

MEETING THE ASSUMPTIONS OF FORAGING MODELS: AN EXAMPLE USING TESTS OF AVIAN PATCH CHOICE

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Abstract. Birds have been widely used to test predictions of foraging theory. The accuracy of such tests depends on whether birds feed in a manner consistent with the assumptions of the foraging model being tested. If the feeding strategy of a species does not conform to the model's assumptions, the conclusions reached from the test are weakened. I discuss whether birds in general conform to the assumptions of various models of patch choice. These models examine an organism's decision to leave a patch in which it is foraging. Many birds appear to forage in ways consistent with three of five assumptions of the marginal value theorem (MVT). The MVT assumptions most often violated by birds are those of random search and the decline of foraging success with time in patch. Several alternatives to the MVT assume that decisions to leave patches are based on simple measures of the forager's expectation of success in a patch. These "expectation models" contain less explicit assumptions than the MVT, and most assumptions are consistent with the foraging of birds; however, some assumptions are not. For example, an expectation model based on the number of prey in each patch (the "fixed-number hypothesis") assumes that all patches have the same number of prey, which is rarely true. Virtually all assumptions examined have been violated in at least some of the studies discussed; to avoid this in future studies, tests of predictions generated from patch-choice models must be designed with care.

Key Words: Assumptions; foraging models; hunting by expectation; marginal value theorem; patch choice.

Theoretical models have been widely used in conjunction with studies of the foraging behavior of birds (Krebs et al. 1983; Stephens and Krebs 1986; Stephens, this volume). Models are used to generate predictions of how organisms will respond to a given situation. The strongest test occurs when alternative models give contrasting predictions. The behavior of test organisms can then be examined to determine which model most closely predicts the observed behavior. The strength of any conclusions depends on whether the assumptions of each model are met by the test situation. If the test violates important assumptions of one of the alternative models, then the ability of the test to discriminate between models is severely weakened (Stephens, this volume).

In this paper I illustrate this concern by examining whether birds meet the assumptions of one class of foraging models, those dealing with patch choice. I demonstrate that the most prominent patch-choice model, the marginal value theorem, contains restrictive assumptions that many bird species may not meet. Several alternative models seem more appropriate because their assumptions are more consistent with avian foraging behavior.

PATCH CHOICE

A forager faces a hierarchical series of decisions (Gray 1987). It must first select a habitat for foraging, and then select among the patches within that habitat. The organism must then decide which prey items to eat in each patch and,

finally, when to move to another patch. This last decision is referred to as patch choice, and models have been developed to predict the rules that foragers should use to leave patches. Because birds are easily observed, and readily maintained in captivity, they are often used to test the predictions of patch-choice models (Krebs et al. 1974; Cowie 1977; Pyke 1978a; Lima 1983, 1984; Ydenberg 1984; Ydenberg and Houston 1986).

What is a patch? A general definition that is applicable to all studies is difficult to describe because patches occur at several different scales. For instance, studies of bumblebees (*Bombus* species) have defined patches at three scales: individual flowers (Whittam 1977, Zimmerman 1983), single inflorescences within plants (Pyke 1978b, Heinrich 1979a, Haynes and Mesler 1984), and individual plants with multiple inflorescences (Zimmerman 1981, Best and Bierzychudek 1982, Hodges 1985). Whether a particular model will predict foraging behavior may depend upon the scale employed. For example, bumblebee studies that defined individual flowers as patches often support predictions of optimal foraging models, while studies at the next higher scale (within inflorescences) rarely do (pers. obs.). A general definition of patch, therefore, must be applicable at a variety of spatial scales.

Stephens and Krebs (1986) define a patch as a localized search area in which there is a specified relationship between time spent and energy gained. A predator can control its intake from a patch by controlling its time spent there. Defining a patch this way distinguishes a patch from

a prey item, which is assumed to be eaten entirely. Prey items therefore are assumed to yield a fixed energy gain and require a fixed handling time (Stephens and Krebs 1986). Since patches are distinguished by a specific energy-time relationship, leaving a patch is equivalent to accepting a different energy intake rate. Patches are often thought of as discrete areas of foraging substrate separated from other patches by areas which yield less energy per time. Time spent crossing these less suitable areas is defined as between-patch travel time. A forager may visit many patches during a single foraging bout; in fact, multiple-patch visitation within a bout is an important assumption of some patch-choice models.

THE MARGINAL VALUE THEOREM

The most widely studied patch-choice model is the marginal value theorem (MVT; Charnov 1976b). The derivation of the MVT has been described in detail (Pyke 1984, Stephens and Krebs 1986, Schoener 1987). The MVT proposes that foragers should leave a patch when intake rates decline to the "average capture rate for the habitat" (Charnov 1976b:132). Thus, a forager should stay in a patch as long as its foraging rate in that patch is greater than that attainable, on average, elsewhere. This prediction is derived from a model based on a series of explicit assumptions (Stephens and Krebs 1986). For the purpose of this review, five assumptions are relevant: (1) the environment is repeating; (2) organisms forage randomly; (3) organisms exhibit behavioral choice among foraging options; (4) foraging success declines with time in patch; and (5) foragers maximize net rates of energy intake. I will discuss whether birds in general, and patch-choice experiments using birds, meet these assumptions.

REPEATING ENVIRONMENT

Charnov (1976b) assumed that patch types within a habitat are distributed at random, and that foragers visit many patches of different types during a single foraging bout. This type of habitat (called a "repeating" environment since the forager repeatedly experiences the various patch types as it forages, MacArthur 1972) is a necessary assumption of the MVT because this type of environment is an assumption of renewal theory, from which the MVT is derived.

Many species probably visit a variety of patches during each foraging bout, and therefore meet the assumption of a repeating environment. Towhees, for instance, often move slowly along the ground during a foraging bout, feeding from numerous spots in the leaf litter. If the litter contains areas that vary in prey richness (Greenlaw 1969), and if the birds' behavior at each spot is

considered an independent sample within the overall foraging bout (e.g., Hailman 1974, Burt and Hailman 1979), then the towhees are sampling many patches in a repeating environment.

The foraging of other groups of birds may also conform to this assumption. Hummingbirds feed from many flowers, often on different plants, during a single bout. Some, however, concentrate on a particular plant species, reducing the types of patches visited within a bout. A third example of a repeating environment is Gibb's (1958, 1962) description of the foraging of tits on pine cones. The tits concentrated their search on a single cone at a time, and visited many cones in a foraging bout. Cones varied in prey richness both within and between trees. Thus if the cones are considered separate patches, the tits experienced a repeating environment. Other groups of birds for which the foraging habitat may be repeating include shorebirds (Goss-Custard 1970), pelicans (Brandt 1984), and egrets (R. M. Erwin 1985), all of which have been shown to move through many patches in a single feeding bout.

Sit-and-wait predators tend to survey their hunting grounds from a single spot. Shrikes and buteonine hawks often hunt from a single perch, returning repeatedly to that perch after attacking prey. These birds are not moving through patches in a conventional sense, although it can be argued that "patches" of mobile prey are moving past the predator. More active sit-and-wait predators, such as flycatchers and motmots, change perches relatively frequently. In order to meet the MVT assumption of repeating environments, bout length for sit-and-wait predators should be defined so as to ensure that patches of different types have been sampled during each bout. This could be accomplished by including many perch shifts within each bout, or by extending bout length at a single perch to include the passage of many "patches" of prey.

Experimental designs often do not incorporate a repeating environment. At artificial feeders, hummingbirds (Montgomerie et al. 1984, Pimm et al. 1985) and sparrows (Schneider 1984, Dunning 1986) usually stay at one "patch" (feeder) throughout an entire bout, even if alternative patches are provided. Early laboratory experiments with tits offered the birds artificial "trees" with patches of different prey density on the branches (Krebs et al. 1974, Cowie 1977). These designs constitute a repeating environment, since both rich and poor patches were encountered during bouts. More recent laboratory experiments have presented tits with food appearing along a conveyor belt (Ydenberg 1984, Ydenberg and Houston 1986). In these experiments the birds do not move through more than one patch per bout, unless the birds are considered sit-and-

wait predators with patches of prey moving in front of them on the conveyor belt.

Because birds often forage in a manner consistent with the assumption of a repeating environment, they can be used to test predictions of the MVT. However, care must be taken that the experimental design of such tests, especially laboratory studies, incorporate a repeating environment.

RANDOM SEARCH

The MVT assumes that foragers are as likely to return to a previously examined patch as they are to move to a new patch; that is, they search randomly (Green 1987). An alternative is systematic search, in which the probability of visiting a previously-searched patch is reduced (Kamil 1978, Baum 1987). Most birds that feed on dispersed prey are systematic searchers and tend not to retrace their foraging path (Cody 1971, Lima 1983, Eichinger and Moriarty 1985). Similarly, if prey are strongly clumped, birds often return repeatedly to patches that were particularly profitable (Smith and Dawkins 1971, Krebs 1974, Zach and Falls 1976b). Thus, birds feeding on either dispersed or strongly clumped prey are usually not random searchers. Hummingbirds, the subject of many early patch-choice experiments, also show nonrandom search, since many species often move to patches of flowers in a regular, repeated order, skipping many available flowers (traplining, *sensu* Feinsinger 1976).

I know of no studies that have demonstrated (or imposed) random search with their avian subjects. Birds are not the only group that violate this assumption. Other common subjects for patch-choice experiments also forage nonrandomly, including bees (Thomson et al. 1982, Heinrich 1979b, Marden 1984, Wetherwax 1986) and invertebrate stream predators (Waage 1979).

This is an important deviation from the assumptions of the MVT for two reasons. First, systematic searchers experience a constant rate of finding prey within a patch, since they do not search areas already depleted (Green 1987). The MVT assumes that rates of finding prey within patches decrease exponentially, and that this decreased rate of success triggers the decision to leave a patch (see below). Second, foragers using nonrandom search often should leave patches using different rules than do foragers searching randomly (Green 1987). This difference between the rules may be quantitative in some cases, but the predicted rules can be qualitatively very different. Since the way foragers search within patches can have a major effect on the predictions being tested (Green 1987), species that search systematically seem inappropriate for testing MVT predictions.

BEHAVIORAL CONTROL

An implicit assumption of the MVT is that the forager is able to forage in more than one patch type, and has the ability to compare intake rates in order to decide when to abandon a patch. In other words, the predicted response is assumed to be within the behavioral repertoire of the forager. That this assumption is true for most birds seems trivial; however, an instructive example exists within the patch-choice literature.

Bumblebees collect nectar from inflorescences in a stereotyped manner: they start at the lowest flower, move straight up the inflorescence, and quit before reaching the top. Since the lowest flowers usually hold the most nectar, this strategy seems consistent with energy maximization, and was cited as confirmation of one optimal foraging model (Pyke 1978b). However, the same behavior is used by bees on inflorescences in which the bottom flowers do not have the most nectar, and in flowers in which the nectar gradient was experimentally reversed (Waddington and Heinrich 1979, Best and Bierzychudek 1982, Corbet et al. 1981). In fact, pollen-collecting bumblebees also move from the bottom up, even though pollen levels are highest in the topmost flowers (Haynes and Mesler 1984). The stereotyped path taken by bees appears to be an invariant response, shaped not just by distributions of nectar, but also by the position assumed by bees while foraging and the need to reduce revisits to the same flower. Since the bees are apparently not responding to differences in intake rates, this system is not really appropriate for testing MVT models.

Many birds show behavioral flexibility in their foraging repertoire and quickly adapt their strategy to take advantage of temporary or novel sources of food. Some species are quite stereotyped, however. The avian equivalent of the bumblebee might be the Brown Creeper (*Certhia americana*). This surface-gleaner flies to the bottom of tree trunks, moves upward as it searches for insects among the cracks in bark, and leaves the trunk before reaching the top. Although this search pattern might be an optimal response to some particular distribution of insects on the surface of the tree, it is more probably a consequence of the posture adopted by the bird while feeding, and the potential interference from branches at the top of the tree (Franzreb 1985). The behavioral repertoire of the bird must be considered carefully when designing patch-choice experiments using stereotyped foragers such as Brown Creepers, crossbills (Benkman 1987a), or wintering Worm-eating Warblers (*Helmitheros vermivorus*, a dead-leaf specialist, Greenberg 1987b).

Interspecific comparisons of patch-choice behavior can be affected by the degree of foraging

specialization shown by the species being compared. Species whose foraging is relatively specialized may not respond to changes in foraging success in the same manner as generalist foragers. Thus, specialist and generalist species may show differences in foraging not predicted by a model which does not incorporate such variation. I found an example of such differences in my study of patch choice in towhees (Dunning 1986). I placed individuals of three towhee species in an artificial foraging arena that contained patches of different litter types. The towhees preferred to feed in one litter type, initially ignoring other available litters. I used this preference to examine foraging success rates before and after birds changed patches.

In each of a series of trials spread over consecutive mornings, a bird had a choice of feeding on a variable amount of seed under a preferred litter type, or a constant, abundant amount of seed under a non-preferred litter. Preferred and non-preferred litters were selected for each individual bird during preliminary trials. Initially 35 g of seed were available under the litter in both patches at the start of each trial. Each morning I reduced the amount of seed under the preferred litter by 5 g per trial, while maintaining the abundant levels under the non-preferred litter. Thus each bird experienced increasingly lower seed densities if it remained in the preferred litter. Eventually all birds switched to using the non-preferred litter.

The three species differed in the timing of the switch from preferred to non-preferred litter. Canyon Towhees (*Pipilo fuscus*), a foraging generalist found in Arizona in relatively food-poor desert washes and canyons, started using the non-preferred patches relatively quickly in the series of trials (Fig. 1). I also studied Rufous-sided Towhees (*P. erythrophthalmus*), montane sparrows of oak and pine-oak woodlands, and Abert's Towhees (*P. aberti*), which are restricted to desert riparian systems in southern Arizona. Each of these two species depends more on a specialized foraging technique, double-scratching in leaf litter (C. J. Harrison 1967), than does the Canyon Towhee (Davis 1957; Marshall 1960, pers. obs.). All individuals of the two relatively specialized species began using the non-preferred patches on trials later than the slowest-switching Canyon Towhee.

The differences in timing of patch switching among the species were not due to interspecific differences in foraging success rates experienced in the trials (Dunning 1986). Instead, I believe that the two more specialized species reacted in a qualitatively different manner to the changes in foraging success within the preferred patch, perhaps by using different decision rules (Dun-

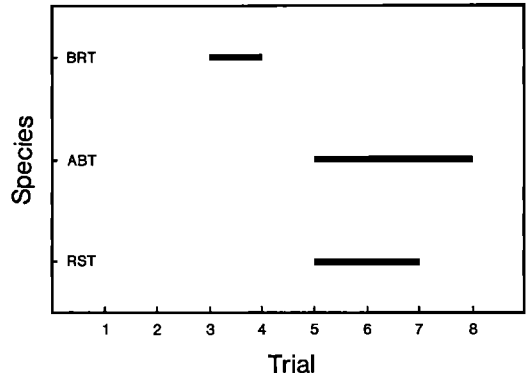


FIGURE 1. Range of trials over which individual towhees switched from use of preferred litter to use of non-preferred litter. BRT = Canyon Towhee, ABT = Abert's Towhee, RST = Rufous-sided Towhee. Notice that the range for Canyon Towhee did not overlap that of the other two species.

ning, in prep.). Since different decision rules can lead to different predictions of patch-choice behavior (Green 1987), my ability to test specific patch-choice predictions through comparison between towhee species was reduced. Studies comparing foraging behavior between species should therefore consider the effect of interspecific differences in foraging specialization on the predictions being tested.

DECREASING REWARD WITH TIME IN PATCH

The MVT assumes that as a predator stays in a patch, it depletes the patch of food items, and correspondingly, its intake rate declines. This decline is crucial to the model, since it is the decline in intake rate that motivates the forager to move to another patch. Birds may not conform to this assumption in several ways. As noted before, systematic searchers (such as many birds) may not experience a decrease in intake rate during search within a patch. In addition, not all patch types would be expected to be depleted by predation, regardless of the type of searching by the predator. For example, prey density in the area scanned by a sit-and-wait predator is variable with time since mobile prey move in and out of the predator's range. Also, a predator in a patch with superabundant resources might not have its intake rate decrease as it feeds. Hummingbirds, for example, feeding at large artificial feeders probably experience no decrease in intake rate until the feeder is drained. A forager feeding on superabundant resources may leave a patch only when satiated.

Data demonstrating that capture success decreases with time in a patch for wild birds are limited. Capture success may have declined with

time for wild Snowy Egrets (*Egretta thula*), but did not for Great Egrets (*Casmerodius alba*) (R. M. Erwin 1985). Intercapture intervals at the end of foraging bouts by American Kestrels (*Falco sparverius*) are longer than earlier intervals, implying that foraging success declined during the bout (Rudolph 1982). However, inspection of the data presented by Rudolph shows that intercapture intervals actually were constant throughout most of the bout, dropping only at the end. This same pattern has been shown in laboratory studies of White-throated Sparrows (*Zonotrichia albicollis*; K. Johnson, pers. comm.).

Sparrows feeding on patches of seed deplete the seed levels with time, eventually prompting patch switching (Schneider 1984, Dunning 1986). However, this depletion may occur over many foraging bouts, and so is qualitatively different than the depletion assumed by the MVT. (Note that with the assumption of random search, a forager is unlikely to return to one patch repeatedly until depletion.) Foragers showing this type of systematic search may be using an expectation patch-choice rule to determine when to stop returning to previously-used patches (Dunning 1986).

The use of microcomputers in laboratory studies to control delivery of food items allows the researcher to control the depletion of patches (Ydenberg 1984, Kamil et al. 1985, Ydenberg and Houston 1986, Hanson 1987). In these studies, a bird initiates the beginning of a foraging bout by landing on a feeding perch, or striking a control key. With the initiation of the bout, food is delivered at a decreasing rate until the bird ends the bout. Delivery rates are reset to the original starting rate for the initiation of the next bout. Thus, in certain controlled situations, use of this kind of apparatus can ensure that intake rates decline when a forager stays in a patch.

The importance of meeting this assumption may vary with the specific test of the MVT. Species which feed on superabundant resources (e.g., hummingbirds at feeders) are clearly not suitable for MVT tests, since their feeding rates are constant over time. Species which experience a constant intake rate initially upon entering a patch may conform to a modified version of the MVT (the "combined patch and prey model," Stephens and Krebs 1986). Predictions of Charnov's (1976b) version of the MVT require a forager that experiences a decreasing intake rate as it feeds in a patch; testing the model with foragers that do not meet this requirement weakens the conclusions reached from the test.

MAXIMIZATION OF ENERGY INTAKE

The most prominent assumption incorporated into the MVT is that organisms seek to maximize

their net rate of energy intake (E_n). The role that this assumption has played in the development of foraging theory is considered at length by Stephens (this volume). I would like to add one point to his discussion. Strictly speaking, organisms should seek to maximize fitness, and the maximization assumption essentially assumes that maximizing E_n is the short-term equivalent of maximizing fitness (Sih 1982). This should not be accepted automatically in all cases, as the following example demonstrates.

A field test of the relationship between fitness and intake in birds examined diet and reproductive success in breeding Herring Gulls (*Larus argentatus*; Pierotti and Annett 1987). This study addressed which habitat a gull should forage in, and which prey items to eat. These are different hierarchical foraging decisions than patch choice; however, I discuss the study here because it is a particularly elegant example of how energy maximization may not maximize fitness. Individual gulls feeding in different areas specialized on mussels, garbage, or storm-petrels. Garbage provided the greatest E_n , while mussels provided the least. In spite of this, mussel specialists fledged more than double the number of young fledged by garbage specialists. Pierotti and Annett suggest that mussels provided limiting nutrients to the egg-laying females, allowing them to lay more clutches and hatch more young. Thus, in this system, gulls with the highest intake rates did not have the highest fitness.

Nevertheless, some studies examining use of patches have demonstrated that some birds adopt a strategy that seems to maximize intake rates. Ydenberg and Houston (1986) compared intake rates of captive tits at the start of foraging periods with the rates of the same birds later in the period. The birds' combination of handling, travel and patch residence times at the start of each period maximized intake rates relative to other combinations of these variables. Intake rates declined later in the period due to conflicting demands for territorial defense. Studies of diet composition of birds are sometimes able to demonstrate that observed diets conform to the energy maximization assumption of optimal diet theory (e.g., Pulliam 1980, Benkman 1987b). Fewer studies of patch choice examine the assumption of E_n maximization, perhaps because of the difficulty with which intake rates in a variety of patches can be estimated.

Montgomerie et al. (1984) investigated which of two functions were maximized by hummingbirds. They suggested that in most situations, maximizing net energy per volume consumed (NEVC) would yield more energy than maximizing E_n . They devised a test which showed that hummingbirds preferred patches that yield-

ed high NEVC over those yielding high E_n . However, Montgomerie et al. concluded that both functions would be maximized simultaneously in most situations.

Some studies examining energy maximization as a foraging goal have been unable to demonstrate that this goal is attained (see Stephens, this volume). However, it is now recognized that most organisms face multiple demands, and it may be rare that a forager can adopt a strategy of unconstrained energy maximization. Recent developments in foraging theory have added realistic constraints to foragers' ability to maximize intake rates, and examine how these constraints change patch-choice decisions (Caraco 1982; Getty and Krebs 1985; McNamara and Houston 1985; Lima and Valone 1986; Stephens, this volume). These extensions of the original patch-choice models may be more useful in examining patch choice in species for which the maximization assumption is not valid. Testing of models assuming energy maximization is still important, however, because deviations from such models' predictions can identify important constraints.

ALTERNATIVE MODELS OF PATCH CHOICE

FIXED-NUMBER AND FIXED-TIME HYPOTHESES

The main alternatives to the MVT have been models in which the decision to leave a patch is based on the forager's expectation of success. These expectations of success are based on simple measures of the environment, such as the number of prey in a patch or the amount of time normally needed to deplete a patch. The first such "expectation models" were the fixed-number and fixed-time hypotheses (Gibb 1962, Krebs 1973, Krebs et al. 1974), which proposed that foragers stay in a patch until they found a certain number of prey (fixed-number) or until a certain time had elapsed (fixed-time).

The fixed-number hypothesis was suggested by Gibb (1962) to explain certain unusual foraging characteristics shown by wintering tits. The only explicit assumption of this hypothesis is that patches contain a specific number of prey, such that the forager can develop an accurate expectation of the number of prey within a patch. This expectation could be learned from past experience, or be genetically programmed by natural selection. It is unlikely that wild birds routinely forage on prey distributed in such a regular manner. In fact, Gibb's earlier studies (1958, 1960) demonstrated that the resource base of the tits, for which Gibb originally suggested the fixed-number hypothesis, did not meet this assumption (Krebs 1973, Krebs et al. 1974). Green (1987) proposed that a fixed-number strategy is optimal

for foragers that search randomly for regularly-distributed prey, but systematic searchers should vary their patch-leaving rules as time in a patch increases. Since most birds probably violate both the fixed-number hypothesis' assumption of regular prey distribution, and the related implicit assumption of random search, birds are not appropriate for testing predictions of this model. I know of no experimental study with birds that supports a fixed-number hypothesis.

The fixed-time hypothesis was proposed by Krebs (1973) to explain the foraging patterns observed by Gibb. Krebs suggested that Gibb's tits stayed in each patch for a set period of time, rather than until a set number of prey were captured, basing this suggestion on the logic that animals are better at measuring time than at counting (Krebs et al. 1974). Recent theoretical models have demonstrated that leaving a patch after a fixed time can be a profitable strategy when prey are distributed randomly among patches (i.e., when prey have a Poisson distribution; Iwasa et al. 1981, Green 1987). This is true regardless of whether the forager searches randomly or systematically; however, random searchers should quit patches before systematic searchers, all else being equal (Green 1987).

Although many prey types for avian foragers may be strongly clumped (i.e., some seed types, fish schools, flowers), some prey types may approximate a Poisson distribution. Prey of foliage-gleaners, for instance, may be randomly distributed among leaves of a tree. Several studies of birds have at least partially supported a fixed-time hypothesis. Krebs et al. (1974) were unable to conclusively reject the hypothesis that tits in an artificial arena were leaving patches at a fixed time. Although the tits tended to spend more time in richer patches (a result allowing rejection of the fixed-time hypothesis if significant) in four different experiments, the differences between patches were significant in only one experiment. Since the birds tended to spend more time in richer patches, Krebs et al. concluded that an optimal foraging model based on giving-up times was better supported by the data (but see McNair 1982 for a reinterpretation of the data).

Zach and Falls (1976d) examined the movements of Ovenbirds (*Seiurus aurocapillus*) hunting for dead flies on an artificial feeding board. They compared predictions of a fixed-number hypothesis, a fixed-time hypothesis, and a giving-up time hypothesis based on the MVT. The fixed-number and giving-up time predictions were clearly rejected. Search by the Ovenbirds violated both the random search and probably the patch depletion assumptions of the MVT. One of three predictions from a fixed-time hypothesis was supported. Zach and Falls conclud-

TABLE 1. EVIDENCE THAT BIRDS USE PRIOR KNOWLEDGE FROM PREVIOUS WITHIN-PATCH FORAGING TO DETERMINE CURRENT FORAGING STRATEGY. PRIOR KNOWLEDGE IS INFORMATION POTENTIALLY AVAILABLE TO BIRDS FROM PREVIOUS EXPERIENCE. EVIDENCE OF EXPECTATION ARE OBSERVED BEHAVIORS CONSISTENT WITH USE OF WITHIN-PATCH EXPERIENCE

Source	Organism	Prior knowledge	Evidence of expectation
Smith and Dawkins (1971)	Great Tit	Estimate of variability in patch quality	Tits showed time lag in response to changes in patch richness.
Smith and Sweatman (1974)	Great Tit	Location of four patches of variable quality	When locations of richest and poorest patches were switched, tits moved to second richest patch.
Zach and Falls (1976b)	Ovenbird	Location and quality of patches	Search patterns based on previous, not current, prey distributions.
Lima (1983)	Downy Woodpecker	Distribution of seeds in feeders	Search pattern based on previous seed distributions; time lags before changes in searching to match current seed distributions.
Dunning (1986)	Towhees	Quality of two types of leaf litter	Birds left preferred patches after large decrease from previous within-patch success.

ed the data weakly supported a time expectation model.

Valone and Brown (unpubl.) used the amount of seed left in a patch after visits by a forager (the "giving-up density," J. S. Brown 1986) to compare predictions of four foraging strategies potentially used by a variety of desert granivores. The giving-up densities of Gambel's Quail (*Callipepla gambelii*) and possibly of Mourning Doves (*Zenaida macroura*) were most consistent with predictions of a fixed-time hypothesis.

WITHIN-PATCH HYPOTHESIS

Another expectation hypothesis proposes that a forager changes patches when success in the current patch has declined to a threshold (as envisioned by the MVT), but that the thresholds are based only on the forager's past and present experience within its current patch type. I call this the within-patch hypothesis, since only information gained by the forager in a single patch type is used to determine when to leave. Previous foraging within the patch type establishes an expected rate of intake from patches of that type. The forager leaves its current patch when success there drops below expectations. A forager's expectation (and therefore its threshold) is altered by large scale changes in patch characteristics, since expectations are updated with new information during each foraging bout. When success drops below the threshold, the forager leaves the patch and samples other available patches to determine if a higher rate is available elsewhere.

This hypothesis is very similar to the MVT. In both models, foragers are assumed to be able to monitor current success, and to compare this success with a threshold rate based on past experience. The main difference between the two

models is that the MVT predicts thresholds based on experience in all available patch types, usually in the form of an average habitat success rate. Thus, the MVT predicts that foragers compare success rates between patch types, while the within-patch hypothesis predicts that patch switching is based on changes in foraging success within the same patch type. The within-patch hypothesis may be more realistic for organisms that forage in complex or variable habitats, in which the information needed to make comparisons of foraging success between all potential patches may require an omniscient forager.

The major explicit assumption of the within-patch hypothesis is that foragers respond primarily to changes in prey distribution or foraging rates within patches. There is extensive evidence supporting this assumption (Table 1). I will discuss two studies as examples. Lima (1983, 1984) examined the use of artificial feeding logs by wild Downy Woodpeckers (*Picoides pubescens*). He found that, with experience, the woodpeckers matched their searching pattern to the distribution of prey in the logs. The birds generally started at the bottom of each log, and moved up, leaving when their expectation of prey distribution indicated that no more prey were available. When Lima abruptly changed the prey distribution, the woodpeckers continued to search the logs in a manner consistent with the previous prey distribution, clearly showing the birds were reacting to their expectations of where the prey were. Within several days (the time frame of the trials), the woodpeckers altered their foraging to match the new prey distributions.

In my study of patch use by captive towhees, I looked specifically for evidence of thresholds based on between-patch or within-patch com-

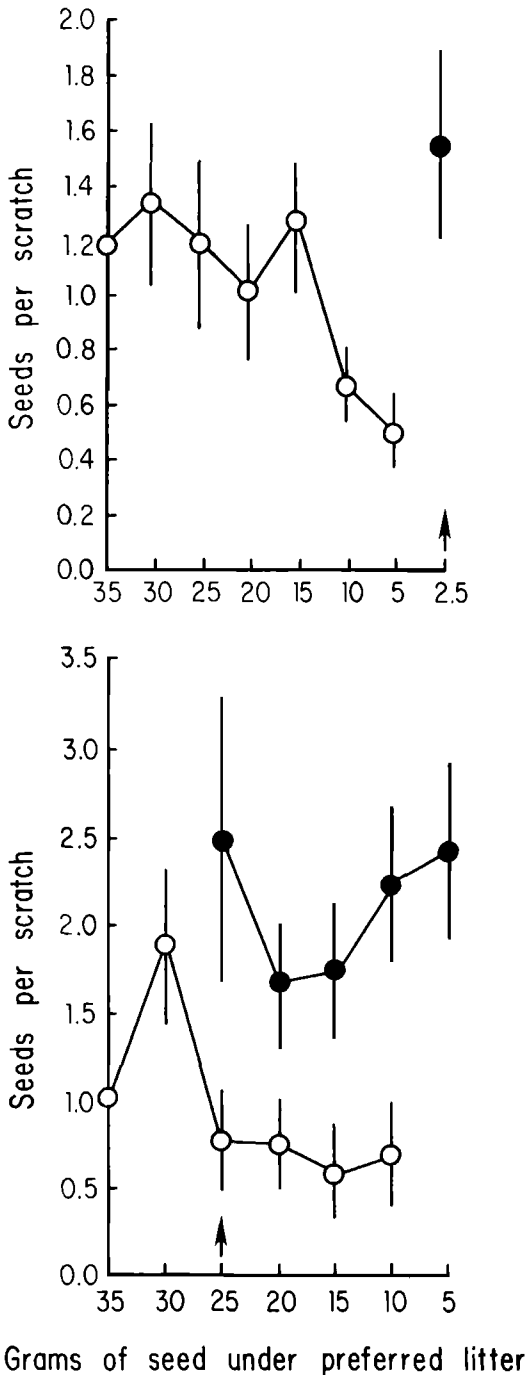


FIGURE 2. Foraging efficiency per trial for two representative towhee individuals: Upper graph is data for an Abert's Towhee; lower graph is data for a Canyon Towhee. Open circles = seeds per scratch in preferred litter; closed circles = seeds per scratch in non-preferred litter. Vertical lines = 95% confidence limits. Trials 1-8 are listed on the x-axis by the amount of seed present in the preferred litter patch during that

parisons of foraging success (Dunning 1986, in prep.). As described before, individual towhees of three species were placed in a foraging arena where they could feed on a variable amount of seed under a preferred litter type, or on a constant, abundant amount of seed under a non-preferred litter. All birds initially concentrated their foraging in the preferred patch, then eventually shifted their foraging to the non-preferred patch. If the towhees were comparing success rates in both patches, then the birds should have switched patches when success in the preferred litter dropped below that available in the non-preferred patch. None of the 12 birds that I observed fit this pattern (see examples in Fig. 2). Instead, changes in patch choice appeared to be associated with large drops in success within the preferred patch itself. This was especially true for Canyon Towhees (Fig. 2b), since three of four individuals of this species switched at the first significant drop in within-patch success (Dunning 1986). Since the patches were adjacent to each other within the foraging arena, and did not appear to differ in exposure or any other factor, I concluded that the birds were not using information from previous trials on success rates in non-preferred patch to determine when to leave the preferred litter. Patch choice by the towhees was most consistent with a decision rule based on changes in within-patch foraging success.

SYNOPSIS

Models of patch choice predict that foragers leave patches based on particular decision rules. These models incorporate assumptions about how foragers behave. The suitability of a particular species for testing predictions of these models depends on how well the foraging of the organism meets the assumptions (Maurer, this volume). Care must be taken in designing experiments that test the predictions of theoretical models, because the conclusions are weakened if underlying assumptions are violated.

Of the assumptions considered in this paper, the one that is probably met least often by birds is the random search assumption of the MVT and (implicitly) the fixed-number hypothesis. Since many bird species studied do not search patches randomly, birds may not be appropriate test organisms for MVT predictions. Green (1987) suggests the theoretical emphasis on random foraging is misplaced, and develops several patch decision rules based on systematic search. These rules deserve empirical testing.

← trial; arrow indicates trial during which bird switched patches. Notice that switching followed large drops in foraging efficiency in preferred patch.

A variety of birds also do not appear to forage in a manner consistent with the MVT assumption that foraging success declines with time in patch. Patch-choice in these species may be better studied by considering modified versions of the MVT that reflect different patterns of how intake rate changes with time in a patch (Stephens and Krebs 1986).

Some expectation models of patch choice incorporate assumptions which may be realistic for many bird species. The fixed-time hypothesis is most appropriate for birds that feed on randomly-dispersed prey, while the within-patch hypothesis was proposed for foragers that use decision rules based on within-patch changes in success. The latter model may be especially appropriate for birds in habitats that change rapidly, where information from all patches in the habitat may be difficult to gather. The uniform environment assumption of the fixed-number hypothesis makes this expectation model less applicable to birds.

One area currently being explored is the incorporation of realistic constraints into patch-choice models (Stephens, this volume). Constraints have been added to optimal diet theory,

leading to a better understanding of diet selection under realistic conditions. Constraints on foragers' ability to collect and use information, for instance, lead to predictions of partial preferences in diet selection, a commonly observed phenomenon (Getty and Krebs 1985, McNamara and Houston 1987b). Incorporation of realistic constraints into optimal patch theory is leading to better understanding of time lags in patch switching (Lima 1984) and sampling strategies (Lima 1985).

Birds have proven useful for testing a variety of foraging models. As illustrated by these models of patch choice, careful consideration of the assumptions underlying theoretical models will improve a researcher's ability to use birds, or any other organism, to understand foraging better through the use of theory.

ACKNOWLEDGMENTS

I thank Brent Danielson, Michael Kaspari, Ron Puliam, Richard Hutto, C. J. Ralph, Joseph Jehl, and Michael Morrison for constructive comments on this paper. The Institute of Ecology, University of Georgia, provided logistic and financial support during the preparation of the manuscript.