predation relationship.

This discussion of alternative mechanisms demonstrates how mechanism and function can be closely related. If the Tinbergen search image hypothesis is correct, then the effect would be limited to cryptic, hard-to-find prey. Improvements in the ability to detect prey should only be important when detection is difficult. If the patch use hypothesis is correct, then crypticity should be irrelevant. Finally, it should be noted that these two hypotheses are not mutually exclusive.

Critically evaluating Tinbergen's search image hypothesis presents substantial methodological difficulties. In order to test the hypothesis, experiments have to control the order in which prey types are encountered. Although there have been some clever and informative tests with animals in the field (15) and in open field environments in the laboratory (16), these attempts have been limited by an inability to control the exact order and timing of encounters with prey. This is a problem we have used operant techniques to overcome.

The story of how we came to think of this technique may be of interest as a case study in how interdisciplinary ideas actually occur. In Spring, 1973, my students and I were auditing a course on predator-prey interactions being taught by my colleague at University of Massachusetts, Ted Sargent. One of the major topics Ted covered was the search image concept and the data relevant to it. We felt that the idea was a fascinating one, but that the data collected to date was not definitive. We wanted to work on the idea, and felt that we had a really good predator-prey system available for studying search image. We had been working with blue jays (*Cyanocitta cristata*), an omnivorous and highly visual predator, for some time. Among the prey taken by these birds in nature are Catocala moths, highly cryptic, background matching animals (Figure 1). We had an interesting theoretical problem and a good predator-prey system for testing it; all we lacked was a good experimental procedure.

Then one of those lucky coincidences took place. Richard Herrnstein came to campus to give a colloquium on his research on 'concept formation' in pigeons (17). In this research, many different slides are shown to pigeons. These slides can be divided into two classes based upon the presence or absence of a class of objects, e.g., trees. If an example of the concept (a tree) is present, the bird is occasionally reinforced for pecking at it. If no example is present, the pigeon is never reinforced for pecking. After training, the birds learn to peck at examples and not peck (or peck less) at non-examples, even when slides are shown that the bird has never seen before. The nature of the learning responsible for this ability to discriminate novel examples is still largely not understood (18). However, the technique itself offers many possibilities for research on interesting problems.

As we sat listening to Herrnstein it occurred to us that his procedures were perfect for search image work. All we needed to do was substitute blue jays for pigeons and cryptic moths for trees. If the birds could learn to respond appropriately to the presence or absence of moths, we would then have a procedure with which we could precisely control the order of encounter with different prey types by controlling the order in which slides were shown to the jays.

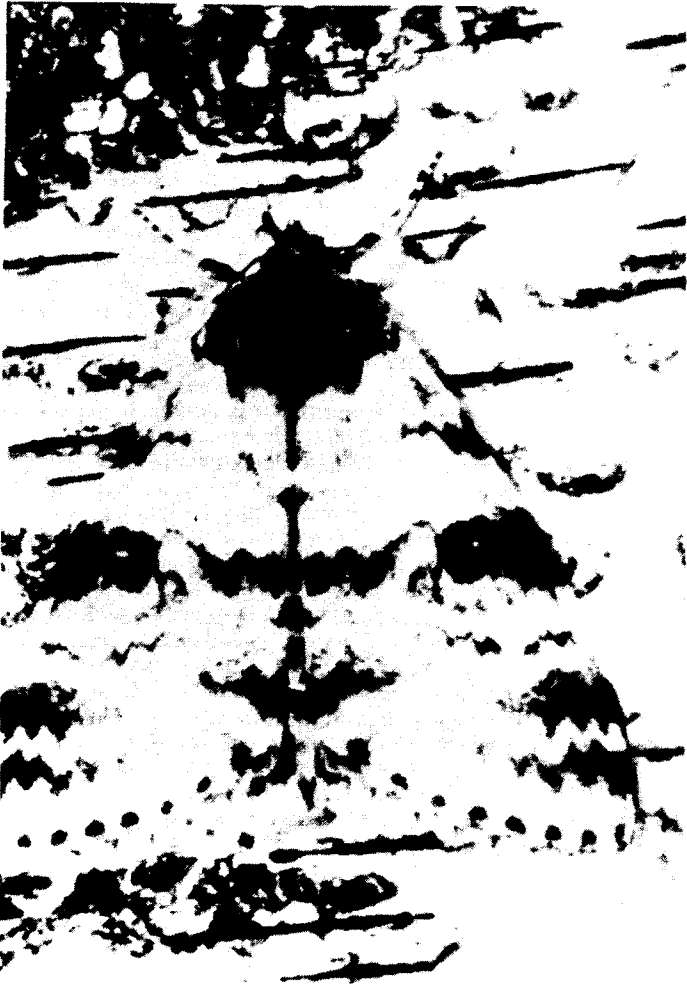


Figure 1. A close-up view of a *Catocala relictata* moth on a birch tree.

In our first study Pietrewicz and I (19) set out to determine if the jays would learn the concept of moth. We prepared a set of slides in which each of three *Catocala* species were photographed on three different backgrounds at various distances. For each picture of a moth, we also made an identical picture of the same scene without the moth. These slides were then presented to the birds in random order. Because we wanted the jays to give unambiguous responses to indicate whether or not they saw a moth in a slide, we used different response contingencies than Herrnstein had used. The slides were projected onto a large, rectangular pecking key. A small round pecking key was located below the rectangular one. The essence of the procedure was that the jay could say 'yes, I see a moth' by pecking at the rectangular key, or could say 'no I don't see a moth' by pecking at the round key. Correct yes responses produced a mealworm after

a handling time requirement was satisfied. Incorrect yes responses produced the handling delay, but no mealworm. Correct no responses resulted in the next trial beginning within a few seconds (needed to allow the slide projector to advance). Incorrect no responses resulted in a 30 sec penalty before the start of the next trial.

All of the jays learned the task, performing with overall accuracy scores as high as 85%, even when new slides they had never seen before were introduced. We were quite confident that the birds were actually detecting the moths. There was a slide without a moth (a negative) exactly identical to each slide with a moth (a positive) in the set. In addition, the performance of the birds was very orderly with respect to the visual characteristics of the moth. Performance declined as the moth-to-camera distance increased. Moths were detected less frequently when they were presented on their species-specific background which best matched the appearance of their forewings. Thus, for example, *Catocala relictata*, a white species with disruptive black coloration was detected less often when presented on white birch than when presented on oak (19).

Having demonstrated that these procedures produced orderly data on the detection of cryptic prey, we proceeded to test the search image hypothesis (20). Each day, each jay received a foraging session during which it responded to 24 slides. The crucial test occurred with slides 5-20. These 16 slides always included 8 slides of moths and their 8 empty counterparts, in random order. During the experimental conditions, the 8 moths were of the same species. In the control condition, they included 4 of each of two species, in random order. If Tinbergen (12) was correct, then prey detection should improve during the experimental condition, as the jays encountered the same prey type several times in a row, but should not improve during the control condition.

As shown in the top panel of Figure 2, this is exactly what happened. The probability of detecting a moth increased significantly after 3-4 consecutive experiences with the same species. As shown in the bottom panel of Figure 2, the birds also became more accurate at correctly rejecting empty slides as search image formation took place. This pattern of improvement in accuracy on both types of images provides convincing evidence that the birds' ability to detect the moths improved when they encountered a run of the same prey type.

Recently, Guilford and Dawkins (21) have suggested that a variety of experimental results, including those of Pietrewicz and Kamil (20), can be explained by changes in search speed rather than changes in the ability to detect prey. However, their arguments ignore, or attempt to sidestep, several aspects of the data of Pietrewicz & Kamil (20, 22). Two points seem particularly critical. First, Pietrewicz (22) recorded the speed with which the jays made each decision. She found that speed of response was actually faster during runs than non-runs, although the effect was not statistically significant. In view of these data, it is difficult to imagine how a slowing of search speed could account for the increase in prey detection observed.

Second, the argument of Guilford and Dawkins depends, in part, on the two prey types being of differing difficulty. The data of Pietrewicz and Kamil do not seem to indicate any differences in detectability between the species of moth. Guilford and Dawkins (21) approach this problem by emphasizing the data from a different experiment, one conducted with naive birds. They suggest that the data of Pietrewicz and Kamil (14) indicate that the two moth species did differ in detectability. However, these data

were collected with during the acquisition of the ability to detect the moths, and with a somewhat different stimulus set. The most relevant data to the issue of relative detectability are presented in the original Pietrewicz and Kamil (20) search image paper. As shown in Figure 2, the detection rates for the two prey types were equal in this experiment. Thus although the interpretation of Guilford and Dawkins (21) is technically possible, in the absence of positive evidence for their hypothesis, it seems unlikely that their hypothesis accounts for our data on search image formation.

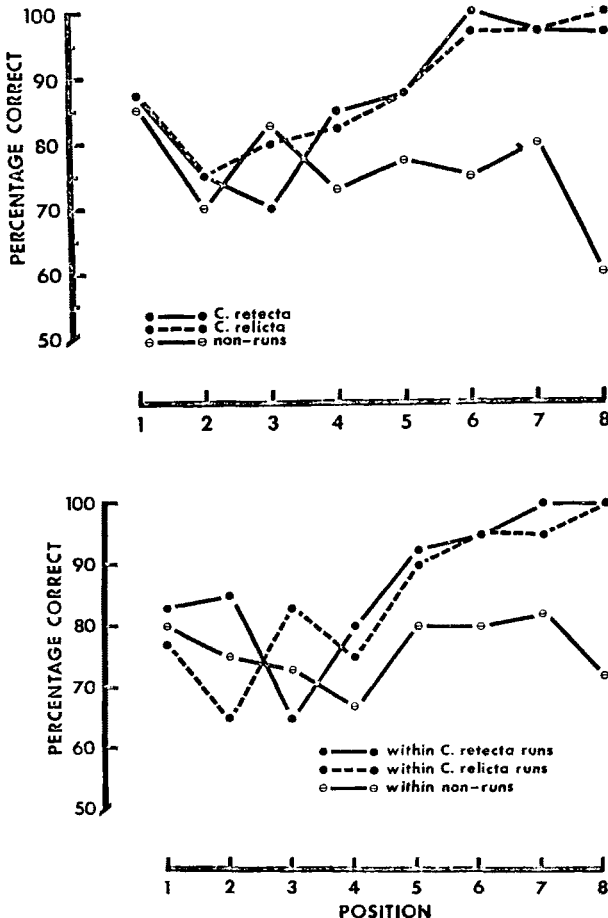


Figure 2. The results of the search image experiment. The top panel shows the the ability to detect moths improved in the runs condition. The bottom panel shows that the ability to correctly reject images without moths increased at the same time.

Bond (23) has recently studied the ability of pigeons to detect cryptic grains, using operant techniques similar to those we have developed as well as situations in which the pigeons searched for grains on differing backgrounds. These studies have produced effects generally similar to those obtained with the jays. Most importantly, perhaps, improvements in detection by the pigeons were accompanied by increases in the speed of detection. This provides further evidence against the Guilford and Dawkins hypothesis (21).

These procedures for studying cryptic prey detection are not limited to testing the search image hypothesis. For example, we have tested the application of a version of the marginal value theorem (24) to the cryptic prey detection situation (25) and the effects of increasing prey crypticity on detection (26). There are many fascinating biological problems surrounding the phenomenon of prey detection, including the evolution of polymorphisms and warning coloration, to which these techniques can be applied. This is particularly true with the development of computer equipment which can be used to capture digitized images from a TV camera, edit those images and display them to animals in high resolution with realistic color. We are currently beginning to use these capabilities to further investigate the search image question and test the Guilford and Dawkins (21) hypothesis.

3. OPERANT STUDIES OF PREY DEPLETION

In our operant studies of cryptic prey detection, the questions and hypotheses arise largely from ecology and natural history. Another important source of predictions about foraging behavior that are eminently testable through operant techniques is provided by optimal foraging theory. For example, one approach has been to adapt various schedules of reinforcement so that they simulate the situations modeled by various OFT models (27). Other researchers have used discrete trial procedures to test these models, particularly the diet selection model (28).

In my own laboratory, we have been particularly interested in an issue that arises from OFT, but is not specific to any one OFT model. What 'rules of thumb' do animals use to decide when to leave a depleting patch. This is a particularly appropriate area for interdisciplinary research because the question is of central interest to both behavioral ecologists and psychologists. To a psychologist, the question is one of stimulus control. That is, the psychologist asks what events (stimuli) control the patch departure decision.

To behavioral ecologists, when to leave a depleting patch is one of the classic problems of OFT. It is the problem addressed by the marginal value theorem, and many other theoretical papers (8, 29). Most models of patch departure use complex mathematics to predict the optimal leaving time. It is well-recognized, however, that animals do not use calculus to make decisions. Therefore, there has been strong interest in identifying the simpler 'rules of thumb' that animals may use, and how well these rules approximate the optimal solutions to problems under various conditions (see 8 for extensive discussion).

Attention has focused largely upon two kinds of rule, which are often treated as mutually exclusive: number of prey obtained (or hunting by expectation (30), and runs-of-bad-luck (31). A simple number-of-prey rule would be to always leave after a certain, fixed number (or amount of) prey had been found. A simple run-of-bad-luck rule would be to always leave after a certain amount of time (or number of consecutive instances) without

success. Because each rule would have different functional implications in different settings, this provides another interesting case of mechanism-function interaction. We decided to use operant procedures to study the patch departure decisions of blue jays.

The basic idea behind the procedures we developed was to provide the jays with two patches. One patch always provided a constant but mediocre rate of return. The other patch was a depleting patch which produced a high rate of prey encounters at first, but then depleted suddenly. Before depletion it was better than the constant patch, but after depletion it was worse. Hopefully, the birds would learn to begin each foraging bout in the depleting patch, then switch to the nondepleting patch after depletion had occurred. If this behavior took place reliably, in bout after bout, we would have an excellent paradigm with which to study patch departure in the face of depletion.

In order to implement this concept, we added a second patch to our prey detection paradigm, which could be considered a single patch procedure, by providing a second set of keys. Each of the two sets of pecking keys represented a patch, each containing a pair of pecking keys, one large and rectangular, the other small and round. Each rectangular key had a slide projector which could project images with or without moths onto the key. The two patches were placed on either side of a central food cup. Figure 3 diagrams the arrangement and shows the events of each trial. Each trial began with the illumination of both round keys. The jay chose which patch to hunt in on that trial by pecking at one of the round keys, which made the other set of keys become dark and inoperative for the rest of the trial. The peck to the round key started a travel time requirement. When the travel time was over, the display on the round key changed and the next peck initiated the search stage. During this stage, a slide was projected onto the rectangular key which might or might not contain a noncryptic moth, and the round key was illuminated. As in our search image work, the jay could peck the rectangular key, which after handling time, produced a mealworm if a moth were present. Alternatively, the jay could peck the round key which ended the trial immediately whether or not a moth was present on the rectangular key. Because the moths were noncryptic, the jays rarely made errors.

The major advantage of this procedure was that the quality of each patch could easily be controlled by the placement of slides in the projector slide trays. In all of our experiments to date, the depleting patch begins with a probability of prey being present on each trial of 0.50, which declines to 0 in a single step at the depletion point. The nondepleting patch had a constant 0.25 probability of containing prey throughout the foraging bout, which consisted of 36 trials.

Our first experiment (32) was designed to evaluate this approach to studying the patch departure problem. Four jays were trained with these procedures. Adapting a suggestion of Iwasa et al. (33), we varied the point of depletion. For two of the jays, depletion always occurred after exactly 6 prey, but a variable number of trials (prey were in random order). For the other two jays, depletion always occurred after the 12th trial, but a variable number of prey.

The jays responded in an orderly and sensible manner to these conditions. They learned to begin each foraging bout in the depleting patch and switch to the nondepleting patch soon after depletion had taken place. There were no differences between the birds receiving a constant number of prey and the birds receiving a constant number of trials before

depletion. The birds were extremely efficient. At the end of the experiment they were obtaining a mean of 10.7 prey per session. An omniscient predator that always switched on the trial immediately following depletion would have obtained a mean of 12 prey per session.

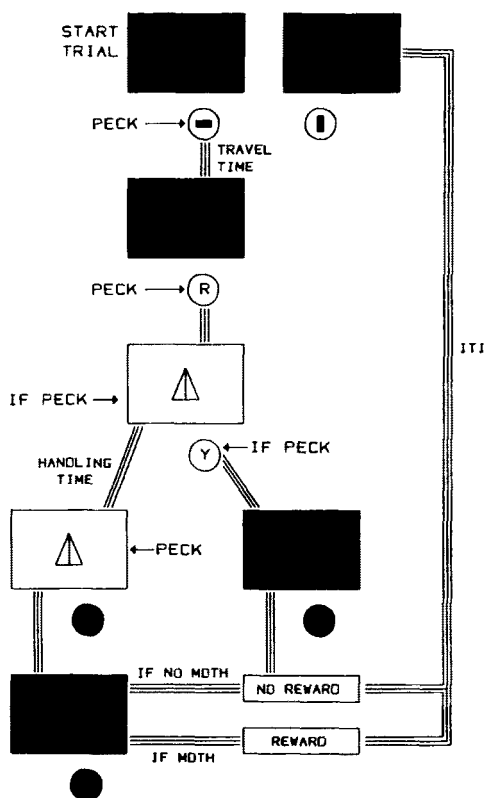


Figure 3. This flow diagram summarizes the two-patch procedure used during our patch depletion experiments, as described in detail in the text.

Although the data of this experiment did not allow a determination of the exact rule the birds were using to switch from the depleting to the nondepleting patch, there were two interesting pieces of evidence relevant to this issue. First, runs-of-bad-luck clearly played a role because switches out of the depleting patch were usually preceded by non-moth trials, and this tendency increased as the experiment proceeded. Second, different rules were used for switches in the two directions. While switches from the depleting to the depleting patch tended to be preceded

by negative trials, the opposite was true for switches in the other direction. By the end of the experiment, over 80% of the switches from the nondepleting to the depleting patch were preceded by trials during which a prey was found.

A second experiment (34) was designed to more thoroughly investigate the rules underlying patch departure. Five jays were exposed to the same basic procedures as before. There were 4 stages of the experiment, during each of which the jays received fixed numbers of prey before depletion. During the first stage there were 9 prey in the depleting patch; during the second stage, 6 prey; during the third stage 3 prey; and during the last stage 9 prey again. Each of the first three stages continued for 120-150 sessions to ensure that there was enough data available to carry out detailed analyses of the events preceding switches out of a patch.

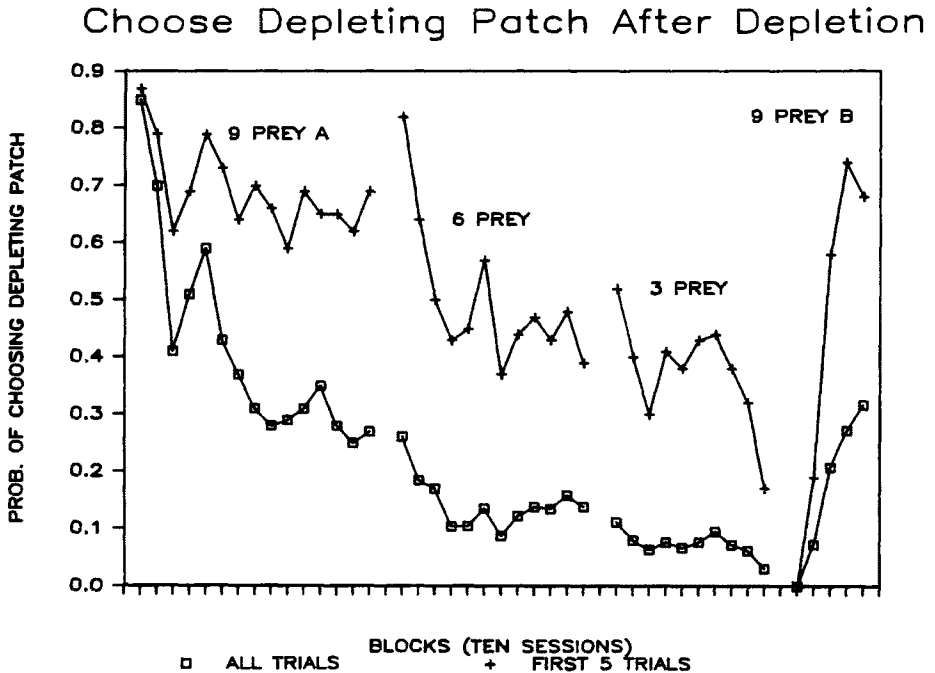


Figure 4. Mean probability of choosing the depleted patch on all trials and on the first five trials after depletion during each condition of the experiment.

The birds again behaved efficiently, adjusting their behavior to the changing conditions (Figure 4). For example, the critical switch trial (that switch after which at least 80% of subsequent choices were in the same patch) went from 23 when there were 9 prey before depletion to 13 when there were 6 prey, to 7 when there were 3 prey. The overall effects of

changing the number of prey between conditions suggested that the birds were using neither a number expectation nor a run-of-bad-luck rule in isolation. If they were depending completely on a run-of-bad-luck rule then they should have adjusted immediately to decreases in the number of prey before depletion. For example, a bird that always left after 4 negative trials in a row would have left four trials after the last prey the first time that the 6 or 3 prey condition was encountered. On the other hand, if they were using a strict number expectation, adjustment to the change from 3 to 9 prey at the end of the experiment should have been slow or nonexistent. The implication is that the birds may have been using both expectation and run-of-bad luck jointly.

This implication received strong support from a detailed analysis of the events preceding switches out of the depleting patch (Figure 5). The conditional probability of patch departure was calculated for each combination of number of prey already found and run-of-bad-luck length for each condition of the experiment. Both number of prey and ROBL had highly significant effects, as did their interaction. Within any condition, patch departure was a joint function of the number of prey found and ROBL length.

Departure Rule – by Condition

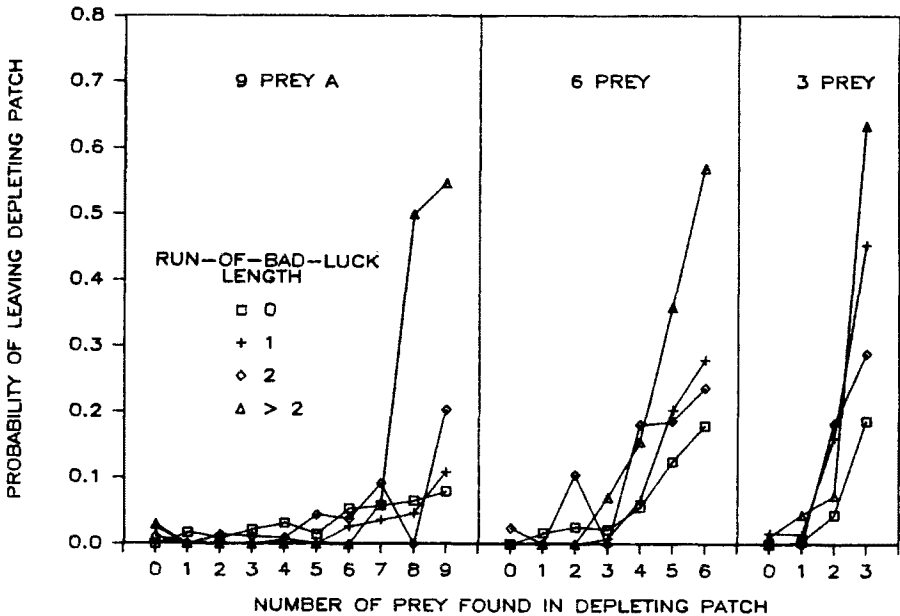


Figure 5. The probability of leaving the depleting patch as a joint function of the number of prey already found and the length of the run-of-bad-luck throughout each of the first three conditions of the depletion experiment.

From a psychological point of view, these results raise interesting questions about mechanism. The birds' behavior varied consistently as a function of the number of prey found and the number of consecutive negative experiences. Although there is no reason to suggest the birds were literally counting these two quantities, how these are monitored remains an interesting question. From an ecological, functional point of view, the birds' behavior suggests that they use a rule-of-thumb which is fairly efficient. The jays obtained over 90% of the prey available most of the time. This joint rule is not as simple as some authors seem to have suggested that rules of thumb ought to be. But this joint rule has the advantage of flexibility. It leaves the animal sensitive to changes in prey availability in both directions. These results provide another case in which the nature of the decision rule of the animal has important functional implications.

A more recent experiment suggests that the jays are strongly committed, in some sense, to the joint rule. During this experiment (35), depletion occurred after a randomly varying number of prey, so that number of prey obtained had very limited information value. Nonetheless, the birds continued to use both ROBL and number of prey, even though a simple ROBL rule would have produced more efficient foraging. These studies are beginning to reveal the mechanisms the birds use to make patch departure decisions. And the functional value of these mechanisms is also beginning to become clear. We plan a series of experiments that are designed to explore how different rules of thumb for patch departure function in the face of environmental change during the coming year.

In summary, these experiments on prey detection and patch departure demonstrate how the operant techniques developed by psychologists can be used to investigate questions about the decisions of foraging animals. In the course of such studies, we can learn a great deal about the behavioral processes involved in foraging behavior. The results of such studies have important functional and mechanistic implications.

4. SPATIAL MEMORY IN FOOD-CACHING BIRDS

In the examples above, psychological techniques were applied to biological problems. In this section, I will discuss another area of research that is generated by interdisciplinary contact. In this case, information from natural history and ecology is used to select species for psychological study.

The issue of species selection has been a sometimes heated and controversial one in psychology (36). I do not intend to review that issue here. Instead, I will give an example of an approach that has not often been used by psychologists (see 3 for an extended discussion of the logic underlying this approach). The basic idea is to explicitly choose animals for study on the basis of their natural history and ecology. Psychologists have tended to avoid such selection in the past because they thought that the results of such experiments might be limited (37). However, there are advantages to this mode of species selection. Selecting species for comparative study on the basis of divergence in natural history can contribute to understanding the evolution of cognitive abilities. In addition, if we want to explore the limits of the abilities of animals, testing animals in the context of the demands placed upon them by their natural history should prove a valuable and important strategy.

An excellent example of this approach is provided by research on spatial memory in food-storing birds (38). To date, research has

concentrated upon two groups, the parids (39) and the corvids (40, 41). The parids tend to scatter-hoard, with cached food being retrieved within 24-48 hr (42). In contrast, the food cached by corvids is often not recovered for many months. The most specialized corvids are the two species of the nutcracker genus, the Eurasian nutcracker (*Nucifraga caryocatactes*) and the Clark's nutcracker (*N. columbiana*). In a typical fall, a single Clark's nutcracker will cache about 30,000 pine seeds in 5-6,000 separate locations in the ground. These cached seeds are then recovered and eaten throughout the winter and spring, providing virtually all of the food of the parents and their young during the breeding season (43). There are several morphological specializations which support these behavioral ecological measures. For example, Clark's nutcrackers possess very long, stout beaks which allow them to open pine cones before they ripen. They also possess a sublingual pouch which allows them to carry as many as 80 pine seeds at a time.

Tomback (44) collected data which gave an indirect estimate of the accuracy of the cache recovery of nutcrackers. When nutcrackers dig up their stored pine seeds, they often leave a conspicuous hole in the ground. If they have found seeds, they usually husk them on the spot. Therefore, Tomback was able to count the number of holes with and without husks next to them. She found that 35-65% of the holes has husks. This can be regarded as a minimum estimate of the recovery accuracy of nutcrackers in the field. It is a minimum estimate because sometimes rodents steal caches, and sometimes the birds fly away before husking the seeds. More recently, direct observations of nutcrackers recovering caches in the wild have produced similar results (45) to those reported by Tomback. It is hard to imagine how a randomly searching bird could have such high probabilities of coming up with seeds when it probed the ground. How does the nutcracker find its seeds?

Evidence from three separate studies clearly demonstrates that memory plays an important role. Balda (40) was the first to study nutcracker cache recovery under controlled laboratory conditions. He studied a single Eurasian nutcracker in a dirt-floored room. The bird was allowed to store seeds, and then recover them 9-18 days later. The bird performed very well, recovering the cached seeds with accuracy far above anything that could be expected by chance. Then, in a critical control procedure, Balda allowed the bird to cache, carefully mapped the locations of the caches, removed all of the seeds and thoroughly raked the floor. This must have removed all cues possibly emanating directly from the seeds, especially odors. The bird accurately returned to cache locations under these conditions.

Vander Wall (41) studied two Clark's nutcrackers in an outdoor aviary. He also found that they would cache under laboratory conditions and recover their caches seeds accurately. He extended Balda's findings in several important ways. First, he found that a nutcracker that was present when another bird cached was very poor at finding the seeds cached by another bird. Second, when two birds were allowed to cache in the aviary at different times, and then later allowed to recover (separately) with both sets of caches present, each bird only recovered the caches it had made. These findings offer strong support for the contention that memory is used. Finally, Vander Wall found that when he moved prominent landmarks in the aviary between caching and recovery, the birds ability to recover was disrupted. This indicates that spatial memory based on landmarks is used.

Kamil & Balda (46) devised a technique that allows extensive control

over the selection of cache sites. We built a room with a plywood floor with many small holes cut into it. Each hole could be equipped with a sand-filled cup, or capped with a wooden plug. The birds would readily cache and recover from the sand-filled cups. In several experiments, we have tested the cache recovery accuracy of nutcrackers after caching in holes largely selected by the experimenter (46, 47, 48). During these experiments, we allow nutcrackers to cache with only a few of the holes uncapped. Then during recovery sessions 7-10 days later, the birds re-enter the room for recovery with all of the holes open. The birds perform accurately. In two experiments (47, 48) we have tested the same birds with both very few holes available during caching, and with many holes available during caching. The cache recovery accuracy of most nutcrackers (10/12) was completely unaffected by this manipulation. These results demonstrate that even when the birds are not allowed to express any general preferences or movement patterns during caching, they can still find their seeds successfully.

The evidence for the use of spatial memory by nutcrackers recovering their seeds is quite convincing. This phenomenon raises many questions for both psychologists and biologists. The most basic question for biologists is why should the birds use memory? Does the use of memory have any functional advantage over alternative modes of cache recovery such as odor or systematic cache placement? The most likely answer is that the use of memory allows the bird to scatter its caches in an unpredictable way so as to minimize losses to inter- or intraspecific competitors. Again, the behavioral mechanism used has important functional implications.

If these functional implications are correct, we might expect to find other cases in which memory plays a role in creating unpredictable food distributions that will be relatively immune to exploitation by competitors. Some nectar feeding birds feed from flowers that contain relatively small, slowly replenished supplies of nectar. In at least some cases (49), these birds remember which flowers they have emptied. Direct measurements of efficiency have shown that the resident bird systematically avoids flowers that it has depleted, thus achieving higher rates of intake than intruders that have no information about nectar distribution. Although the manner in which the food distribution is created is quite different for the nectar feeding bird, the end result of using memory is the same as for the seed-caching bird - the creation of a food resource distribution that can be best exploited by the individual creating the distribution.

The most important mechanistic question raised by the spatial memory ability of Clark's nutcrackers is whether or not this ability of nutcrackers is 'special'. The word special has two possible meanings in this context. First, it could mean special relative to other species. Because of their unusual natural history, with the tremendous premium placed on successful recovery of cached pine seeds, the spatial memory of nutcrackers may be systematically better in some way from that of other species. Second, it could mean special in the sense of specialized. That is, the nutcrackers may possess a memory system for storing spatial locations that is used only for cache recovery, but not for other spatial memory tasks. In order to test these possibilities, it will be necessary to study the memory abilities of nutcrackers, and other species, in several different contexts.

The specialization hypothesis will also require multiple tests of the memory abilities of nutcrackers in several different paradigms in order to

determine if the characteristics of their memory vary across situations. The comparative hypothesis will similarly require several paradigms. If species differences are found with any one procedure, it is always possible that the differences are due, not to species differences in memory but to some 'contextual variable' specific to the paradigm (50, 3). However, if the results from several different procedures are congruent, no single contextual variable is likely to be responsible.

We have begun the long process of testing these ideas. In our first comparative experiment (48) we selected three corvid species, all of which cache pine seeds, but which differ in the extent of their dependence upon and morphological specialization for caching food. Pinyon jays are also very specialized for pine seed caching and recovery. Individuals cache about 20,000 seeds per year, and they possess an expandable esophagus in which they can carry 25-30 seeds. Scrub jays are much less dependent upon cached food, caching only about 5,000 seeds per year. They also can only carry a few seeds at a time in their mouth and crop. Thus on the basis of degree of specialization on cached food, one would expect nutcrackers to perform best, pinyon jays a close second and scrub jays the worst.

All three species were tested with the cache-recovery procedures we developed with nutcrackers, described above. We obtained relatively large and significant differences between species. The pinyon jays and nutcrackers consistently recovered their caches more accurately than did the scrub jays. Although this is largely consistent with the ecological differences among the species, it cannot be taken as providing conclusive evidence of differences in spatial memory ability.

The problem is that the species differed in ways that could have affected the characteristics of the task as a test of memory per se. Two behavioral differences were particularly important, number of visits to a site and the use of space during caching sessions. (1) During caching sessions nutcrackers loaded their sublingual pouch with seeds and rarely visited any cache site more than once even though they placed multiple seeds in most sites. Pinyon jays and scrub jays, in contrast, only carried one seed at a time and frequently visited a cache site more than once. It is well-known in the operant literature that repeated responding at a stimulus improves memory for that stimulus (51). Therefore the memorial demands on the scrub and pinyon jays may have been reduced by their repeat visits to cache sites. (2) Pinyon jays tended to cluster their caches close together in space. This may have allowed the pinyon jays to use an area-restricted search during recovery which would improve their accuracy levels.

These species need to be compared with other tests of spatial memory ability. One step in that direction has been taken by developing an open-field analog of the radial-arm maze for use with these species (52). In this experiment, we used 8 of the holes in the floor of our cache-recovery room, arranged in a circle. Many logs and bricks were placed between the holes to make it difficult for the birds to go directly between nearest neighbor holes. A trial consisted of two stages. During the information stage the bird was released into the room with 4 randomly chosen holes open. Each open hole contained a seed buried beneath the sand. After the bird removed the four seeds, the lights were turned off and the bird left the room for a retention interval. During the retention interval, the experimenters entered the room, cleaned up any signs of digging, opened all 8 holes and placed a seed in each of the four holes that had not yet been visited. After the retention interval, the bird reentered the room.

Correct responses were visits to holes that had not been visited earlier. This procedure is directly analogous to studies with rats (53) in radial arm mazes, and pigeons in open-field analogs of the radial arm maze (53).

The nutcrackers performed very well, showing little retention loss even after 6 hr. This performance is much better than that of pigeons (54), and roughly equivalent to that reported for rats (53). It will be of particular interest to use this radial arm maze analog to compare nutcrackers, scrub jays and pinyon jays.

While the radial maze performance of the nutcrackers was quite good compared to other species, it was quite poor when measured against another standard - the performance of nutcrackers during cache recovery tests of memory. There are two broad classes of explanation for this difference. First, it may be that the difference is due to the many methodological differences between radial arm and cache-recovery tests of memory. The most obvious is the difference in the opportunity for proactive interference to build up during radial maze testing. Second, the nutcrackers may be using different memory systems during the two tasks. These two possibilities can be differentiated by varying the parameters of the two test situations. We will soon begin a series of experiments that manipulate proactive interference during radial maze testing as a first step in this process. The results of such tests will contribute heavily to the resolution of the specialization issue.

In order to further explore both the comparative and the specialization issues, we have also begun a series of experiments on performance in nutcrackers, scrub jays and pigeons in operant tests of spatial memory, using a spatial nonmatching-to-sample procedure. Nutcrackers have performed spectacularly well, easily tolerating delays of 80 secs and longer. Scrub jays and pigeons have performed much more poorly. Much more work remains to be done. But these preliminary data suggest that the nutcracker may perform better than scrub jays (and pigeons) in a wide variety of tests of spatial memory. If this pattern holds up after repeated tests, it will indicate that there are species differences in spatial memory that correlate with the degree of ecological dependence on, and morphological specialization for cached food. Furthermore, if nutcrackers consistently outperform other, less specialized species in noncaching tests of spatial memory, this will suggest that their spatial memory abilities are general, and not specialized for use during cache recovery alone.

5. CONCLUSIONS

The two research programs described in this paper clearly demonstrate the advantages of research strategies that combine concepts and methods from experimental psychology and behavioral ecology. In the first program, operant conditioning techniques developed by experimental psychologists were applied to hypotheses and theories originating in behavioral ecology. We were able to test the search image hypothesis in a particularly powerful way and the resulting data helped understand data generated from less controlled field experiments. In our research on patch departure we were able to demonstrate the use of mixed rules of thumb based on two environmental parameters, ROBL and number of prey obtained within the patch. This use of a mixed rule enables the forager to be efficient while maintaining sensitivity to potential environmental change. Our research on spatial memory in Clark's nutcrackers and other corvids raises two issues that challenge traditional psychological views. First, the cache

recovery abilities of the nutcracker (and the caching parids, 39) are much greater than the spatial memory abilities of animals have been thought to be. The laboratory data, combined with the field data, indicate that these birds can remember thousands of locations for months at a time. Second, the preliminary findings that nutcrackers perform extremely well in several different tests of spatial memory suggest that a specific adaptation may have affected a general cognitive ability. Further studies of the cognitive abilities of animals in which animals are rigorously tested for abilities that are highly significant in their natural environments will probably contribute to dramatic changes in how we conceive of the limits of the mental abilities of animals (3).

ACKNOWLEDGMENTS

The research reported in this chapter, and the preparation of the chapter, were supported by NSF grants BNS-8418721 and BNS-8519010.

REFERENCES

1. Lakatos, I. (1974). The Methodology of Scientific Research Programs. Cambridge: Cambridge University Press, (1974)
2. Shettleworth, S. J. (1982). Function and mechanism in learning. In: M. Zeiler & P. Harzen (Eds.) Advances in Analysis of Behavior, Vol. 3. Biological Factors in Learning. New York: Wiley Sons. Kamil, A., & Yoerg, S. (1982) Learning and foraging behavior. In: P.P.G. Bateson & P.H. Klopfer (eds.) Perspectives in Ethology, Vol. 5, New York: Plenum Publishing Co.
3. Kamil, A. C. (1988). A synthetic approach to the study of animal intelligence. In: D. W. Leger (Ed.), Comparative Perspectives in Modern Psychology: Nebraska Symposium on Motivation, Vol. 35. Lincoln, Nebraska: University of Nebraska Press.
4. Skinner, B. F. (1977). Why I am not a cognitive psychologist. Behaviorism, 5, 1-10.
5. Rescorla, R. A. (1985). Associationism in animal learning. In: L. Nilsson & T. Archer (Eds.), Perspectives on Learning and Memory, Hillsdale, N.J.: Erlbaum.
6. Krebs, J. R., & Davies, N. B. (1981). An Introduction to Behavioural Ecology. Oxford: Blackwell Scientific Publications.
7. MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. American Naturalist, 100, 603-609.
8. Stephens, D. W., & Krebs, J. R. (1986). Foraging Theory. Princeton, N.J.: Princeton University Press.
9. Krebs, J. R. (1973). Behavioral aspects of predation. In: P. P. G. Bateson, & P. H. Klopfer (Eds.), Perspectives in Ethology. New York: Plenum Publishing Co. Krebs, J. R. (1978). Optimal foraging: Decision rules for predators. In: J. R. Krebs & N. B. Davies (Eds.), Behavioural Ecology. Oxford: Blackwell Scientific Publications.
10. Schoener, T. W. (1987). A brief history of optimal foraging ecology. In: A. C. Kamil, J. R. Krebs, H. R. Pulliam (Eds), Foraging Behavior, New York: Plenum Publishing Co.
11. Kamil, A. C., Krebs, J. R., & Pulliam, H. R. (1987). Foraging Behavior. New York: Plenum Publishing Co.

12. Tinbergen, L. (1960). The natural control of insects in pinewoods. 1. Factors influencing the intensity of predation by songbirds. Archives Neerlandaises de Zoologie, 13, 265-343.
13. Mook, J. H., Mook, L. J., & Heikens, H. S. (1960). Further evidence for the role of "searching image" in the hunting behavior of titmice. Archives Neerlandaises de Zoologie, 13, 448-465.
14. Pietrewicz, A. T., & Kamil, A. C. (1981). Search image formation in the blue jay (*Cyanocitta cristata*). Science, 204, 1332-1333.
15. Croze, H. J. (1970). Searching image in carrion crows. Zeitschrift fur Tierpsychologie, Supplement 5, 1-85.
16. Dawkins, M. (1971a). Perceptual changes in chicks: Another look at the "search image" concept. Animal Behaviour, 19, 566-574.
16. Dawkins, M. (1971b). Shifts in "attention" in chicks during feeding. Animal Behaviour, 19, 575-582.
17. Herrnstein, R. J., & Loveland, K. H. (1964). Complex visual concept in the pigeon. Science, 146, 549-551.
18. Herrnstein, R. J. (1985). Riddles of natural categorization. In: L. Weiskrantz (Ed.) Animal Intelligence, Oxford: Clarendon Press.
19. Pietrewicz, A. T., & Kamil, A. C. (1977). Visual detection of cryptic prey by blue jays (*Cyanocitta cristata*). Science, 195, 580-582.
20. Pietrewicz, A. T., & Kamil, A. C. (1981). Search image formation in the blue jay (*Cyanocitta cristata*). Science, 204, 1332-1333.
21. Guilford, T., & Dawkins, M. S. (1987). Search images not proven: a reappraisal of recent evidence. Animal Behaviour, 35, 1838-1845.
22. Pietrewicz, A. T. (1977). Search Image Formation in the Blue Jay (*Cyanocitta cristata*). Unpublished doctoral dissertation, University of Massachusetts, Amherst, MA.
23. Bond, A. B. (1983). Visual search and selection of natural stimuli in the pigeon. Journal of Experimental Psychology: Animal Behavior Processes, 9, 292-306. Bond, A. B., Riley, D. A., & Ranganathan, S. (1989). Selective attention during visual search for natural stimuli in the pigeon. Journal of Experimental Psychology: Animal Behavior Processes, in press.
24. Charnov, E. L. (1976). Optimal foraging: The marginal value theorem. Theoretical Population Biology, 9, 129-136. Fitzpatrick, J. W. (1978). Foraging Behavior and Adaptive Radiation in the Avian Family Tyrannidae. Unpublished doctoral dissertation, Princeton University, Princeton, NJ.
25. Kamil, A., Lindstrom, F., & Peters, J. (1985). Foraging for cryptic prey by blue jays. I. The effects of travel time. Animal Behaviour, 33, 1068-1079.
26. Getty, T., Kamil, A. C., & Real P. G. (1987). Signal detection theory and foraging for cryptic or mimetic prey. In: A. C. Kamil, J. R. Krebs & H. R. Pulliam (Eds.), Foraging Behavior, New York: Plenum Publishing Co.
27. Hanson, J. (1987). Test of optimal foraging using an operant analogue. In: A. C. Kamil, J. R. Krebs, & H. R. Pulliam, (Eds.) Foraging Behavior. New York: Plenum Publishing Co.
28. Fantino, E. (1987). Operant conditioning simulations of foraging and the delay-reduction hypothesis. In: A. C. Kamil, J. R. Krebs, & H. R. Pulliam (Eds.), Foraging Behavior. New York: Plenum Publishing Co.

29. Green, R. (1987). Stochastic models of optimal foraging. In: A. C. Kamil, J. R. Krebs, & H. R. Pulliam (Eds.), Foraging Behavior. New York: Plenum Publishing Co.
30. Gibb, J. A. (1962). L. Tinbergen's hypothesis of the role of specific search images. Ibis, 104, 106-111.
31. Krebs, J. R., Kacelnik, A., & Taylor, P. (1978). Test of optimal sampling by foraging Great Tits. Nature, 275, 27-31.
32. Kamil, A. C., & Yoerg, S. I. (1985). Effects of prey depletion on patch choice by foraging blue jays (*Cyanocitta cristata*). Animal Behaviour, 33, 1089-1095.
33. Iwasa, Y., Higashi, M., & Yamamura, N. (1981). Prey distribution as a factor determining the choice of optimal foraging strategy. American Naturalist, 117, 710-723.
34. Kamil, A. C., Yoerg, S. I., & Clements, K. C. (1988). Rules to leave by: Patch departure in foraging blue jays. Animal Behaviour, 36, 843-853.
35. Yoerg, S. I., Clements, K. C., & Kamil, A. C. (1989). Effects of variable patch quality on departure rules in blue jays. Behavioral Ecology and Sociobiology, in press.
36. Hodos, W., & Campbell, C. B. G. (1969). Scala naturae: Why there is no theory in comparative psychology. Psychological Review, 76, 337-350.
37. Seligman, M. E. P. (1970). On the generality of the laws of learning. Psychological Review, 77, 406-418.
38. Balda, R. P., Bunch, K. G., Kamil, A. C., Sherry, D. F., & Tomback, D. F. (1987). Cache site memory in birds. In: A. C. Kamil, J. R. Krebs, & H. R. Pulliam (Eds.), Foraging Behavior. New York: Plenum Publishing Co.
39. Sherry, D. (1982). Food storage, memory and marsh tits. Animal Behaviour, 30, 631-633. Sherry, D. (1984). Food storage by black-capped chickadees: Memory for the location and contents of caches. Animal Behaviour, 32, 451-464. Shettleworth, S., & Krebs, J. (1982). How marsh tits find their hoards: The roles of site preference and spatial memory. Journal of Experimental Psychology: Animal Behavior processes, 8, 354-375.
40. Balda, R. P. (1980). Recovery of cached seeds by a captive *Nucifraga caryocatactes*. Zeitschrift fur Tierpsychologie, 52, 331-346.
41. Vander Wall, S. B. (1982). An experimental analysis of cache recovery in Clark's Nutcracker. Animal Behaviour, 30, 84-94.
42. Cowie, R., Krebs, J., & Sherry, D. (1981). Food storing by marsh tits. Animal Behaviour, 29, 1252-1259.
43. Vander Wall, S., & Balda, R. (1981). Ecology and evolution of food-storage behavior in conifer-seed-caching corvids. Zeitschrift fur Tierpsychologie, 56, 217-242.
44. Tomback, D. (1980). How nutcrackers find their seed stores. Condor, 82, 10-19.
45. Vander Wall, S. B., & Hutchins, H. E. (1983). Dependence of Clark's nutcracker (*Nucifraga columbiana*) on conifer seeds during the postfledgling period. Canadian Field Naturalist, 97, 208-214.
46. Kamil, A., & Balda, R. (1985). Cache recovery and spatial memory in Clark's nutcrackers (*Nucifraga columbiana*). Journal of Experimental Psychology: Animal Behavior Processes, 11, 95-111.

47. Kamil, A. C., Balda, R. P., & Grim, K. (1986). Revisits to emptied cache sites by Clark's nutcrackers (*Nucifraga columbiana*). Animal Behaviour, 34, 1289-1298.
48. Balda, R. P., & Kamil, A. C. (1989). A comparative study of cache recovery by three corvid species. Animal Behaviour, in press.
49. Kamil, A. C. (1978). Systematic foraging by a nectar-feeding bird, the Amakihi (*Loxops virens*). Journal of Comparative and Physiological Psychology, 92, 388-396.
50. Bitterman, M. E. (1960). Toward a comparative psychology of learning. American Psychologist, 15, 704-712. Macphail, E. M. (1982). Brain and Intelligence in Vertebrates. Oxford:Clarendon Press.
51. Sacks, R. A., Kamil, A. C., & Mack, R. (1972). The effects of fixed-ratio sample requirements on matching-to-sample in the pigeon. Psychonomic Science, 17, 483-488. Roberts, W. A. (1972). Short-term memory in the pigeon: Effects of repetition and spacing. Journal of Experimental Psychology: Animal Behavior Processes, 6, 217-237.
52. Balda, R. P., & Kamil, A. C. (1988). The spatial memory of Clark's nutcrackers (*Nucifraga columbiana*) in an analog of the radial-arm maze. Animal Learning and Behavior, 16, 116-122.
53. Beatty, W. W., & Shavalia, D. A. (1980). Spatial memory in rats: Time course of working memory and effect of anesthetics. Behavioral and Neural Biology, 28, 454-462.
54. Spetch, M. L., & Edwards, C. A. (1986). Spatial memory in pigeons (*Columba livia*) in an "open-field" feeding environment. Journal of Comparative Psychology, 100, 279-284. Spetch, M. L., & Honig, W. K. (1988). Characteristics of pigeons' spatial working memory in an open-field task. Animal Learning and Behavior, 16, 123-131.