

*Observations, Sample Sizes, and Biases*

FOOD EXPLOITATION BY BIRDS: SOME CURRENT PROBLEMS AND FUTURE GOALS

DOUGLASS H. MORSE

*Abstract.* Food exploitation is usually addressed in two major contexts in population and community studies of birds: (1) in consideration of niche relationships (niche theory) and (2) in choice of foods or feeding sites (foraging theory). The two approaches may be, but seldom have been, combined. Studies of niche relationships focus on comparisons of foraging performance. Food-choice or feeding-site (patch) studies compare foragers' performance with an optimum, usually based on maximizing resource intake. Both niche and foraging studies typically assume that resources (food) are limiting, but this assumption is seldom verified. Failure to test for resource limitation weakens most foraging studies, but this failure will be difficult to rectify. Few studies have concentrated on periods during which food limitation is likely to be most serious.

Foraging studies must determine how resources should be defined, when and how often foraging activities should be measured, which members of a population should be studied, how to compare foraging results with resource availability, and what effect other species' densities will have on foraging. Foraging theory evaluates efficiency in resource use. Failure of birds to realize foraging predictions may point to the mechanisms that shape foraging behavior. Studies combining niche and foraging theory should advance understanding of how communities develop structure. All of the studies discussed need to be evaluated in terms of fitness considerations. It is not sufficient merely to assume that selection exists for foraging variables independent of other life-history variables.

*Key Words:* Competition; fitness; food limitation; food exploitation; foraging; niche theory; optimal foraging theory.

The study of food exploitation, including foraging (searching and selecting) has been a major preoccupation of avian ecologists and behaviorists over the last 35 years. One might thus think that little work remains to be done, but a closer look will quickly change that impression. I will focus here on an evaluation of past and current work, and suggestions for a future agenda.

I will discuss four major areas: (1) food limitation and related competition; (2) some major foraging variables that often do not receive adequate attention; (3) the hiatus between optimal foraging theory and niche theory; and (4) fitness considerations. I have worked extensively in all of these areas, for the first three in studies of paruline warblers and mixed-species foraging flocks (reviewed in Morse 1980a), and for the first and fourth in current studies on other animals, primarily crab spiders (reviewed in Morse and Fritz 1987).

These topics deal with three distinct hierarchical levels: individual, population, and community. Food exploitation involves many different variables that interact to predispose a bird to forage where, when, and how it does. As such, it is a complex topic to study.

Much of the early work on foraging attempted to establish how species' ecologies differed and how these differences were related to coexistence. Often these studies compared the foraging patterns of coexisting species and used the resulting

data to infer ecological relationships among the participants. In my opinion, these studies are unlikely to provide much further insight into basic understanding of community ecology. More recently, interest has shifted to optimal foraging, a subject largely concerned with how individuals can enhance or retain their efficiency in gathering food. This work focuses on the individual, rather than the community hierarchical level. As a result it has usually been treated as an issue distinct from niche partitioning studies; however, it is important to link these two bodies of study.

FOOD LIMITATION AND COMPETITION

Studies of niche partitioning deal with problems in which competition, often taken to be for limited food resources (or places to hunt for it), is assumed to be a driving force in niche differentiation. Few studies, however, have directly addressed the problem of food limitation.

The obvious way to test for food limitation is by manipulating the food supply. A few workers have attempted this technique with passerine birds (e.g., Krebs 1971), and in a non-controlled way we do so when we set up a feeding station. Most food supplementation studies have been done during the winter, perhaps for two reasons: because the investigator can readily manipulate the food (usually seeds), and because it is believed by many (e.g., Lack 1954, Pulliam and Millikan 1982) that northern residents are lim-

ited during this season. Unfortunately, foraging studies have not accompanied most food supplementation studies (but see Grubb [1987] for data on flock foraging). A logistical problem in studying food limitation may be that periods of limitation ("crunches") are infrequent events (Wiens 1977, Dunham 1980), so even carefully designed experiments on food limitation may not accomplish what the investigator intended.

Winter is not the only time that food limitation may occur, however. It is probably easiest to view this possibility from the perspective of total lifetime fitness. Foraging studies have focused on the short-term survival of adults, especially for species provided with winter food supplements. Yet, winter survival constitutes only part of the birds' problem; another major factor is fecundity (reproduction), which may not be directly related to winter food considerations. Reproduction in the vast majority of passerine birds, at least temperate-zone species, occurs during the spring and summer. At the period most advantageous for breeding it is just as important that conditions permit birds to accumulate the additional resources required for breeding as it is for birds to survive the winter. The ultimate result of failure to reproduce during the summer or to survive the contingencies of the winter is a net fitness of zero. Failure of an iteroparous individual to breed successfully during a given summer clearly is not equivalent to failure of the same individual to survive a winter, in the former instance it can try again. However, since many passerine species have high mortality rates, the mean number of seasons to breed may not greatly exceed one, so that the importance of breeding and winter contingencies may not differ greatly. Depending on the relative importance of winter or summer limitation, pressure on foraging efficiency may differ. Experimental tests of problems such as these would prove daunting in the field.

The crisis can thus occur at either season. Consecutive, catastrophic, breeding seasons at my Maine coast study areas (1972 and 1973) were associated with a population decline of up to 50% for some warbler species in certain study areas (Morse 1976a). I interpreted this poor level of success to the parents' inability to feed young during extended periods of stormy weather, with resultant high juvenile mortality (Morse 1971a, 1976a). Thus, although breeding contingencies may not be food-based, they can be. Sorting out these relationships requires that more attention be paid to these problems.

Thus, the problem of limitation is complex, and it probably differs among species, within species, spatially, and from one time to the next. Apparent niche shifts do not qualify as strong evidence for competition, notwithstanding the

extensive pleading to parsimony that sometimes occurs (for example, see Diamond [1978:327]). Equally inappropriate are statements that since few satisfactory experimental demonstrations of competition exist, we may assume that competition is not an important structuring factor in communities (see Connell 1975). What *is* clear is that tests of food limitation or competition are not easy to perform in the field, especially for certain groups of animals, unfortunately including birds. Nevertheless, Connell's arguments, as well as those of Simberloff and his colleagues (e.g., Connor and Simberloff 1979), have had the salutatory effect of encouraging workers to address these problems seriously. It is encouraging to see Schoener's (1983) report of some 150-odd studies in which he concluded that competition was adequately demonstrated experimentally in the field, although only seven of them came from birds (probably partly because of the extreme difficulty of performing the appropriate studies, and partly because investigators have not been in the habit of attempting to do so).

This difficulty should encourage us to look for indirect evidence. For instance, more food probably exists during insect outbreaks, such as spruce budworm (*Choristoneura fumiferana*) infestations, than birds can eat; perhaps that could form the basis for comparison with situations in which such a visible outbreak does not occur. Similar assumptions may be valid in instances of temporal ecological release; that is, when the exploitation patterns of an individual change from moment to moment with the presence or absence of another one or more individuals (see Morse 1967a, 1970, 1980a). These observations provide stronger evidence than Diamond's (1978) putative niche shifts, in that the same birds can be observed both in the presence and absence of other individuals.

Two other observations have to be made here. First, behavior normally associated with limiting situations, such as aggressive behavior, either intra- or interspecific, may occur even if resources themselves are not directly limiting. For instance, one can observe hostile interactions among spruce-woods warblers during major insect outbreaks, and that behavior may affect foraging patterns. This seemingly inappropriate behavior could be a consequence of these birds existing under limiting conditions at other times, with behavioral repertoires that function effectively then. During periods of superabundant food, the seemingly inappropriate venting of aggressive behavior may not exact a significant decrease in foraging efficiency. The important point is that interpreting aggressive behavior uncritically as evidence for resource limitation may lead to error. It is important, however, to ask whether

one can assume the existence of unlimited resources if hostile encounters lower success. Numbers of some species of spruce-woods warblers may actually decline during spruce budworm outbreaks (e.g., Morris et al. 1958). These declines could be either a response to declines in the numbers of alternative prey or to the warblers themselves.

The second point is that competition takes place at an individual level, as do its consequences, even though ecologists have generally considered it as a population, or community, level phenomenon. This perception is largely a consequence of interest in population densities or species diversity. However, Martin (1986) has stressed that the concern to an individual is related to the pressures it personally experiences. If it is territorial, those concerns are pressures on its territory, rather than events going on in other parts of its population. This consideration assumes major importance if a strong gradient of food or habitat acceptability exists (the ideal free space of Fretwell and Lucas 1970). It should assume less importance in an ideal (hypothetical) homogeneous habitat, where the obvious solution is to space out. However, given that habitats are heterogeneous and individuals exhibit preferences for a part of the habitat, the ideal homogeneous habitat seems unlikely. The significance of competition as a between-individual phenomenon in the community remains to be worked out. Assuming that resource limitation exists in places, populations and communities can be divided into two categories of individuals, those that exist under varying levels of competitive stress and those that do not. This difference is a potential selective force, even if its consequences at population and community levels are not clear. For our present purposes, it may mean that we should separate these two groups of individuals for studies of food or foraging. To what degree are these individuals otherwise randomly distributed within a population, as in their food choices and foraging repertoires? If habitat or resource gradients are worth contesting, dominant and submissive individuals may experience secondary selective pressures for somewhat different patterns of resource exploitation.

Food limitation thus probably affects foraging strongly, but that result has seldom been directly demonstrated in bird populations. Bird populations exhibit a variety of characteristics, such as apparent niche shifts, which can be interpreted as evidence for competition, often food-based competition, and the tendency has been to accept as sufficient, far weaker evidence than I feel is appropriate. The constancy of the studies cited supports the importance of food-limitation and competition, but most of the individual studies

in themselves provide only weak backing for this explanation.

#### SOME COMMENTS ON FORAGING VARIABLES

Potentially ecologically distinct categories have often been lumped in foraging studies. This procedure may produce erroneous conclusions, but probably more often, equivocal, no-difference results that may obscure major variables upon which natural selection may act. If these studies are to have an evolutionarily relevant context, it is important to identify and concentrate on such variables. If they are difficult to study, that is a serious problem, but if they are to be explored in a bird system, there may be no alternative to hard work. I will consider several foraging variables; the following list is not complete, but it should suffice to make my point. They can be broken down into two basic categories: (1) problems of scale and (2) problems of individual variability.

#### FORAGING CATEGORIES

The most basic sampling problem in studies of food exploitation is the investigator's selection of foraging categories (foraging sites, foraging motions, etc.). This problem is one of scaling: dividing the habitat into either too many or too few components will misrepresent the way in which foraging birds respond to it. Prior to MacArthur's (1958) study, ecologists seriously entertained the possibility that the spruce-woods warblers provided an important counterexample to the competitive exclusion principle, since these birds coexisted, in high diversity and large numbers, in seemingly homogeneous spruce forests. However, MacArthur quickly established that this conception grossly misinterpreted the warblers' space allocation patterns, for they do not respond to the forest as a single homogeneous entity, but as a highly divisible one. That conclusion indicated the necessity of using a scale similar to those used by the birds themselves. I will largely confine discussion to within-habitat divisions, but between-habitat distinctions may be important as well.

To select foraging categories from the viewpoint of adaptive or fitness considerations, the investigator should assume the perspective of the foraging bird. Detailed pilot studies may help to resolve the problem of which foraging categories to adopt, although they may greatly increase the effort necessary. In their calculations of foliage-height diversity, MacArthur and his colleagues (MacArthur and MacArthur 1961, MacArthur et al. 1962) attempted to discover what features were important for the presence of different species. Although their initial results were prom-

using, attempts to extrapolate from some eastern forests and their inhabitants to other communities did not prove to be very successful. These were ambitious attempts to discover simplification and generality, and they may have foundered on those points. Their techniques assigned birds to habitats on the basis of a very few kinds of information, and now knowing that extensive within-habitat partitioning takes place in some groups (but not others), it is not surprising that they did not generally succeed. Their efforts were nevertheless important because they explored new methodologies. In contrast, if one selects too many categories in a mechanistic quest to establish whether quantifiable (although questionably biologically-based) differences occur among species, the data sets necessary may become prohibitively unwieldy, and the likelihood of finding spurious correlations increases.

Two apparent alternatives exist. The first is to divide foraging sites into what appear to be biologically meaningful subdivisions (e.g., crown, understory, ground, and perhaps with within-layer categories like trunk and large limb). The second may be not to attempt such biological divisions at this point, but to separate the habitat into arbitrary categories of such a size range that the members of the community as a whole will use all so-designated parts with reasonable frequency. Height intervals could be used (e.g., 3-m heights), and horizontal (within-layer) separation might be by distance, or by dividing the range of available substrate sizes into several categories. Both methods have their advantages and disadvantages; the first may be botanically relevant, but partition the habitat in a way that the bird never would; the second may avoid any unwarranted assumptions about a species' biology, but at the possible expense of creating biological redundancy and biologically irrelevant categories. The latter technique has the redeeming feature of presenting results that have not incorporated major, and possibly fallacious, biological assumptions into the data gathering at this early stage. Pilot studies that initially record data on a small scale may help to resolve this difficulty.

A related sampling problem concerns how foraging data are gathered. Many workers have gathered substantial numbers of observations from single individuals, an expedient way to obtain the large data sets needed for quantitative analysis. A positive feature of this technique is that it minimizes bias associated with the different visibility of individuals in different parts of the habitat. If an individual is more easily discovered in some parts of its habitat than in others, the larger the number of subsequent observations gathered on it, the less the data should

reflect the bias of initial observation (the "spotting" bias). But, these are not independent data points. The problem of independence of foraging data points is usually ignored (but see Morrison 1984a; Hejl et al., this volume), so that such studies present artificially (and incorrectly) inflated  $n$ 's, and the specter of pseudoreplication. Ideally such difficulties can be redressed with analyses that compare bouts of foraging among individuals, but that has often not been the approach.

#### FOLIAGE SAMPLING AND BIRD FOOD CHOICE

A question of central interest to students of insect-gleaning birds is, "Do these birds specialize on certain types of food, and if they do, how?" Many and varied efforts have been made to sample the food supply in order to answer these questions. They differ in accuracy, difficulty, and human effort. Even if they sample the foliage accurately, that does not mean that the birds sample it in the same way, however (see Hutto, this volume). For instance, in some of my work in which I used exhaustive methods of foliage analysis that appeared to be very accurate (Morse 1976a, 1977), I found that Black-throated Green (*Dendroica virens*) and Yellow-rumped (*D. coronata*) warblers specialized strongly on large caterpillars that they gathered on spruce foliage, even though these caterpillars sometimes appeared in very low frequencies in the foliage samples. These same studies showed that large numbers of insects less than 2 mm in length, mostly psocids, regularly occurred in the samples, but seldom in the stomach contents. This absence might simply result from their not being visible in the stomach remains, but more likely, judging from their behavior, the birds did not perceive these insects because of their small size, or they eschewed them. If they were not profitable prey, not seeing them might actually improve the birds' foraging efficiency, in terms of energy gain per unit time. More time-efficient, but less accurate, estimates of insect standing crop raise additional questions and debate over how far one can extrapolate; for instance, what data from sticky traps can tell us, since these traps take highly biased samples (Southwood 1978). Thus, it is important not to interpret bird food intake from foliage studies alone, even accurate ones.

#### THE EFFECT OF ABUNDANCE OF SPECIES ON THEIR COMMUNITY IMPACT

The foraging impact of a species on its own members and on other species will differ with its abundance. This factor may assume considerable importance at the community level, but is often ignored, although it enjoyed considerable atten-

tion in the theoretical literature under the term of "diffuse competition" (MacArthur 1972). Thus, an abundant species that overlaps another species slightly may have a considerably heavier impact on it than will a third species that is relatively uncommon but overlaps it heavily. Ulfstrand (1976) has emphasized the importance of this role for the Willow Warbler (*Phylloscopus trochilus*), an abundant species in many parts of Europe. Since the density of this migratory species may greatly exceed that of any resident species, its impact upon them is likely to be major. In a collective sense the same relationship may exist between the spruce-woods *Dendroica* warblers, whose numbers may make up 70% or more of the total summer bird fauna, and the permanent residents. In both Europe and North America, some of the residents exhibit habitat shifts between seasons that strongly suggest competitive displacement.

#### TEMPORAL VARIATION

Temporal variation may also compromise the precision of foraging studies. It may occur at several time scales. Short-term studies run a high risk of presenting misleading results, for they may record only part of the variation inherent in a system, and possibly a very atypical part at that. The scales in question may range over several time frames: part of a day vs. an entire day, part of a season vs. an entire season, part of a year vs. an entire year, or one year vs. more than one year.

Some atypical periods, or the intervals between them, considerably exceed one year. They include both the "crunches" (periods of shortage) to which Wiens (1977) refers and periods of temporary superabundance. Representing the greatest inflections from a long-term mean, these two kinds of fluctuations are of great overall importance to the birds.

Extreme droughts may have a devastating effect on foraging opportunities. Grant (1986:191) found that drought affected the foods available to Darwin's finches, with many of the foods normally taken becoming unavailable, necessitating concentration on certain others. A severe population decline followed, with accompanying selection for individuals best able to exploit the remaining food types.

In my study of mixed-species foraging flocks I observed a major shift in foraging associated with a periodic mast crop of longleaf pine seeds (Morse 1967a). Foraging by Brown-headed Nuthatches (*Sitta pusilla*) changed markedly with this gradation; they shifted from a primarily insectivorous diet to one of over 80% seeds. To get the pine seeds they worked farther out into the foliage than they did at other times. There they came into frequent contact with the abun-

dant and aggressive Pine Warbler (*D. pinus*). Simultaneously, fights between these two species increased markedly. The consequences for the nuthatches may not have been significant, because of the abundant source of food available to them; however, the consequences to the Pine Warblers, in terms of energy and time expenditure, may have been more severe. The warblers did not feed heavily on seeds, and thus probably profited marginally if at all from them. One might be somewhat at a loss to explain this strong hostile response, which obviously detrimentally affected the warblers' foraging efficiency, if one had conducted the study only during the one winter of the three that I devoted to this system. Mast years of longleaf pine occur every six years or so (Wahlenberg 1946).

Gradations over a somewhat longer time scale, or with highly mobile species, may result in striking population changes, which in turn are bound to affect interactions, and consequent food choice and foraging patterns as well. Sustained spruce budworm outbreaks, sometimes lasting a few years, produce marked shifts in the abundance of their predators. Three-fold increases in numbers of warblers and other insectivorous species may occur during budworm years, as revealed by comparing Kendeigh's (1947) censuses during a budworm outbreak at Lake Nipigon, Ontario, with those of Snyder (1928) and Sanders (1970) when few budworms were present. Aggressive behavior does not disappear during an outbreak, even among the budworm specialists, the Bay-breasted (*D. castanea*) and Cape May (*D. tigrina*) warblers. These interactions might even be responsible for the declines in numbers of some species at this time, such as Blackburnian Warblers (*D. fusca*).

Foraging shifts may occur over shorter periods, also. Foraging may change during the course of a "normal" breeding season under equilibrium conditions, as in the activities of female spruce-woods warblers during the incubation period and at other times. At incubation time, the females forage at an unprecedentedly rapid rate, which probably affects the types of substrates used, their efficiency of using them, and the abundance of resources required for success. This contingency comes about because the females perform all of the incubation and also must hunt for themselves, resulting in an intensity of foraging unmatched at other times (Morse 1968).

Major changes may even occur over the period of a day. Holmes et al. (1978) found that the American Redstart (*Setophaga ruticilla*) changed its frequency of flycatching strikingly over the day, a shift correlated with the activity of its insect prey. Early in the day, while it was cold and the number of flying insects low, redstarts remained relatively inactive and did little fly-

catching; as it became warmer and the day drew on, flycatching became the prevalent technique. This type of shift in foraging behavior may be widespread in flycatching species. I have observed a similar pattern in Yellow-throated Warblers (*D. dominica*) (Ficken et al. 1968), which concentrated their activities on insects hiding in old pine cones during the cold of the early morning, but reverted to flycatching as the air warmed on early spring mornings and insects became active.

The social environment may affect the foraging patterns of these birds as well. Members of mixed-species foraging flocks exhibit this relationship especially clearly (Morse 1970). Members of socially subordinate species shift their foraging patterns in the presence of dominant species, and this change should affect the resources available to them. Even more important for many species are intraspecific dominance patterns (e.g., Black-capped Chickadee [*Parus atricapillus*], Glase [1969]). The effects of both interspecific and intraspecific flock relationships often shift over a period of minutes, and the results that one obtains inside and out of flocks may also differ markedly.

The tendency to participate in a mixed-species foraging flock may itself depend on food considerations, or perhaps predator avoidance is of primary importance. Social groups may also shift in character as a consequence of changes in climatic conditions. For instance, on warm winter days members may leave the groups, usually to take up a territory. The largest species, presumably the least vulnerable to surface-volume ratios of heat loss, quit the flocks first during warm stretches of winter weather (Morse 1978a).

Weather can strongly affect foraging patterns in other ways. Wet foliage may be one of the most serious factors for foliage gleaners, and the conclusions that one draws from observing foraging on wet and dry foliage may differ markedly. Carolina Chickadees (*P. carolinensis*) (Morse 1970) shifted from foliage-gleaning to large-limb hunting during rainy periods in the winter, thereby sparing their plumage from the wet foliage. Since the temperatures during these observations were near freezing and were preceded by freezing temperatures, these foraging shifts are unlikely to result from insect movements.

The problem of wet foliage assumes fundamental importance during the stormy weather that sometimes occurs while spruce woods warblers are incubating or feeding nestlings. They are extremely vulnerable to the loss of nestlings at this time (Morse 1971a, 1976a, 1977), and they, too, concentrate their foraging away from wet foliage, using areas such as the inner parts of branches, where most of them seldom forage at other times. This shift may also affect the one

species that normally uses these areas most frequently and might therefore appear least vulnerable, the Yellow-rumped Warbler. Being the most subordinate of the *Dendroica* warblers in these communities, one might expect the added interactions to affect them adversely. More work needs to be done on the wet-foliage problem (also see Morrison et al. 1987a), but it is often difficult to gather these observations. Students of foraging tend to gather foraging data only on good days, and even if those data accurately portray the usual foraging patterns, they probably do not adequately represent the "crunch" situations. Birds may forage most efficiently when the foliage is dry and may even lack strong adaptations for the wet conditions, which could be so severe as to obviate the possibility of feeding young, anyway. If so, the birds are playing a game of chance during the breeding season, in which the odds favor escaping these extremely inclement conditions in any given breeding season.

#### VARIABILITY AMONG THE MEMBERS OF A POPULATION

Members of bird populations are not homogeneous in their characteristics, which leads to predictions of differences in foraging patterns and possibly in food secured. This must be considered in any study program. Size varies profoundly within species of many animal groups; for instance, as foragers, most fishes or salamanders vary over several orders of magnitude of mass during a lifetime (Werner 1977, Fraser 1976). The case of metamorphosing anurans, which shift from herbivorous to carnivorous existences at metamorphosis, is even more dramatic.

In contrast, within-population differences of birds are modest; indeed, with few exceptions passerine birds do not become foragers until they have reached full size. Even so, a number of ecologically significant differences in foraging occur regularly within bird populations, and they may turn out to be commonplace. I will consider two, male-female differences and adult-immature differences. Note, too, that dominance-related differences often have a size- or age-related element.

Male-female foraging differences may seem most likely to occur in association with marked sexual dimorphism. Differences in foraging repertoire between male and female Hispaniolan Woodpeckers (*Centurus striatus*), in which males and females differ in beak length by over 20% and tongue length by nearly 35% (Selander 1966), are thus not surprising. However, marked between-sex foraging differences are not confined to strikingly dimorphic species. They occur among monomorphic male and female spruce-woods warblers during the breeding season (Morse 1968), with males foraging higher in the

vegetation than their females. The male heights matched their display heights more closely than those of the nest sites. Female foraging heights, in contrast, resembled nest heights more closely than male display heights. Only the females incubate. Others have subsequently found similar differences in several warblers (e.g., Sherry and Holmes 1985) and in vireos (Williamson 1971). Perhaps the most interesting example is that male Black-throated Blue Warblers (*D. caerulescens*) forage lower than their females, a difference that is associated with a tendency to display in open areas below the canopy (Sherry and Holmes 1985). Thus, an adequate display site, rather than height alone, seems to be the governing variable in this partitioning.

Adults and immatures may differ in foraging success, a likely consequence of the difficulty of learning how to forage. Such differences may not be apparent in most species; however, if they involve particularly difficult foraging repertoires, significant differences in success rates as well as in foraging patterns, foraging time, or items caught may exist. These differences have been reported for various seabirds (Ashmole and Tovar 1968, Orians 1969a) and wading birds (Recher and Recher 1969). I do not know of similar examples among territorial species of small birds. However, passerine fledglings learn by trial-and-error and narrow their foraging repertoires in the process (e.g., Davies and Green 1976). Further, heavy mortality often occurs at this time (e.g., Lack 1966), probably largely due to the inefficiency of foraging by these birds as they become completely independent. Consequently, although brief, this period may be one of fundamental importance and involve some of the most critical foraging decisions of a lifetime.

Thus, a diverse range of variables may affect the foraging patterns of birds. Not all will be of concern to each individual or at all times. Part of the challenge involves determining when such variables constrain success and when they do not. Knowledge of them and when they apply can provide insight to major fitness considerations.

### OPTIMAL FORAGING THEORY

These niche-related studies differ from those of basic food-choice and foraging strategies. The latter type of work follows from the recent popularity of optimal foraging theory, the proposition that animals forage in a way that optimizes their success. In practice, workers usually substitute "maximize" for optimize, and energy gain per unit time for success, and implicitly use foraging success as an estimate of fitness. This work operates at the level of the individual, albeit with strong population implications.

Most of these studies are really not tests of optimal foraging theory (Krebs et al. 1983, Pyke 1984). Rather, they state whether their results are consistent with the predictions of a particular model, even though they may claim to do more. Nevertheless, these studies are of importance here, because my main concern is food choice and foraging behavior at the individual and population levels, rather than testing theory. These studies, as well as the more direct tests, reveal a variety of complications at the individual level, also. The first optimal foraging theory models were simple ones with no constraints and, depending on whose interpretation one accepts, were either quite successful (e.g., Pyke et al. 1977) or not very successful (Gray 1987). Quantitative predictions often were only approximate, suggesting complications. These deviations from theoretical predictions are generally attributed to constraints not built into the models, including inadequate memory, predator-avoidance, competition, dietary constraints, morphological constraints, and risk-minimizing. The nonconformities should not be surprising, but are of interest because they provide possible insight into the food and foraging problems discussed above, and their resolution may help to predict which species can prosper in different situations. Here I will put these studies into the context of food exploitation and suggest how to relate them to niche theory studies.

For these purposes one may divide optimal foraging theory studies into those concerned with diet-choice and those concerned with patch-choice. Patches deal directly with the use of space, which equates them somewhat with the niche relationships I have already discussed. Diet studies deal directly with food acquisition, rather than substrates exploited. Foods are ranked according to their energy value to the foragers, and foragers are expected to take only those items that will improve their overall energy balance (reviewed in Pyke et al. 1977). This general pattern often holds, although foragers frequently take items relatively low in value more often than predicted (e.g., Krebs et al. 1977). Krebs et al. attributed this deviation to the birds sampling the environment in a way that favored a long-term strategy; that is, obtaining information on food characteristics for possible future use when conditions have changed, such that these items might assume high positions on the birds' list of preferences. This simple model does not take into account such problems as memory; knowledge of the intricate detail necessary to make perfect choices; the problem that items are often discovered sequentially, rather than simultaneously, in many sorts of foraging situations; or the substantial hunting times required to find cryptic organisms, which will enhance the probability

that most cryptic items, once found, will be taken despite an otherwise low value. Cryptic organisms are less likely than others to require substantial handling times or special physical abilities to exploit, which would further favor eating them once discovered.

This simple approach thus brings several problems with it. However, my purpose here is not to critique simple optimal foraging theory models, but to show that difficulties in fitting results to models indicate the existence of variables of basic importance. This work exposes a deficiency of understanding about foraging and related factors. Problems of learning and manipulation have received considerably more attention, primarily from the psychologists. It is in this area between experimental psychology and behavioral ecology that the lacuna exists (Kamil and Sargent 1981).

Patch-choice studies make similar predictions, but relate to aggregation of food items in space and strategies necessary to exploit them with maximum efficiency. Distances between patches, sizes of patches, and the like will have major effects upon decisions to move. If the forager has incomplete information on the alternatives available, this deficiency will complicate the result. Many of the same variables as those associated with diet choice will affect the patch-choice decisions made.

Several other optimality problems, such as optimal flock participation, are related in varying degrees to food choice and foraging. However, they tend to incorporate parts of the diet and patch-choice considerations, or play off food-patch contingencies against other demands such as reproductive considerations and social relationships, and therefore I will not discuss them.

Food availability differs considerably in its predictability, which confounds the probabilities of accomplishing feeding or foraging "goals." Birds require a high minimum energy input, and it may be necessary for them to adopt foraging strategies that incorporate this constraint. The alternatives are often referred to as risk-prone and risk-averse. When food is the critical variable, starvation is the crisis that they must avoid. Life cycles will be heavily influenced by the patchiness of the environment as well as the abundance of resources. Risk-prone and risk-averse strategies assume major importance with high temporal variation in foraging conditions. If predictability of finding food is low, but overall resource availability is adequate to support the individuals present, individuals should adopt a risk-averse pattern; that is, they should use techniques that minimize the probability of starving because of an inability to locate food within the habitat. Strategies might include flocking, in which many eyes search for the occasional large reward that might feed all of the members of the

flock. (If an individual cannot defend such an item, one need not invoke group-selective advantages for this system to operate.) However, if the average food availability is inadequate to feed an individual, it pays to play a risk-prone game (if one cannot leave the area). If one adopted a risk-averse strategy "successfully," the inevitable results would be starvation. A risk-prone strategy gives it a chance to survive and should be adopted by individuals in imminent danger of starvation. Indeed, the behavior of some individuals suggests that this is the case; at least, traits such as predator avoidance may largely disappear at this time. Whether their disappearance constitutes more than a physiological consequence of poor body condition is not always clear.

Risk assessment is a relatively new area of interest in foraging, and has not been developed extensively for ecological problems. However, Caraco (1981b), Clark and Mangel (1984), and others have studied it from the viewpoint of winter flock participation. Foragers may also adopt similar strategies in comparable, if not so extreme, situations. Moore and Simm (1986) reported that migrating Yellow-rumped Warblers adopted a risk-prone strategy when rapidly fattening, choosing variable rewards over constant ones of the same average abundance, consuming more items in a foraging bout, handling them more rapidly, and selecting especially profitable ones. However, upon attaining maximum body mass, they shifted to a risk-averse strategy, selecting predictable rewards rather than unpredictable ones of the same average abundance.

Diet-choice, patch-choice, and predictability thus all appear likely to play a major role in determining the food-choice and foraging strategies adopted by birds. The general guidelines of optimal foraging theory may provide a good framework from which to start, recognizing that the goal is not to test optimal foraging theory, but to use it as a tool to generate testable hypotheses about food and foraging choices.

These optimal foraging theory studies thus help to identify the spatial and temporal patterns and mechanisms by which animals obtain food. In turn, they should provide insight into how populations and communities are composed if food is a limiting resource.

## FITNESS

Optimal foraging theory rests on the assumption that animals foraging as predicted maximize their fitness. Foraging animals may satisfy this assumption, but it is short-sighted to treat energy gain, or some other measure of foraging success, as an adequate or sufficient estimate of fitness, because it is an extremely indirect estimate. The behavior in question is often separated from



eventual fitness payoffs by the better part of a life cycle. Considerable question exists, for example, about whether the strongest selective pressures occur in the winter or summer. Several workers have argued that winter is the critical time for some permanent residents (Lack 1966, Fretwell 1972), and this may hold for some species that remain at high latitudes. But, the question of payoffs will only be resolved in terms of reproductive success, and since the breeding season is remote from the time at which winter crunches occur, the matter may receive little attention. Lifetime fitness is what matters. If individuals survive several breeding and winter seasons, these periods all have to be taken into consideration, which makes isolated bouts of foraging behavior difficult to evaluate. It seems impossible to demand such information routinely, but the central nature of this assumption must be recognized. Lifetime fitness information, especially that put in the context of foraging repertoires or success, is virtually lacking; in fact, only a few studies of lifetime fitness have been made (Clutton-Brock et al. 1981, Arnold and Wade 1984). Birds, as iteroparous, supra-annual, highly mobile and often migratory animals, present especially difficult problems, but even partial tests, such as comparing the relationships of high foraging success at certain times with reproductive success, would advance foraging studies to a more critical level. If foraging considerations were not correlated with reproductive success, assumptions made in optimal foraging theory studies, and in niche-level studies as well, would have to be re-evaluated.

Grant (1986) has found that factors associated with feeding play a dominating role intermittently in the survival and consequent fitness of Darwin finches during serious drought periods. He also demonstrated that finch populations underwent strong directional selection at this time. However, if directional selection occurred then, one wonders what other factors normally act to produce a population not maximally adapted to these drought conditions in the first place. Other forces may dominate through the rest of their lifetimes, and possibly in ways that counter this feeding-related advantage of certain individuals (large beaks that facilitate feeding on seeds that smaller beaks cannot crack). If different forces really do act at different times, one should be very careful in interpreting optimal foraging theory results.

#### INTEGRATING FORAGING THEORY AND NICHE THEORY

Little effort has been made to integrate niche theory and foraging theory. My suggestions are largely based on Werner (1977), who used op-

timal foraging theory techniques to derive predictions about niche relationships and coexistence among three centrarchid fishes (bluegill [*Lepomis macrochirus*], green sunfish [*L. cyanellus*], and largemouth [*Micropterus salmoides*]).

Werner constructed cost curves of prey under controlled laboratory conditions, using data from the pursuit time, handling time, and capture efficiency of several food items by different-sized individuals of the three predatory species. Using estimates of resource distribution and abundance from the field and calculating cost-benefit ratios from the prey capture—handling data and caloric estimates of these prey—he set boundaries on the predators' predicted niche dimensions (food-size axes). The fishes' shapes and sizes affected the results strongly. These results can be matched against predictions from species-packing theory (niche overlap), thereby facilitating the introducing of food-exploitation patterns into predictions of community structure. Species-packing theory (MacArthur and Levins 1967, MacArthur 1972, May 1973) addresses the problem of how closely species can be fit into a community if sustained on one principal resource axis.

Werner's technique allows insight into mechanisms that drive community-level organization, and provides a link among morphology, efficiency of resource use, and overlap in resource use. Werner's food-size axes predicted the presence and abundance patterns of these species well; typically small lakes supported two of the three species, the smallmouthed bluegill and the largemouthed bass; the intermediate species' (green sunfish) absence was usually predicted. The latter species was uncommon and coexisted only by habitat segregation. The bluegill and bass totally overlapped in habitat, but were complementary along the food-size axis; the green sunfish strongly overlapped the other two species on the food-size axis, but where it coexisted it was largely confined to a shallow fringe of habitat along the shore that was seldom used by the other species.

I will not discuss Werner's procedures in detail, because they are unlikely to be useful for food studies of birds. Gleaning species of birds may expend considerable time and effort in finding individual food items, so that once they are found, they will probably be taken. Selectivity of discovered prey items should thus not be as high as for consumers with relatively low searching costs, like sunfishes, although specialized hunting procedures could lead to a food intake unrepresentative of the standing crop. Nevertheless, it may be profitable to adopt an approach analogous to Werner's, especially to explore patterns of coexistence among closely related bird species, or for ecologically similar members of a community. Comparisons of species groups ex-

hibiting high (spruce-woods warblers) and low (*Empidonax* flycatchers) levels of coexistence would assume particular interest.

Since birds do not share the complications of the tremendous intraspecific size variation seen in fishes and in many other animal groups, they have an important compensating advantage for studies conducted at a population or community level. If birds concentrate on a relatively few food types, as my Yellow-rumped and Black-throated Green warblers did (Morse 1976a), the problem of modeling efficiency may be tractable. Approximate energetic costs of different activities are known for several birds (e.g., King 1974), and can be readily estimated. Holmes and his colleagues (Holmes and Sawyer 1975, Holmes et al. 1979a) have estimated energy expenditure of several northern passerines. Their results suggest that it would be feasible to concentrate on the foraging strategies of different co-occurring species and to generate cost curves for exploiting the various stations recognized in bird foraging studies. These curves would be based on food availability and foraging efficiency (the major problem) in different sites and, similar to Werner's curves, could be used for predicting the presence or absence of species. Measuring food intake would constitute the most difficult aspect of such a study, but the procedure nevertheless warrants serious attention.

If one can establish the conditions under which species coexist, it should be possible to focus on which situations are the limiting ones and how they act in limitation. This approach should also provide insight into the conditions that permit the insinuation of non-equilibrium species (Bay-breasted and Cape May warblers among the spruce-woods *Dendroica*), as well as why some equilibrium species decline at these times.

Werner recognized foraging generalists and specialists, and habitat generalists and specialists, in his fish community. Members of bird communities also clearly differ in this way (Morse 1971a, 1977, 1980a). Some bird species may even differ in their tendencies to specialize or generalize along different foraging axes, thereby presenting potentials for segregation (Cody 1974, Ulfstrand 1977, Morse 1978a). For instance, the participants of English mixed-species foraging flocks that I studied (Morse 1978a) varied in relative specialization and separation from each other along dimensions of foraging substrate (e.g.,

limb, twig), height, and tree species. In contrast, species-poor North American flocks did not clearly separate along a tree-species gradient (Morse 1970). Thus, bird communities offer many opportunities for disentangling problems of niche complementarity and coexistence.

#### SYNTHESIS

Integration of work done at different organizational levels (community, population, individual) is needed to maximize advance in the understanding of food exploitation. Studies of niche-partitioning, as it relates to foraging, are well developed in their basics, although often suspect in light of questions about resource limitation or competition. They require considerable attention, however, to accommodate a wide range of variables in ways that focus attention on foragers at the level of the individual, in this way reflecting the action of selection. In that sense, a substantial part of the work needed might be considered corrective. In particular, this work needs to be focused toward periods of unusual demands or want, the "crunches" of Wiens (1977).

Although optimal foraging theory itself is not concerned with the mechanisms by which foragers make choices, it addresses foraging problems at a level that draws attention to these matters. An understanding of these mechanisms seems vital to comprehending fully the decisions that determine resource exploitation patterns and why some apparent options are exercised and others not (morphogenetic and phylogenetic constraint). Optimal foraging theory also addresses questions at a level that permits one to relate the behavior to fitness, a subject in great need of attention, both as it relates to foraging and to other problems. By doing so, it may be possible to start piecing together the events and interactions taking place in a community in a way that will reflect the action of initial selective pressures, adjustments to them, and possibly, evolutionary change.

#### ACKNOWLEDGMENTS

I thank W. M. Block, M. L. Morrison, S. D. Openheimer, and J. C. Robinson for commenting on the manuscript. The National Science Foundation has supported much of my work on warbler foraging and mixed-species foraging flocks.