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The Ecology of Foraging Behavior: Implications for Animal Learning and Memory

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Introduction

In his recent *Annual Review of Psychology* article, Snowdon (1983) discussed the synthesis of ethology and comparative psychology. A similar synthesis of behavioral ecology and animal learning is beginning to take place. This article reviews developments in the behavioral ecology and ethology of foraging behavior relevant to psychological research on animal learning. The psychological literature shows that animals possess a wide range of learning abilities, including "simple" classical and operant conditioning; they acquire spatial, nonspatial, and temporal discriminations; they exhibit various forms of rule learning (e.g. matching-to-sample and learning set), and may even in certain senses learn language. Why does this widespread animal ability to modify behavior on the basis of previous experience exist? The answer to this question must include both a mechanistic (proximate) and a functional (ultimate) aspect (Tinbergen 1951; Alcock 1979). The mechanistic answer seeks to explain learning in terms of the mechanisms and processes that enable the animal to learn. The functional answer seeks to explain learning in terms of the role learning plays in conferring a selective advantage on organisms possessing those mechanisms.

Psychological investigations of animal learning have emphasized mechanistic explanations whereas ecological and ethological investigations have tended to emphasize functional explanations. Complete understanding requires both kinds of answers, however, and the synthesis of behavioral ecology and psychology suggested here provides a basis for both kinds of analysis.

Several recent articles have discussed the relationship between behavioral ecology and animal learning in general terms (Johnston 1981, Kamil & Yoerg 1982, Shettleworth 1983, 1984). Here we review those portions of the ecological and ethological literature on foraging behavior most relevant to animal learning and memory.

On Optimal Decision Theory

MacArthur & Pianka (1966) introduced the notion that animals seeking food are attempting to solve a maximization problem, obtaining the maximum amount of food per unit time. They suggested that foraging animals could be conceptualized as optimal decision makers. Because optimal decision theory is central to understanding recent developments in the study of foraging, it deserves discussion in the present context (see also Maynard Smith 1978).

Life is a compromise. It is a compromise among competing demands (e.g. whether to spend time seeking food or seeking a mate) and among potential and realizable goals. Every behavior has both costs and benefits, and the animal must always compromise between minimizing costs and maximizing benefits.

According to modern views of evolution, the successful organism is the one that maximizes its contribution to the gene pool (e.g. Wilson 1975, Dawkins 1976). Life, in this view, is also a maximization problem, as expressed in the tautology that animals have been selected so as to maximize their fitness. From these two premises, compromise and maximization, comes the essence of optimality theory. The optimal decision maker adopts the compromise that maximizes fitness given the organism's limitations.

If there were no competing demands on an organism—if it had only one life problem to solve—then its life (and ours) would be simple. For example, if an organism's single problem were to get as much food as it could, then the most successful organism would be the one that got the most food. Even if life were so simple, however, no animal could possibly obtain food at an infinite rate and thereby achieve infinite fitness. Its life would still be a compromise between its goal of an infinite food intake rate and the practical limits on food intake. We usually think of these limits as constraints. Among the constraints that prevent an animal from achieving a "perfect" solution to its optimization problem are (a) "accidents" of its ancestry, (b) limits on the speed with which it can change the form of its compromises, (c) limits on the ability to obtain information from the environment, and many others (Roitblat 1982a). Optimality theory seeks to determine not whether organisms are "nicely adapted to their environmental niche" but what competing demands and constraints they face and what means they employ to meet them.

As psychologists we tend to concentrate on one kind of constraint: that produced by limits on the organism's ability to process relevant information. Some organisms, for example deal with a range of situations by using such relatively rigid mechanisms as reflexes and fixed action patterns. Many approaches to foraging behavior, however, imply that organisms have more dynamic mechanisms for assessing and responding to changes in the environment. For example, many of the models considered below assume that organisms can measure both time and the density of prey items in a patch. Although animals in the laboratory have been found to discriminate time and number, their performance on these two dimensions is seldom perfect (e.g. Gibbon & Church 1981, 1984; Church & Meck 1984). Imperfections in either of these estimation tasks would yield less than perfectly efficient behavior.

Optimal decision models of an activity like searching for food in a patchy environment represent assumptions about the compromises being effected by the organism, about its limitations and constraints, and about the maximization problem(s) it faces. Given these important assumptions we can specify, in a formal and often mathematical way, what that organism should do in various situations. The observations we then make in those situations are tests of the assumptions in the model; they do not test the optimization principle itself (e.g. Maynard Smith 1978, Roitblat 1982a).

Behavioral ecologists have varied in the extent to which they are explicit in specifying the type and content of information they suppose a predator to possess. Some models assume the predator to be less than omniscient. These are sometimes called "rule of thumb" models. This application of the phrase seems inappropriate (Krebs et al 1983). However, if it suggests that the animal is "satisficing" (Simon 1956)—i.e. merely choosing a course of action that is "good enough." Such models are not rules of thumb in this sense. A rule of thumb, as the term is used here, is not a rule that does well enough but rather a hypothesis about the best choices the organism can make, assuming various constraints.

By a rule of thumb model, then, we mean a hypothesis that specifies precisely the variables controlling the animal's behavior, the information it has, and how that information is represented (Roitblat 1982b). For example, Hubbard & Cook (1978) found that the parasitoid *Nemeritis canescens* allocates its search time for hosts approximately as specified by an optimal decision model based on an ability to measure the rate at which it encountered hosts. Waage (1979) subsequently found that this parasitoid's "rule" for "deciding" when to stop searching in a particular patch is based on its habituation to the host's scent. Laying eggs results in dishabituation, after which searching resumes until a certain level of habituation is again reached. Thus a potentially complex ability—i.e. to keep track of one or more intercapture intervals—is instantiated by a relatively simple mechanism.

Rules of thumb differ in the extent to which they approximate "ideal" performance (Houston et al 1982; Krebs et al 1983). For example, all other things being equal, a predator with more information about the distribution of prey will do better than one without that information (Iwasa et al 1981). The ability to process additional information, however, is not itself without costs. At some point, the marginal benefits (ultimately in terms of increased fitness) of additional information processing capacity may not justify its costs (e.g. Janetos & Cole 1981; Orians 1981). This argument is also an optimality argument, not an argument against optimality.

Psychologists are particularly well suited to discovering the kinds of information used by a predator and the mechanisms it has for dealing with that information. For example, laboratory studies of sequential patterns of reinforcement indicate that animals do not simply average the outcome of a set of trials. Rather, different patterns of reinforcement and nonreinforcement, each leading to the same average rate, can result in widely different patterns of behavior, such as resistance to extinction (Capaldi 1966, 1971). Application of such laboratory findings to foraging situations will elucidate both foraging and the mechanisms of animal learning (Kamil & Yoerg 1982).

Although all organisms must ultimately maximize their fitness, measuring fitness and the effects of various individual actions on it is problematical. For this reason, students of animal behavior typically make simplifying assumptions. For

example, many of the models described below assume that animals attempt to maximize their net rate of energy intake, usually measured in calories per unit time. This is a simplifying assumption dictated by the difficulties of estimating the effect of a behavior on the organism's ultimate fitness, the complexity of solving multidimensional maximization problems (McCleery 1978), and so forth. We must recognize, however, that the animal faces a situation far more complex than our simplifications. For any real predator, energy intake always competes with many other demands. These competing demands include balancing the danger of becoming prey against the success of obtaining prey (e.g. Milinski & Heller 1978, Sih 1980, Grubb & Greenwald 1982). That the world is less simple than our models does not falsify the optimization hypothesis, but it does make the process of developing optimal decision rules more difficult. Fortunately, many systems can be studied in which our simplifying assumptions do not invalidate analysis.

Patch Selection

In nature, food is often distributed in discrete patches (e.g. different trees, branches, pieces of lawn, etc.). When food is not uniformly distributed in the environment, the predator must decide in which of these concurrently available patches to forage and how long to spend in each.

The nature of the predator's problem depends on the reliability of the distribution of prey within patches. In order to maximize food intake, the predator must identify and then choose the patch that will yield the highest rate of return. In some cases, the predator can determine the richness of a patch before it begins to forage, by means of perceptual cues or memory. Quite another problem arises when the quality of a patch can vary significantly in a stochastic manner. In that case, the predator must "invest" effort to discover the value of the available patches before it can concentrate on the richer patches.

Foraging in Reliable Patches

Predators have been found to take advantage of uneven prey distribution. For example, redshank (*Tringa totanus*) tend to concentrate their search for worms in areas containing relatively high prey densities, selecting areas that appear to maximize their rate of food intake (Goss-Custard 1981). Wagtails (*Motacilla flava* and *M. alba*) select foraging sites as a function of prey density (Davies 1977a). Blackbirds (*Turdus merula*) and song thrushes (*Turdus philomelos*) choose foraging sites on the basis of location and time of day (Greenwood & Harvey 1978). As the shadows cast by trees moved during the day, the prey density and the preferred foraging sites of the thrushes also moved. The reliability of these diurnal variations presumably allowed the birds to take advantage of their past experience and

to allocate their foraging effort in response to variations in patch quality. Similar behaviors have been observed in ovenbirds (*Seiurus aurocapillus*; Zach & Falls 1976), great tits (*Parus major*; Smith & Sweatman 1974), kangaroos (*Macropus giganteus*) and wallaroos (*Macropus robustus*; Taylor 1984), and in bees (*Apis mellifera*) selecting among flower types (Waddington & Holden 1979).

Foraging in Variable Patches

When the quality of a patch is not predictable, a predator must invest effort to discover value of the patch. There should be an optimal tradeoff between time spent assessing and time spent exploiting patches. This expectation has begun to be studied in the laboratory (Krebs et al 1978; Kacelnik 1979).

Foraging in concurrently available patches resembles the problem faced by a laboratory animal on a concurrent reinforcement schedule. These schedules have been studied extensively in the operant laboratory (de Villiers 1977, Staddon & Motheral 1978, Herrnstein & Heyman 1979, Heyman & Luce 1979, Staddon 1980). Kamil & Yoerg (1982) have questioned the generality of these studies because of peculiarities of the schedules employed. They argue for cautious interpretation of the operant studies because of peculiarities of the variable interval schedules typically selected for study.

The patch-selection problem faced by a foraging predator is also similar to that studied in probability learning (for reviews see Bitterman 1965, 1969, Mackintosh 1969).

Laboratory studies of patch selection typically use concurrent variable ratio (VR) schedules. Despite controversy over many other combinations of concurrent schedules, there is widespread agreement (Rachlin et al 1976) that the optimal response pattern on concurrent VR schedules is to respond exclusively to the alternative with the richer schedule (i.e. the lower average response requirement). Laboratory studies of patch selection differ from typical operant studies, however, in that the schedule associated with a given response varies stochastically from one session to the next. At the start of a patch-selection session, the predator typically does not know which alternative is associated with the richer VR schedule. Such studies concern the process by which information about the schedules is acquired, rather than the steady-state behavior of the organism following acquisition.

Strategies that maximize reward on these schedules have been explored by mathematicians in the form of the "two-armed bandit" problem (Bellman 1956, Lindley & Barnett 1965, De Groot 1970, Jones 1976, Wahrenberger et al 1977). Each alternative is conceived as a slot machine (or one-armed bandit) with a fixed but unknown probability of payout. By extension, a "machine" with two alternatives is called a two-armed bandit. The problem is to find a rule specifying which arm to choose in order to maximize the overall rate of return in a fixed number of trials. The fixed number of trials is called the time horizon.

Optimal terminal performance on a two-armed bandit problem allocates all responses to the alternative with the higher probability of reinforcement. To achieve this, the predator must first discover which alternative is better, sampling the two until a decision can be made. Hence, the task can be divided into a sampling phase and an exploitation phase; the problem is to determine how much time to spend sampling.

The optimal sampling time depends on the difference between the reward distributions on the two alternatives and on the total time available for foraging. The more of its limited time the animal spends sampling, the less time it will have to exploit the better patch; the less time it spends sampling, the higher the probability of exploiting the wrong patch. Even small differences in the reward probabilities can have a substantial effect as they cumulate over the exploitation period. The cumulative difference between the richer and the poorer alternative is the cost of concentrating on the poorer alternative. The optimal duration of the sampling period is a trade-off of the probability of a correct decision against the cumulative effects of that decision, and depends on the number of responses or time that can be spent—the time window. With longer available durations, the sampling period is expected to be longer (Krebs et al 1978, Kacelnik 1979).

Kacelnik (1979) tested great tits (*Parus major*) who foraged by hopping on one of two perches. Each perch was associated with a characteristic, but unknown, variable ratio reinforcement schedule. The probabilities of reinforcement assigned to the two alternatives varied randomly from session to session. Sessions were terminated when 90% of a sequence of 100 hops were to one of the alternatives or when all 72 of the available reinforcers were obtained without reaching this criterion. The last hop before the beginning of a block of 100 responses with a bias of more than 90% was taken to be the switch point separating the sampling from the exploitation period.

Kacelnik found that the birds' sampling performance fit very closely an optimizing model based on a time window of 150 responses, which was the modal number of responses emitted in a session before reaching one of the stopping criteria. The greater the difference between the probabilities of reward on the two responses, the sooner the birds switched from sampling to exploitation. Furthermore, explicit manipulation of the session duration, in a second experiment, resulted in changes in the estimated time window, and in the duration of the sampling period. Finally, Kacelnik also found that the birds' performance was poorly fit by a momentary maximizing model (Shimp 1969), which predicted choice of the alternative with the currently higher expected reward probability.

Such studies raise a number of interesting possibilities for future research. First, unlike typical operant experiments, these are concerned with the dynamic rather than steady-state properties of animals' behavior. There has been little operant research, for example, on concurrent variable ratio schedules because terminal performance on them presents a trivial problem. Studies on foraging,

in contrast, show that the means by which animals arrive at this trivial solution can itself be interesting.

Two further opportunities for research derive from an elaboration of the simplifying assumptions used in designing the experiments on patch selection. For example, all the patch-selection experiments known to us have used only two alternatives. Leaving one "patch," therefore, is equivalent to entering another. Although this simplification makes the mathematics of prediction tractable, it risks simplifying the problem out of existence. At least three alternatives are probably necessary to mimic, in any significant sense, the kind of situation faced by a predator in the field.

A second limitation in the methods used so far is the lack of a variable representing significant travel costs between patches. Although these studies generally assume that multiple patches are simultaneously available, outside the laboratory it takes time and energy to move from one patch to another. If the effort required is significant, it will have an important impact on the pattern of behavior observed.

The importance of travel time and its impact on the validity of using concurrent reinforcement schedules to mimic patch choice is most apparent when "central place" foragers are considered. These animals must travel frequently between a foraging site and a central place, such as a nest or den. A pair of brooding birds, for example, must frequently bring food gathered in a distant patch back to their nestlings. The significant time spent traveling between the central place and the foraging sites presents special problems (Orians & Pearson 1979, Andersson 1981, Bryant & Turner 1982, Evans 1982, Giraldeau & Kramer 1982, Kasuya 1982, Aronson & Givnish 1983, Kacelnik 1984).

Patch Persistence

In the previous section we assumed that multiple patches were concurrently available; the value of each patch was predictable and stable. Effort may have been required to discover the value of a patch, but during exploitation that value remained stable. None of these assumptions is universally appropriate. For many predators it is more reasonable to assume that the predator encounters patches one at a time (e.g. because of substantial costs of traveling between patches), that the value of patches is a random variable, and that the marginal or conditional within-patch capture rate declines with foraging time (e.g. because the predator consumes or frightens off the available prey). Under these conditions, the predator cannot rationally control the selection of patches, but it can control time spent in each.

In general, an efficient predator should search a patch only so long as the expected rate of return (e.g. measured in prey captured per minute) for remaining

in a patch is higher than the rate of return that can be expected after leaving the patch. The predator (and anyone trying to understand it) must devise rules for inferring future events (i. e. expected rates of prey capture) from past experience. One of the first hypotheses attempting to describe the rules used by predators in determining how much time to spend searching a patch was the marginal value theorem proposed by Charnov (1976; see also Krebs et al 1974, Charnov et al 1976 for simplified versions of the theorem).

The marginal value theorem assumes: (a) The predator spends all its time either searching for prey within a patch or traveling between patches. (b) The patches vary in their profitability. (c) The rate of food intake for the patch declines gradually as the predator depletes it of prey. (d) The number of prey present in a patch cannot be observed directly but must be "discovered" by sampling. Therefore, the expected value (number of prey) of a patch before it has been visited is simply the average value of all patches. (e) The predator has information about the overall average capture rate and the instantaneous marginal capture rate (i.e. conditional on the time already spent in the patch). The theorem predicts that the predator should leave a patch when the marginal value has declined to the average rate of intake for the habitat. Time spent within patches and time spent traveling between patches are both included in calculating the average rate of intake for the habitat.

The marginal value theorem assumes prey are captured continuously and an instantaneous rate of capture can be calculated. For most predators, however, a more reasonable assumption is that prey are captured at discrete instances and the predator can only approximate the continuous distribution. Krebs et al (1974) and others have suggested that predators can use the interval between successive captures as a measure of the capture rate. According to this "rule of thumb" (see above), the predator should leave a patch when the interval since the last prey capture exceeds a criterion period; this period should be constant and independent of the actual value of the patch (see McNair 1982).

Krebs et al (1974) investigated this optimal "giving-up-time" hypothesis with chickadees (*Parus atricapillus*) foraging in an indoor aviary. Patches were artificial "pine cones," made from small blocks of wood with holes drilled in them and pieces of meal worm concealed in these holes. The birds were initially trained with one prey per patch and then tested in a mixed environment with two kinds of patches containing either one or three prey per patch. Krebs et al (1974) compared the predictions of their giving-up-time version of the marginal value theorem with a hypothesis that predators hunt by expectation (Gibb 1958, 1960, 1962; see also Hodges 1981, Lima 1983). According to the expectation hypothesis, predators learn how many prey they can expect in a patch and stop searching when the expected number of prey have been found. Contrary to the expectation hypothesis, however, during the mixed condition the birds studied by Krebs et al (1974) did not give up immediately after finding the single prey they had

learned to expect. Rather, they searched longer when a patch contained three, as opposed to one prey. Their giving-up time depended on the average number of prey per patch (i.e. it was longer in the mixed than in the single-prey condition) but not on the number of prey in any particular patch. The same giving-up time was observed in both one-prey and three-prey patches. These results are all consistent with the predictions of the marginal value theorem and with the optimal giving-up-time rule of thumb.

Cowie (1977) investigated these hypotheses further in a test designed to simulate the effects of travel time (the amount of time necessary to leave one patch and begin foraging in another). Longer travel time between patches reduces the average profitability of an environment without affecting the rate of capture within a patch. The greater the travel time, therefore, the longer the predator should spend in a patch. Cowie tested great tits in an indoor aviary. Patches consisted of cups filled with sawdust in which pieces of mealworm were hidden. Long travel times were simulated by covering all cups in the environment with tight-fitting lids. Short travel times were simulated by covering all cups in the environment with loose-fitting lids. The birds spent more time searching in a patch when all patches were covered by tight lids than when they were covered by loose lids. Thus when the energetic costs of searching and traveling between patches were considered, the data fit closely the quantitative predictions of the marginal value theorem.

Other experiments, using methods similar to that used by Krebs et al (1974), have yielded results inconsistent with the optimal giving-up-time version of the marginal value theorem. Zach & Falls (1976) tested ovenbirds (*Seiurus aurocapillus*) in an artificial environment consisting of six "golf-course" patches made of plywood, each containing 99 holes in which freeze-killed flies were hidden as prey. Zach & Falls found no evidence that the birds used either a number-of-prey or a searching-time expectation to control the time they spent in searching a patch. The birds spent more time searching patches when the environment as a whole contained more prey, but, contrary to the optimal giving-up-time hypothesis, their giving-up time did not depend on the overall prey density.

Hypotheses that do not rely on the assumptions of the marginal value theorem have also been used to predict how long an efficient predator should continue searching a patch. In a field experiment analogous to that of Krebs et al (1974), Lima (1984) studied free-ranging downy woodpeckers (*Picoides pubescens*) foraging for sunflower seeds in artificial patches. Each patch was made by drilling 24 holes in a piece of log. During pretraining, a single seed was placed in each hole, then covered with masking tape, and the birds learned to retrieve the seeds. The birds were then tested with patches containing either 0 prey or a fixed number of prey. The bird could not predict which of the patches contained prey without pecking through the masking tape covering

some of the holes. Hence, this experiment provided the birds with a stochastic environment in which the number of prey in a patch was a random variable (with a value of 0 or n).

By simulation, Lima predicted the number of holes a bird should peck open to optimize its discrimination between empty and nonempty patches. This number varied with the number of prey hidden in the nonempty patches. He found that the birds quit an empty patch after searching approximately the predicted number of holes but continued to search a nonempty patch until all of the holes had been opened. Thus their performance on empty patches was approximately as predicted, but their performance on nonempty patches was not. This result may indicate that the birds could not change their searching strategy from the one appropriate during pretraining, when all patches were full. Alternatively, these data could mean that the birds "knew" the average prey density in the environment as a whole but could not keep track of the individual counts within a certain patch. A number of mechanisms that do not rely on counting prey might provide an estimate of the overall value of an environment (e.g. stomach load, energetic gain, etc.).

Knowing the average density, but not the number of prey already found within the patch, would allow an optimal giving-up strategy on empty patches but would not be sufficient to yield an optimal giving-up strategy on nonempty patches. The difference between the predicted optimal strategy and the observed strategy could be attributable to an information constraint (see also Lima 1983). When information about the exact number of prey already found in a patch is not available, then the optimal strategy (in Lima's experiment as in that of Krebs et al 1974 and that of Zach & Falls 1976) is to search every available site exactly once. Without information that the last prey has been discovered, the predator's best guess is that the probability of a prey in the next hole remains constant.

Iwasa et al (1981) showed that the stopping rule to maximize the number of prey captured per unit foraging time depends on the distribution of prey in the patches. An optimal giving-up-time rule of the sort investigated by Krebs et al (1974) is best when the variance of the prey distribution is high, but worst when the variance is low. Iwasa et al showed that if the prey are binomially distributed, then the optimal stopping rule says to quit after discovering a fixed number of prey. If the prey are Poisson distributed, then the optimal stopping rule is to quit a patch after a fixed time spent. Because different rules are appropriate with different prey distributions, we should expect predators to show stopping rules characteristic of the distribution patterns of their typical prey.

The general model underlying the predictions by Iwasa et al (1981) is related to the stochastic giving-up-time model proposed by Oaten (1977) and McNamara (1982). The stochastic giving-up-time model assumes that the predator knows (a) the distribution of the number of prey per patch (i.e. what proportion

of patches have 0 prey, 1 prey, 2 prey, etc.) and (b) the distribution of the intercapture interval, conditional on the number of prey already captured in the patch and on the distribution of the number of prey in the patch. The predator uses this information and the remembered intercapture intervals for the current patch to estimate the expected period until capture of the next prey. Analogous to the marginal value theorem, the stochastic giving-up-time model assumes that the predator will leave the patch when it fails to capture a prey within the expected period. Unlike the marginal value theorem, the stochastic model does not assume any particular relationship between successive intercapture intervals and does not necessarily set the criterial intercapture interval to a constant value such as the environmental average intercapture interval.

Although these stochastic models have not been investigated rigorously, they appear to be more general and potentially more powerful than the marginal value theorem proposed by Charnov (1976). In order to obtain this increased power, however, we must assume that the predator possesses vast amounts of data about both the distribution of patches and its own history on the current patch (e.g. the distribution of numbers of prey per patch, the pattern of intercapture intervals, etc.). Animals can sometimes possess surprising amounts and types of information (e.g. Kamil 1978, Olton 1978, Roitblat 1982b, Shettleworth & Krebs 1982, Balda & Turek 1984, Kamil & Balda 1985, Roberts 1984), so it is not reasonable to dismiss, out of hand, models that assume large stores of data. On the other hand, models that assume less sophisticated cognitive capacities may be more appropriate.

Diet Selection

Theoretical Models

One of the earliest optimal foraging models (MacArthur & Pianka 1966; see also Emlen 1966) analyzed the problem faced by a forager encountering different food types (e.g. different species of insects or seeds), each of which is characterized by a particular handling time (time to approach, capture, and consume) and energetic value. MacArthur & Pianka (1966) found a relatively simple way to calculate which prey types should and should not be included in the diet, provided the forager knows a lot about the prey types and is attempting to maximize its net rate of energy gain.

The MacArthur & Pianka (1966) model is most appropriate for a forager that encounters prey sequentially and must decide, in each case, whether or not to capture and consume it. The model partitions foraging time into search time and handling time. Search time is spent looking for prey, while handling time is spent pursuing, capturing, and consuming it. If the prey types available are ranked from best to worst in terms of energetic value per unit of handling time (E/H), the solution that maximizes net energy intake is easily seen. For a

forager that presently includes only the highest ranking item in its diet, adding the item ranked second highest will have two effects. Search time between items will decrease, since more items are now included in the diet; but handling time per unit of intake will increase, because the second item provides less energetic value per unit handling time than the first. The diet that maximizes rate of intake will add lower-ranked items only when the decrease in search time compensates for the increase in average handling time. This point is reached when the next prey in the ranking has an E/H value less than the rate of intake being achieved without that prey in the diet (this overall rate includes search time in the denominator).

Three of the major predictions of this model are: (a) Under a given set of conditions, a prey type should either always be included in the diet or always excluded. There should be "no partial preferences" in which a prey type is sometimes included and sometimes excluded. (b) The inclusion of any prey type should depend only upon the density of higher-ranked prey types, not on the density of either the prey type in question or any lower-ranking types. (c) By implication, the predator must be able to rank the prey items it encounters in E/H order.

Hughes (1979) developed a model that incorporates recognition time and learning effects. Hughes added a recognition time component to the denominator of E/H and considered how experience might affect the time required to recognize and/or capture a prey type. Ollason (1980) and McNair (1981) have also considered possible learning effects. The McNair paper is particularly interesting because it considers the effects of learning on diet selection in a stochastic environment. Another approach to the diet selection problem has been advanced and tested by Belovsky (1978, 1981, 1984a,b), based on linear programming techniques (see below).

These models have been tested often in both laboratory and field, and the resulting literature is much larger than we can review here, given space limitations (see Pyke et al 1977, Krebs et al 1983 for reviews). Therefore we emphasize some of the papers of most interest to psychologists.

Field Studies

Many studies have tested the predictions of diet selection models in the field (e.g. Davies 1977b, Goss-Custard 1977a,b, Waddington & Holden 1979, Pulliam 1980, Pleasants 1981, Tinbergen 1981; see Krebs et al 1983 for review, especially Table 6.1). In general, these studies have found either qualitative or quantitative support for predictions of the MacArthur & Pianka (1966) approach (but see Goss-Custard 1977b, Schluter 1981, 1982, Zach & Smith 1981). For those first reading this literature, Goss-Custard (1981) and Werner & Mittelbach (1981) provide well-written overviews of extensive research projects on diet selection.

Goss-Custard (1981) studied the behavior of redshanks (*Tringa totanus*) foraging on mud flats for polychaete worms and amphipod crustaceans buried in the mud. Goss-Custard first studied the selection of different size classes of polychaetes by the redshanks. Several of the basic predictions of the MacArthur & Pianka model received support. The proportion of larger worms taken was affected only by their own density, and not by the density of smaller (lower E/H value) worms; but, as predicted, smaller worms were preyed upon by the redshanks only when larger worms were relatively rare. Prey selections were affected by neither day length nor the amount of foraging already accomplished. This is consistent with the model since the birds should always be taking the diet that maximizes rate of intake.

Goss-Custard (1981) also found two major deviations from predictions of the model. The redshanks sometimes showed partial preferences for small or medium-sized worms. In addition, when amphipods were present in the same area as polychaete worms, the redshanks often took the amphipods at a high rate, although the amphipods had relatively low E/H values. This may be because the amphipods provide a needed nutritional component (see Goss-Custard 1977b, Rapport 1981).

Werner and his associates (Werner & Hall 1974, 1976, 1979; Mittelbach 1981, 1983; Werner et al 1981, 1983a,b) have studied the foraging behavior of bluegill sunfish (*Lepomis macrochirus*) feeding on various food, especially *Daphnia*, in natural lakes and artificial ponds. These investigators have sought to understand natural patterns of foraging behavior in bluegills and their implications for species interactions and community structure. In general terms, they have found that a modified form of the MacArthur & Pianka (1966) model accurately predicts the different diet compositions and habitat usages of different size classes of bluegills. The diets of these different classes are different because each size class differs in the size prey it can efficiently handle. These differences, in turn, predict which part of the pond or lake the fish will be found in.

Field tests of optimal diet models suggest that learning plays a central role in efficient diet selection. The factors that affect diet selection, particularly relative prey density, can change rapidly under natural conditions, and predators often deal flexibly with these changes, tracking environmental change closely. "Sampling" behavior, spending time in relatively unprofitable areas (see above, Goss-Custard 1981, Werner & Mittelbach 1981), or occasionally taking a relatively unprofitable prey type, is probably essential to this learning. As Werner & Mittelbach state, "Our studies with fish also call attention to several areas critical to the further development of foraging theory. Specifically the role learning and sampling play in the foraging behavior of animals is crucial" (p. 826; see also Dill 1983 for broader discussion of learning and foraging in fishes).

Belovsky (1978, 1984a, b) has provided substantial data testing a linear programming approach to diet selection that appears to better account for characteristics of the foraging behavior of herbivores than several alternative models (Belovsky 1984a). The linear programming approach allows the inclusion into the model of several factors of particular importance for herbivores, such as constraints upon daily digestive capacity and nutrient requirements. While some have treated such factors as inherently incompatible with optimal foraging approaches (Rappaport 1981), Belovsky's work shows that they can be incorporated into a single maximization model. The model appears to account for the diet selection of moose (Belovsky 1978, 1981), beaver (Belovsky 1984b), kudu, and microtine rodents (Belovsky 1984a). The evidence for the importance of nutritional constraints suggests that important connections to the psychological literature on "nutritional wisdom" could be made (e.g. Rozin & Kalat 1971).

Laboratory Studies

Tests of the predictions of diet selection models under laboratory conditions (e.g. Krebs et al 1977, Elner & Hughes 1978, Erichsen et al 1980, Houston et al 1980, Jaeger & Barnard 1981, Kaufman & Collier 1981, Moermond & Denslow 1983) generally support such models, at least qualitatively (but see Hughes & Elner 1979, Rappaport 1980, Barnard & Brown 1981).

Only Moermond & Denslow (1983) have rigorously tested the assumption that foragers rank their food types in a monotonic fashion. These researchers offered individual fruit-eating, wild-caught birds choices between pairs of different fruits in an aviary. The birds were sensitive to fruit differences, showing preferences on 67-100% of the trials. In addition, the choices of the birds were transitive; if the birds preferred fruit A to fruit B, and preferred fruit B to fruit C, then they always preferred fruit A to fruit C. These data strongly support the hypothesis of an underlying monotonic ranking. Moermond & Denslow (1983) also obtained data suggesting that the concept of handling time is too simple. Relatively small changes in the accessibility of fruit above or below the branches on which the birds stood sometimes had large effects on choice, even though the effects on handling time were small. Thus time may sometimes be an inappropriate measure of the costs of handling food items. In this case, the risk of falling or the physical difficulty of movement may play a large role in determining the denominator of the E/H ratio.

Krebs et al (1977) tested the diet selection model with great tits (*Parus major*) in an interesting and clever experimental apparatus. The bird sat on a perch while prey went by on a conveyer belt. The prey were large and small pieces of mealworm. As predicted, when the encounter rate with prey was low the birds were nonselective, taking both sizes, but they specialized on the large prey when

the encounter rate was high. However, the birds did not switch from mixed to a pure diet in a single step. Krebs et al suggest that this may represent sampling by the birds.

In another experiment utilizing the same apparatus, Erichsen et al (1980) tested the model of Hughes (1979). They placed large and small pieces of mealworm inside opaque and clear pieces of plastic straw, respectively, which were then placed on the conveyor belt along with opaque straws containing only string. The larger prey thus resembled "twigs." In this same twig-like guise the birds might also find pieces of straw containing only string. The birds could only discriminate between the string-filled "twigs" and the large prey by picking up the straw and inspecting it. As predicted by the model, the birds switched their preference from the larger to the smaller prey as the proportion of mealworm pieces present in the opaque straws on the conveyor belt decreased.

Lea (1979) used more traditional operant procedures to test the diet selection model with pigeons. Each trial consisted of a series of events designed to mimic search time and handling time. After completing a preliminary fixed interval (FI) search requirement, the birds were presented with one of two stimuli (the prey types), each associated with a particular FI requirement (short or long) that produced access to food at the end. The pigeon could choose either to include the prey by pecking at the colored key or to exclude it by pecking at another key. This procedure gave Lea control over several parameters relevant to diet selection models: E/H values could be manipulated by varying either the FI requirements or the food access; relative density could be manipulated by controlling the probability of the long and short FI schedules. The results were qualitatively in agreement with diet selection model predictions, but there were significant departures from the MacArthur & Pianka (1966) predictions. As usual, partial preferences were observed, and the birds showed a marked bias against accepting the long PI (low E/H) alternative. The density of the worse prey type affected the choices of the birds.

Abarca & Fantino (1982) used similar techniques but employed a variable interval (VI) schedule for search rather than an FI. Their results were qualitatively similar to those predicted both by diet selection theory and by the delay-reduction hypothesis (Fantino 1981). Using operant procedures to investigate the diet selection model in pigeons, Snyderman (1983a) found that extended exposure to a stable set of conditions produced all-or-none prey selection, and that increasing deprivation decreased the selectivity of the pigeons (1983b).

As these studies make clear, the predictions of diet selection theory can be translated into psychological experiments. The critical parameters of the models, such as prey value, handling time, and search time, can easily be mimicked and manipulated with suitable adaptations of operant techniques. It is interesting to note that diet selection models make predictions about successive choice situations in which the predator must decide either to attack or pass up a prey.

This contrasts with patch selection and patch persistence models, which apply to simultaneous choice situations in which the predator must choose between or among patches available at the same time.

Risk-Prone and Risk-Averse Behavior

As discussed earlier, the problem of stochasticity has become a focus for recent theory and research in behavioral ecology. The study of risk-averse and risk-prone behavior has shown that the choices of a forager can be affected by the variability of reward.

Caraco (1980) explored this problem theoretically, using the concepts of utility theory (e.g. Keeney & Raiffa 1976). Caraco analyzed the problem of a forager with a fixed amount of foraging time—e.g. a small bird during winter, with foraging limited to daylight hours. How should the forager allocate its time among the available patch or prey types? Caraco's model predicts that preference for the more variable patch (risk-prone) or for the less variable patch (risk-averse) should depend upon resource availability. If resources are readily available, so that the forager can reasonably expect to obtain enough food to meet its needs, Caraco predicts risk-aversion. But if resource availability is low, so that the forager cannot expect to meet its needs, Caraco predicts risk-prone behavior.

One useful if simplified way to conceptualize this model is by thinking in terms not of maximizing energy intake but of minimizing risk of starvation. When things are good, and the average benefit realized from the available patches is sufficient to meet energetic/dietary needs, choosing the more variable patch will increase the risk of starving, through a run of bad luck. If things are bad, and the patch average is insufficient, the gamble of choosing the more variable patch type becomes worthwhile. With a run of good luck, starvation may be avoided.

Other papers have addressed this problem theoretically. Real (1980a,b) has dealt with uncertainty in more general terms. For example, he has explored the idea of variance discounting, in which the mean value of a behavioral option is discounted in proportion to its variance. He finds that under uncertain conditions, organisms should engage in more diverse behaviors, whereas under conditions of certainty, a single behavior should dominate. Stephens's (1981) analytical model, which minimizes starvation risk, agrees with Caraco's (1980) in many respects, including the prediction that the occurrence of risk-prone and risk-averse behavior should depend on mean food availability. One interesting additional implication of this model is that the risk-taking decision may be affected by the number of decisions left to make—by, for example, the time of day with a diurnal feeder. Stephens (1981) suggests that risk-prone behavior may be less likely when few decisions remain. Houston & McNamara's (1982) sequential

version of Stephens's (1981) model suggests that a forager may switch back and forth frequently between risk-prone and risk-averse behavior during foraging, depending upon current energy reserves.

Three papers have reported experiments testing the effects of variability in nectar supply on the foraging behavior of insect pollinators. Waddington et al (1981) gave bumblebees (*Bombus edwardsii*) a choice between two flower types, one offering constant reward, the other variable reward. The mean nectar contents of the two flower types were equal. In each of three experiments the bumblebees preferred the more constant flower. Because this risk-aversion developed as the bees gained experience with the flower types, learning appeared to be involved.

In a similar experiment, Real (1981) found that bumblebees (*Bombus sandsoni*) and paper wasps (*Vespula vulgaris*) also preferred constant flowers. In this experiment, flower type was signaled by color. In the initial phase of the experiment, blue flowers were variable while yellow flowers were constant, and the foragers preferred yellow. When these values were reversed, the preference reversed. This again implies learning.

The effects on choice of variance in amount of reward have been studied extensively in small, granivorous birds (see Caraco & Lima 1985 for the most recent review). In most of these experiments, the same basic discrete-choice procedures have been used. Each bird receives a series of tests under different experimental conditions. Each test consists of a preliminary set of forced-choice trials, during which each alternative is presented equally often. These are followed by a preference test, consisting of free-choice trials. On each free-choice trial the bird can choose one feeder.

Caraco et al (1980) tested yellow-eyed juncos (*Junco phaeonotus*) in two experiments. In each experiment, the birds were given a series of tests with constant rewards vs variable rewards with the same mean value. For example, in one test, the juncos received a constant 2 seeds per trial at one feeder, a variable 0 or 4 seeds at the other feeder (with a mean of two seeds). During the first experiment, the birds were food deprived for 1 hr before each session, and there was a delay of 30 sec per seed eaten between trials. These conditions were chosen because they should have maintained the birds in a positive energy budget (intake exceeding expenditures). The juncos showed consistent, significant preferences for the constant feeder—risk-aversion. In the second experiment, the birds were deprived for 4 hr before each session. The intertrial interval was 1 min per seed eaten. These conditions maintained the birds in a negative energy budget (rate of intake below energy expenditures). The birds now showed consistent, significant risk-prone behavior, reliably choosing the more variable feeder. The results support models predicting switches between risk-prone and risk-averse behavior as a function of energy budget (e.g. Caraco 1980, Stephens 1981).

Caraco (1981) obtained similar results with dark-eyed juncos (*J. hyemalis*). These birds also were risk-averse when maintained under a positive energy budget, and risk-prone under a negative energy budget. When tested under a balanced energy budget, the birds showed mixed results, with more indifference than observed in other experiments. The details of the choices of individual birds in this condition suggested that certain mean-variance combinations might be particularly attractive to the birds.

Caraco (1982, 1983) has also worked with white-crowned sparrows (*Zonotrichia leucophrys*), a bird half again as large as a junco. In the first of these papers, Caraco (1982) reported the results of two experiments. In the first experiment, the sparrows, like the juncos, showed risk-aversion under a positive energy budget. In the second experiment, a new procedure was used. All feeders were present simultaneously, and the bird could visit them in any order. The different feeder types were signaled by colored pieces of paper. Under these conditions, one might expect risk aversion to be reduced, since a visit to a low-quality feeder would be less costly—i.e. another feeder can be visited immediately. However, the results again showed risk aversion under positive energy budgets. Caraco (1983) found risk aversion under positive energy budgets, and risk proneness under negative budgets, even when both feeders were variable, but with different variances.

Recently, Caraco & Chasin (1984) extended the general finding that birds are sensitive to the distribution of rewards about the mean. Using the choice procedures developed in Caraco's studies of risk, Caraco & Chasin showed that white-crowned sparrows were sensitive to the skew of the distribution of rewards, with the mean and variance held constant. For example, the sparrows were given a choice between two feeders: Feeder 1 delivered either no seeds with probability 0.25 or delivered 2 seeds with probability 0.75. Feeder 2 delivered either 1 seed with probability 0.75 or 3 seeds with probability 0.25. Each feeder thus had a mean number of seeds per choice of 1.5 and a variance of 0.87, but feeder 2 was positively skewed. The birds showed significant preference for the positively skewed feeders when maintained under a positive energy budget.

What general conclusions of interest to psychologists can be drawn from this work? First of all, many questions about risk-prone and risk-averse behavior in the ecological context remain unanswered. The only experimental demonstrations of risk-prone behavior have been with relatively small seed-eating birds. Several studies with insect and nectar feeders have found only risk aversion (although energy budget was not manipulated directly). It remains to be established whether the phenomenon of switching between risk preference and risk avoidance as a function of energy balance is general among animals. However, the existence of sensitivity to reward variance and skew raises interesting psychological questions. Clearly animals can be quite sensitive to the characteristics

of the distribution of reward about the mean. Psychological experiments with rats have reported risk-prone behavior when number of food pellets was varied (Leventhal et al 1959), but these studies used relatively severe deprivation conditions, and one wonders whether risk aversion would otherwise have been shown. The strength of the risk preference decreased as mean number of food pellets per choice increased (Leventhal et al 1959).

A number of authors (e.g. Krebs et al 1983; Caraco & Lima 1985) have pointed out a potential relationship between the results of (a) experiments on risk and (b) operant experiments investigating preference for variable vs constant ratio or interval schedules (e. g. Herrnstein 1964; Pantino 1967; Davison 1969). This relationship is tenuous because there are so many procedural differences between the two sets of experiments. The biggest difference is that the risk experiments have manipulated the distribution of amount of reward. (It should be noted that in most of Caraco's experiments variable reward was associated with variable intertrial intervals whose duration was defined in time per seed obtained.) Different relationships might hold for other aspects of food delivery. However, because prey types are apparently often ranked on the basis of the ratio of food value to handling time, and interval or ratio schedules may be reasonable simulations of handling time, the effects on preference of the distribution of intervals or ratios within schedules of reinforcement certainly deserve more intensive investigation.

Cache Recovery and Memory in Birds

Field workers have long known that members of two families of birds, the Paridae and the Corvidae, frequently cache food which is later recovered and eaten (e.g. Lohrl 1950, Swanberg 1951, Turcek & Kelso 1968). Most of the experimental research on cache recovery and memory in birds has concentrated upon the *Parus* and *Nucifraga* genera (but see Bossema 1979 for work with the European jay, *Garrulus glandarius*). Since the two genera show somewhat different natural patterns of cache recovery, we review the work with each separately, then conclude with a section on comparative implications.

Parids

The basic pattern of food caching shown by parids is probably best described as scatter-hoarding, dispersing food items over a wide area and making no attempt to defend them (Sherry et al 1982). Most of the cached food is usually recovered and eaten within 24 hr (Cowie et al 1981). Some field data have suggested that parids may find their caches using memory (Lohrl 1950; but because many cache sites are usually involved, others have doubted that memory guides these birds back to the scattered food (Gibb 1960, Haftorn 1974).

This disagreement cannot be resolved through field data alone. One cannot assign a central role to memory until reliance on other possible mechanisms has been eliminated. For example, direct cues emanating from the seeds, site preferences, or systematic patterns of movement could all account for most field observations. The best field data indicating the potential role of memory in cache recovery by parids comes from a clever experiment by Cowie et al (1981). Radioactively labelled sunflower seeds were dispensed to marsh tits (*Parus palustris*) from feeders placed in Wytham wood outside Oxford. Many of these seeds were cached by the marsh tits, and subsequently located by the experimenters using oscillation counters. Control seeds were then placed near (within 10 cm) or far (100 cm) from each located cached seed. Both types of control seeds remained undiscovered longer than the seeds cached by the birds, but this difference was significant only for the far control seeds. Although not conclusive, this evidence is consistent with the hypothesis that memory plays an important role in the cache recovery of marsh tits. Since birds discovered the seeds placed close to the original cached seeds less frequently than they did the original seeds, this argues against use of direct cues. Furthermore, several aspects of the data argue against specific site preferences. For example, although the marsh tits showed preferences for particular types of locations (e.g. moss or tree bark), these preferences often changed from day to day. Nonetheless, only by means of the control offered by laboratory studies can we determine whether or not parids remember cache site locations.

LABORATORY STUDIES. The role of memory in the cache recovery of parids has been clearly established by several laboratory experiments with marsh tits (*P. palustris*) and chickadees (*P. atricapillus*) (Sherry et al 1981, Sherry 1982, 1984a, Shettleworth & Krebs 1982). Individually and collectively, these experiments leave little doubt that memory is a primary mechanism of cache recovery in this genus.

In an aviary experiment, Sherry et al (1981) presented marsh tits with moss trays in which sunflower seeds could be cached. Following the caching session, all seeds were removed by the experimenters, and recovery sessions were conducted 3 and 24 hr after the caches had been created. The marsh tits made more visits to, and spent more time at, the quadrants of the moss trays in which they had cached seeds.

In a second experiment, Sherry et al (1981) tested the effect of interocular transfer on cache recovery. Because in the visual system of birds the two optic nerves show complete decussation at the optic chiasma, memory cues stored using one eye would only be useful if the stimuli to be remembered were again seen by that eye. In this experiment with marsh tits one eye was covered during caching and one eye covered during recovery. In the control condition the same eye was covered during both caching and recovery; in the transfer condition,

different eyes were covered. The marsh tits performed accurately (found their caches) during control tests but randomly when interocular transfer was required. They therefore seemed to be relying on information stored in the brain.

Sherry (1982) extended these results, employing a similar technique using moss trays. In this experiment, he tested marsh tits with two recovery sessions after a single caching session. While cached seeds were present during the first recovery session, all seeds were removed for the second. He found that during the second recovery session, the birds avoided the sites they had emptied during the first.

Memory is clearly important in the cache recovery of marsh tits. Several experiments found accurate performance in the absence of any possible direct cues from the seeds. The lack of interocular transfer suggests that information is stored in the brain. The avoidance of already emptied cache sites during a second recovery session eliminates simple rules of movement, and implies a dynamic memory system.

Shettleworth & Krebs (1982) have further documented the role of memory in cache recovery in marsh tits using a more sophisticated experimental technique. They presented marsh tits with a large set of cloth-covered holes in artificial trees. They replicated many of the findings reviewed above. In addition, they found that the number of errors per seed increased with successive seeds found, that the birds avoid holes in which they have already cached seeds when caching more seeds, and that there was a slight recency effect when recovering seeds cached at two separate times. All of these results are consistent with the use of memory.

Sherry (1984a) has extended research on cache recovery to another parid species, the black-capped chickadee (*P. atricapillus*), employing a technique similar to that used by Shettleworth & Krebs (1982). In addition to replicating many of the results previously obtained with marsh tits, Sherry (1984a) reported two new findings. When given a second recovery session, not only did the chickadees avoid sites they had emptied during the first recovery session, but they also avoided sites they had found to be empty (seeds removed by the experimenter) during the first recovery session. In an experiment in which the chickadees stored two different types of seeds, they tended to visit those containing the preferred seeds during recovery, suggesting memory for the contents of food caches.

Nutcrackers

In contrast to the parids, which appear to recover most of their cached food within 24 hr (Cowie et al 1981), the nutcrackers (the Eurasian nutcracker, *Nucifraga caryocatactes*, and Clark's nutcracker, *N. columbiana*) usually leave food caches in place for months before recovering them. These birds harvest pine seeds and store them in caches in the ground during the late summer and fall

(Tomback 1977, Vander Wall & Balda 1977). These cached seeds then provide most or all of the diet during the following winter and breeding season (Giuntoli & Mewaldt 1978) and are fed to nestlings and fledglings during the following spring and summer (Mewaldt 1956). An individual Clark's nutcracker stores from 22,000 to 33,000 pine seeds a year (Vander Wall & Balda 1977, Tomback 1983), while estimates for Eurasian nutcrackers are as high as 86,000 to 100,000 (Mezhenny 1964, Mattes 1978). The nutcrackers possess a number of morphological and behavioral specializations for the harvesting and storage of pine seeds, including a stout, strong bill and a sublingual pouch used in seed transport (Bock et al 1973, Vander Wall & Balda 1977, 1981, Conrads & Balda 1979).

As in the case of the parids, field observations suggest that memory may be involved in the cache recovery of nutcrackers. For example, since nutcrackers usually husk recovered pine seeds by the cache site, Tomback (1980) was able to estimate what percentage of probes in the ground result in recovery of seeds. Her estimate, 72%, must be regarded as a lower bound since rodents may steal some caches and nutcrackers may sometimes carry unhusked seeds away from cache sites (see also Swanberg 1951, Mezhenny 1964, Mattes 1978).

LABORATORY STUDIES. Four experiments have examined the cache recovery performance of nutcrackers in laboratory settings (Balda 1980, Vander Wall 1982, Balda & Turek 1984, Kamil & Balda 1985). Balda (1980) worked with a single Eurasian nutcracker in an aviary with a dirt floor. Using retention intervals of 7-31 days, he found that cache recovery was highly accurate, even when cached seeds had been removed by the experimenter to eliminate any cues emanating from the seeds themselves.

Vander Wall (1982) allowed two Clark's nutcrackers to cache in a single dirt-floored aviary. During recovery, each bird accurately recovered its own caches but virtually never found caches created by the other. Two additional nutcrackers, which did not cache themselves but were allowed to watch the other birds cache seeds, found caches at levels above chance but well below the levels of the cachers themselves. Vander Wall (1982) also found that when he moved landmarks within the room (logs and rocks), the cache recovery of the nutcrackers was disrupted. In a similar vein, Balda & Turek (1984) found that cache recovery accuracy declined when local landmarks were removed. These results strongly support the memory hypothesis and implicate visual cues as the stimuli controlling recovery performance.

Kamil & Balda (1985) studied four Clark's nutcrackers in a room with 180 sand-filled holes, each of which could be made inaccessible with a wooden plug. Using retention intervals of 10-15 days, they found that the nutcrackers recovered their caches accurately even when the experimenters forced the birds to cache in randomly selected holes. These results show accurate recovery even when site preferences have been eliminated.

Comparative Implications

The data reported to date suggest two important differences between parids and nutcrackers in their use of memory to recover caches. The first is the duration of the memory. The nutcracker experiments have used retention intervals of up to 31 days with good results, and Balda & Kamil have a study in progress using much longer retention intervals and have observed accurate cache recovery after 91 days. The parid experiments have used retention intervals of 3-24 hr. While the parids have not been tested with longer delays, the field data (Cowie et al 1981) strongly suggest that they would not perform well if the interval between caching and recovery were several days or weeks. The second difference concerns revisits to cache sites previously emptied by the birds. Parids avoid such revisits (Sherry 1982, 1984a) while nutcrackers do not (Balda 1980, Kamil & Balda 1985). While both of these differences require further study, they raise substantial comparative questions, especially since the differences appear to correlate with differences in caching behavior shown in the field (Kamil & Balda 1985). These comparative implications, and the relationship between cache recovery and more traditional psychological tests of animal memory, are discussed in more detail by Sherry (1984b). Further research with other caching species, as well as research with caching species in more traditional tests of animal memory, is needed.

Concluding Remarks

The ecological and ethological literatures on foraging behavior contain ideas and data that raise significant issues for the study of animal learning and memory. This functionally oriented literature will not be integrated easily with the mechanistically oriented psychological literature on animal learning and memory. It is always difficult to combine different levels of explanation (Lehrman 1974, Shettleworth 1983, 1984).

Perhaps recent research on kin recognition provides an example of how such integration could occur. Functional considerations led Hamilton (1964) to argue that animals could gain significant adaptive advantage if they could recognize their relatives. That mechanisms for kin recognition exist was later confirmed (Lewin 1984). The foraging literature suggests many learning and memory mechanisms, such as risk sensitivity when rewards vary, and sampling of the environment in the face of uncertainty. Psychologists possess experimental skills and specific techniques well-suited to the investigation of the phenomena implicit in the foraging literature. But in doing such research, psychologists must be aware of the biological, adaptive implications of the research. Such ecologically oriented research will likely alter significantly our ideas about the capabilities of animals.

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