Studies in Avian Biology No. 13:38–43, 1990.

FOOD AVAILABILITY FOR AN INSECTIVORE AND HOW TO MEASURE IT

HENK WOLDA

Abstract. Insect availability is defined as abundance of potential prey items within the microhabitat used by a bird searching for food. Whether an available insect is actually eaten depends on its probability of being detected, its acceptability, and its chances of being pursued, captured and eaten. Availability can be measured by determining (1) the detailed hunting technique of the insectivore, especially selection of microhabitats when searching for prey; (2) identity of potential prey items; and (3) abundance, or changes in abundance, of potential prey insects in appropriate microhabitats. Ideally one may want to monitor absolute abundance of insects, as this provides the most reliable information. However, depending on diversity of prey items and available funds, a more general standard insect collecting technique may have to be adopted. This may be adequate, provided it is carefully selected to focus on microhabitats and insect species used by the insectivore. It is advisable to analyze insect samples at a sufficiently detailed taxonomic level, usually the species level. By pooling preferred species with their non-preferred congeners, a very distorted picture of the abundance and changes in abundance of potential prey items may be obtained.

Key Words: Insectivore; insect availability; prey selection.

As is testified by a large body of literature, availability of food plays a crucial role in the dynamics of natural populations. To understand quantity and composition of an insectivorous bird's diet, to grasp the problems of food preference, prey capture rate, and the effects of food on population dynamics, "availability" of food items is a suitable standard against which performance of a bird can be judged. Typically, researchers identify the items in the diet of a bird and determine availability of those items in the environment.

What exactly is "insect availability" and how can it be measured? Many techniques exist to determine relative or absolute insect abundance (Southwood 1980; Cooper and Whitmore; Dahlsten et al.; Majer et al., this volume). Selection of a suitable technique is a crucial first step in undertaking a study of food availability in insectivorous birds. My objective here is to concentrate on general problems of data interpretation, particularly on how this interpretation is facilitated by better analyses of insect samples.

AVAILABILITY

Various definitions of availability can best be reviewed in the light of a simplified, generalized sequence of steps in the capture of an insect prey: (1) the insect is present in the general area; (2) it is encountered by a bird (i.e., it occurs in a suitable microhabitat and within reach of the predator); (3) it is detected; (4) it is accepted by the bird as a potential prey; (5) it may then be pursued; (6) captured; (7) finally classified as an acceptable food item; and (8) eaten. Some researchers equate availability with presence or abundance of insects in the environment (step 1) (e.g., Earlé 1985, Blancher and Robertson 1987). Some even take catches by a light trap, sweepnet, sticky trap, Malaise trap, or some other general collecting device as a measure of insect availability (e.g., Sinclair 1978, Hutto 1981a, Laurenzi et al. 1982, Turner 1983, Murphy 1986, Lack 1987, Hutto, this volume). At the other extreme, availability of food has also been defined as "food obtained" (step 8) (Van Dijk 1986), defeating the purpose of the concept. Webster defines "available" as "usable, handy, accessible" (Guralnik 1970), suggesting that availability should not be synonymized with mere presence or abundance (cf. MacFadyen 1962, Hutto 1981a).

The definition suggested here is based on step (2) in the above sequence: "Insect availability is the abundance of potential prey items in microhabitats used by an insectivore when searching for food." The crucial terms here are "potential prey items" and "microhabitats used."

Not all insects are necessarily potential prey items to a given insectivore. A bird may take some kinds of insects regularly, others only occasionally, some at certain times or under special circumstances, and others never. The latter category, once established, can be excluded from an investigation. All other insects, whether common or rare in the insectivore's diet, classify as "potential prey." In a given habitat insects may occur in a variety of microhabitats. An insectivore may not search for prey in all microhabitats and those in which it does search may not be visited with equal frequency (Hutto, this volume). Thus, many insects in the environment may not be available, and those that are tend to have different probabilities of encounter. Only insects occurring in the "microhabitats used" by a bird should be classified as "available."

Any study of food availability must be based on a thorough analysis of the bird's feeding ecology, that is, the spectrum of its hunting techniques, the distribution of its searching activities over available microhabitats, and the kind of insects taken as prey (Hutto, this volume). A possible dependence of those parameters on weather, season, abundance of conspecifics, competitors, or prey species needs to be determined (Brennan and Morrison, this volume). For a proper understanding of the interactions between an insectivore and its potential prey items, knowledge of the ecology and behavior of those prey items is also essential.

The eight steps outlined above in the sequence of predator-prey interactions can often be quantified (e.g., Morrison 1980) and the probabilities involved determined. Any differences in those probabilities among potential prey taxa affect the relation between the insects available and the diet of the bird.

Measuring Insect Availability

To measure availability of potential prey to an insectivore, one must determine: (1) hunting behavior of the bird in sufficient detail to estimate relative frequencies of its visits to various microhabitats of the area (e.g., Greenberg and Gradwohl 1980, Morrison 1980, Airola and Barrett 1985, Holmes and Recher 1986); (2) identity of potential prey species; and (3) abundance, or at least changes in abundance, of those species (e.g., Madden 1982) in appropriate microhabitats. If abundance measures cover an area larger than the microhabitats used by birds, estimates must be obtained of the proportion of insects that live in those microhabitats. This procedure should be repeated to document spatial and temporal changes in insect abundance and bird activity (e.g., Tinbergen 1960, Davies and Green 1976, Laurenzi et al. 1982, Waugh and Hails 1983, Greenberg 1987b). Birds can be very flexible and may use different techniques for different insect prey, which adds to the complexity of the study (Davies and Green 1976).

One can study insect availability on a variety of levels. One can try to determine: (1) absolute abundance of each potential prey species in the appropriate microhabitats, to provide the best possible data; (2) relative abundance of potential prey species in the appropriate microhabitats (not as reliable as absolute abundance, but adequate if used with caution); or (3) relative abundance of higher taxa of insects, such as families or orders, or of all insects combined irrespective of taxonomic affinity, rarely permitting sound conclusions.

Absolute Abundance

Many techniques are available to measure absolute abundances of appropriate life stages of various insect species (Southwood 1980). In spite of many problems (e.g., Avery and Krebs 1984, Mallet et al. 1987), absolute abundances usually can be estimated with an acceptable degree of accuracy. In the case of polyphagous insectivores, and many are, several insect species must be studied simultaneously. Obtaining estimates of absolute abundance of each is difficult and labor intensive, but not impossible (Tinbergen 1960, Klomp 1966). However, if many potential prey species are involved, measuring absolute abundances can exceed logistic and financial means. One must then rely on measures of relative abundance and of changes in abundance.

Relative Abundance

Relative abundance of an insect species can be estimated by a suitable standard technique (e.g., pitfall traps, sweepnets, light-traps, transect counts, suction traps; Southwood 1980; Cooper and Whitmore, this volume). Selection of a technique depends on behavior of both birds and prey. However, such techniques may collect from microhabitats that do not overlap with the hunting microhabitats of a bird (Hutto, this volume), so caution in the interpretation of changes in insect abundance observed in samples is in order, and estimates of the distribution of the insect among microhabitats may be needed.

Capture rates of an insect species may not be constant. They may vary seasonally (Rose 1972, Masaki and Walker 1987), in relation to weather (e.g., Avery and Krebs 1984), or as a result of changes in condition of the insects concerned. Gravid females may fly less or not at all and thus not be caught by a method that captures only flying insects (Rose 1972), with the result that catches suggest a diminished general abundance when none occurred. Similarly, seasonal movements and seasonal changes in activity patterns, such as diapause, may bring an important part of the population into or out of reach of the monitoring technique used (Wolda and Wong 1988). This may be precisely what one needs. If a bird takes only flying insects, a decrease in insect abundance is real to that bird, whether the insects disappeared from the area, or a large part of the population stopped flying. In other cases such apparent but nonexistent changes in insect abundance cause confusion.

Some species are far more prone to be captured by a given technique than others, so that relative abundances in a sample may contain little or no information on relative abundances in the field (Cooper and Whitmore, this volume; Hutto, this volume). This problem can be overcome by calibrating the collecting technique with simultaneous measures of absolute abundance. Tinbergen (1960) showed the feasibility of this by measuring abundances of several caterpillar species in a pine wood with frass collectors. Frass pellets were identified to species and instar. These data could be used to estimate absolute abundances, because they were calibrated by simultaneously measuring the densities of caterpillars, by species and instar, on the trees.

Grouping Species Into Higher Taxa

Counting or weighing insect samples as a whole, or after classification to higher taxa, is far easier and much less time consuming than classifying them at the species or morpho-species level, which makes the procedure very popular. This is understandable because of limited time and funds. But for reasons given below, I am convinced that in most cases studies of insect availability are irrelevant unless analyses are done at the (morpho-)species level.

SELECTIVITY OF SAMPLING TECHNIQUES

Insect collecting techniques differ in their efficiency in capturing a given species and this efficiency varies among species. As a consequence, the relative frequencies of insect species in a sample depends on the collecting techniques used (e.g., Fenton and Howell 1957, Mikkola 1972, Tallamy et al. 1976, Service 1977, Dowell and Cherry 1981, Zelazny and Alfiler 1987, D'Arcy-Burt and Blackshaw 1987, Mizell and Schiffhauer 1987, Cooper and Whitmore, this volume, Majer et al., this volume). It is doubtful that any collecting method can produce an unbiased picture of the faunal segment under study (Cooper and Whitmore, this volume; Hutto, this volume; Majer et al., this volume). If the nature of the bias is known, correction factors can be applied, as is done for suction-trap samples (Taylor 1962) and a few other cases (Weseloh 1987). Normally, however, both direction and magnitude of bias are unknown. Relative abundances of the species in a sample may have very little predictive value for those in the field.

ESTIMATES OF TOTAL ABUNDANCE FROM SAMPLES

Because relative abundances of species in a sample may have little relation to relative abundances in nature, they provide unreliable estimates of total abundance. For example, a hypothetical fauna of 10,000 individuals comprises five equally abundant species, A–E (Fig. 1). A given collecting effort obtains a sample of 100 individuals, among which the five species are unequally represented because of different capture probabilities. One species (A) was not captured at all, while another (E) made up 60% of the sample. (Such differences in capture probabilities are probably commonplace.) If any of these five species increases fivefold, from 2000 to 10,000 individuals, the total fauna increases to 18,000 individuals. How this would be perceived in the sample, however, depends on capture frequency (Fig. 2). Here increase in total number of individuals varies from 0 to 240%, depending on which of the five species increased. If individual species were not counted separately, the sample would present a very distorted picture of the natural situation. One can make the model more realistic by allowing some species to increase and others to decrease. A real increase in the total fauna might then very well translate to a decrease in the number of individuals in a sample and vice versa. Unless samples are analyzed at the species level, conclusions about abundance are likely to be erroneous.

THE INSECTIVORE'S VIEW

An insectivore is likely to be at least as selective as an entomologist (Hespenheide 1975, Belwood and Fullard 1984, Sörensen and Schmidt 1987). Probabilities of encounter, detectability, or acceptability are usually different for different insect species. In Figure 3 I show the same hypothetical fauna used in Figure 1. Species are arbitrarily assigned different distributions in the habitat such that different proportions of populations occur in the correct microhabitat and, accordingly, have different probabilities of being encountered by a bird. This results in an "available" fauna different from the total fauna. Similarly, among-species differences in probabilities of being detected and being accepted result in detected and accepted "faunas" with a species composition that is very different from the fauna as a whole (Fig. 3). Diet composition, affected by still more probabilities, may be different again.

A faunal increase of 80%, from 10,000 to 18,000 individuals, with only one of five equally abundant species increasing fivefold (as in Fig. 2) is perceived by a bird as an increase in the number of acceptable prey items, which varies from 0% to 250% depending on which species experienced the increase (Fig. 4). Again, if insects are analyzed at the species level, data provide an accurate picture of which species underwent an increase. If not, the apparent relationship between diet and fauna may be difficult to explain.

SELECTION OF COLLECTING TECHNIQUES

The central problem in selecting a collecting technique is to determine both distribution and abundance of potential prey items. With a collecting technique that monitors potential prey only in appropriate microhabitats, one could directly measure availability, or changes in availability. Some instances seem to approach this

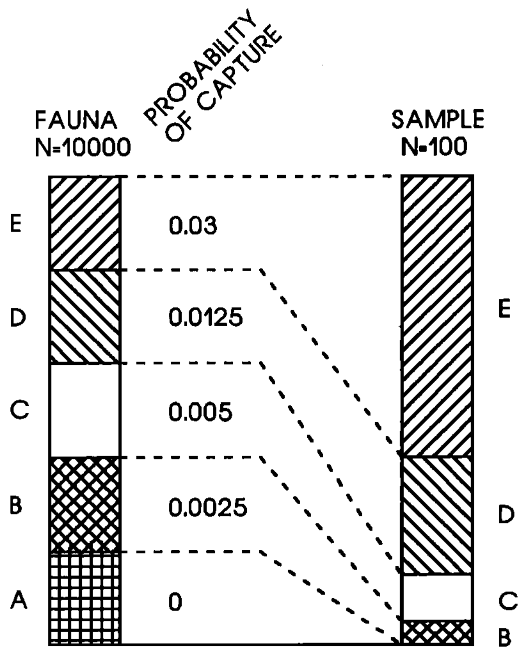

FIGURE 1. Effect of species-specific capture probabilities on the relative abundances of the species in an insect sample of 100 individuals taken from a fauna of 10,000 individuals consisting of five equally abundant species, A–E. Representation of a species in the sample depends on its capture probability.

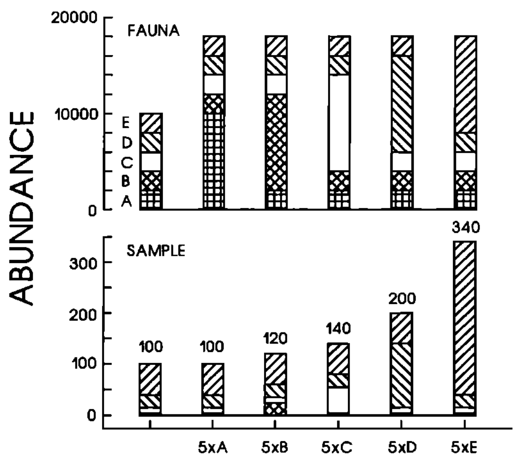

FIGURE 2. Effect of a fivefold increase in abundance of one species of the fauna of Figure 1 on total insect abundance in the fauna as well as that in the sample using the capture probabilities of Figure 1. How the real increase in abundance is perceived in the sample depends on the capture probability of the species that underwent the increase.

ideal. Birds specializing in insects that hide in aerial leaf litter are an excellent example (Rosenberg, this volume). Aerial nets placed at appropriate heights may directly measure availability of prey insects to predators of flying insects (Hespenheide 1975, Bryant and Westerterp 1981, Quinney and Ankney 1985, Hussell and Quinney 1987). Visual inspection of foliage in the understory of a forest may approximate availability of insects for an understory foliage gleaner (Graber and Graber 1983, Karr and Brawn 1988). Often, however, such direct measurements of insect abundance in the correct microhabitats are impossible. In such cases one should select the monitoring technique that comes closest to that ideal, and one that does not select against species important to an insectivore. A splendid example is given by Castillo and Eberhard (1983), who used artificial webs to measure insect prey available to a spider. Finally, one should attempt to calibrate abundances in samples against those in the field (Tinbergen 1960, Cooper and Whitmorte, this volume).

DETAIL OF TAXONOMIC ANALYSES

The level of taxonomic detail needed to analyze an insect fauna and the diet of a bird is determined by the ecology of both bird and insects. Insect taxa that are perceived identically by a bird can safely be pooled, if one can determine the bird's perception. Two species of flies may be alike in appearance, but if one concentrates in microhabitats used by the bird and the other does not, pooling their measures of abundance is unjustified. If they occur in the same microhabitats, but have a different probability of being captured, they are again not identical to a bird.

Whether "similar" prey from our standpoint are identical for a given bird can be determined only if their relative frequencies are determined both in the diet and in the suitable microhabitat. Initial classification into "potential prey" and "nonprey" items depends to a large extent on guesswork. If birds do not take ants, counting ants can be avoided. However, for many taxa the decision is not obvious. A bird may be known to take "small beetles," but it actually may take only a few kinds and avoid others.

When insect samples can be analyzed only at a coarse taxonomic level, extreme care should be taken to interpret the results. One should not expect changes in abundance in one set of species to be "representative" of those in another (cf. Hutto 1985b). In cases where previous studies have established that a bird feeds only in a well-defined microhabitat, takes only a certain category of prey, and does not discriminate among those items, an analysis at the species level is a waste of time. In general, however, one should

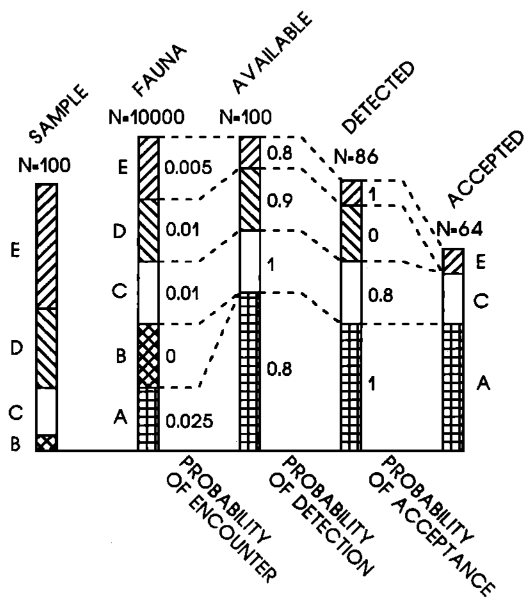

FIGURE 3. Perception of relative abundances of the five species in the fauna of Figure 1 by an insectivore, given species-specific probabilities of encounter, of detection, and of acceptance. Probabilities of pursuit, capture, and being eaten similarly affect the species composition in the diet, but are not included here for sake of simplicity. The sample "taken by the investigator" (Fig. 1) is given for comparison.

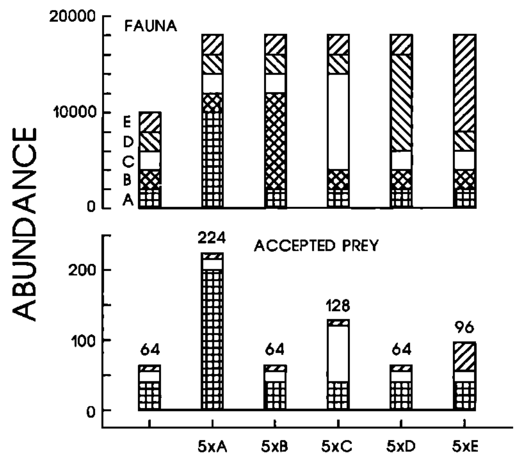

FIGURE 4. Effect of a fivefold increase in abundance of one of the species of the fauna of Figures 2 and 4 on total insect abundance in the fauna as well as that in the category of prey items acceptable to the bird (using the probabilities given in Fig. 4). How the real increase in abundance in the fauna is perceived by the bird depends on the (encounter, detection, etc.) probabilities of the particular species which underwent the increase.

err on the safe side initially and perform the analysis at as detailed a level as possible, preferably at the species level. Pooling of taxa can be done later, but splitting taxa requires a reexamination of the same samples.

In most cases, it is unnecessary to get too involved in insect taxonomy. With the help of an insect reference collection, using code numbers instead of names if convenient, one can classify individuals at a "morphospecies" or "operational taxonomic unit" (OTU) level. The goal is to work at the level of real species, but one should avoid getting bogged down in problems of sibling species or the analysis of genera that can be analyzed only by a specialist. If two individuals cannot be separated on relatively simple external characters, they can be classified as belonging to the same morphospecies. This facilitates the task considerably, and it can be accomplished even in diverse habitats. My assistants and I have been doing it for years in tropical forests in Panama. This procedure has the potential for errors of the kind mentioned above, but I believe its advantages outweigh the disadvantages. The advice of competent insect taxonomists is invaluable when deciding which characters to use in the classification.

A common objection to the (morpho)species approach is economical. However, lack of funds is no excuse for an unsound study. With proper planning, acceptable procedures can be designed that can be executed at a reasonable cost, and defended in grant proposals.

CONCLUSIONS

To obtain reliable results from studies of insect availability for birds, one must be prepared to take time away from birds and spend a considerable proportion of available resources on the insects. Simply putting up some sticky traps or taking some sweepnet samples, and then scoring insects at best at the ordinal level, is insufficient. It is preferable to estimate absolute abundances of potential prey insects. However, measures of relative abundance, using some carefully selected standard monitoring technique, may often provide sufficient information, especially when results are calibrated against field abundance. The more detailed the analysis of the insect samples, the more reliable and the more informative the results. If insects are tallied only at a coarse taxonomic level, the best one can hope for is that nonprey species do not dominate the sample to the extent that existing correlations between insect availability and bird performance are obscured. Loiselle and Blake (this volume) and Blake et al. (this volume) clearly demonstrate the need to classify fruits in birds' diet to the species level.

Whenever possible, one should take the analysis to the morphospecies level and pool species only if it is known that this can be done with impunity.

If, instead of one species, an entire guild of insectivores is under investigation, the situation becomes more complex. Different insectivores are likely to be different in hunting characteristics, and so are likely to have different values of availability, detectability, and so on, for each prey taxon. The overlap in insect taxa constituting "potential prey" and in "microhabitats used" may be small. Composition of the diet of a guild of insectivores is a complex, composite picture of selections made by the component species. Under these conditions an approach that does not distinguish among potential prey species is unlikely to produce useful results.

Trying to avoid problems introduced by an inappropriate collecting technique or a coarse taxonomic analysis by using a variety of techniques simultaneously may be self deception. The assumption that errors will cancel out (e.g., Fenton and Howell 1957) is wishful thinking. Executing a proper analysis of the importance of food for an insectivorous bird is a formidable but rewarding challenge.

ACKNOWLEDGMENTS

I am grateful to Jim Karr, David Manuwal and two anonymous reviewers for critically reading the manuscript.