

## MEASURING THE AVAILABILITY OF FOOD RESOURCES

RICHARD L. HUTTO

*Abstract.* To assess the role of food supply in the biology of forest birds, available food density must be measured with precision. In reviewing 155 recent papers that deal with the role of food supply, I found that most authors justify use of a particular sampling method by intuitive arguments and numerous assumptions. An intuitive approach may be inadequate, however, because (1) we do not perceive food availability in the same manner that birds do, (2) we ignore scale-of-measurement problems, and (3) we measure only standing crop. To avoid those potential problems, I suggest using quantitative measures of behavioral acts that are necessarily correlated with variation in food abundance as a “check” on the reliability of measurements of food availability. These might include a bird’s temporal and spatial attack rate, its mean stop-to-stop movement length, or the proportion of its daily time budget spent foraging. Future studies may be strengthened if such behaviors are used to confirm that a given measure of food availability is appropriate.

*Key Words:* Food availability; prey density; stomach contents; functional response; feeding rates; search tactics; time budgets.

### INTRODUCTION

Of biological parameters that might influence the evolution of adaptations among species, the distribution and abundance of food, predators, and mates are especially important (Krebs and Davies 1987). Virtually every aspect of the life cycle of an individual has been molded to some degree by those variables, as Crook (1964) began to demonstrate in his classic studies of social organization of weaver finches.

Information on food availability alone has contributed to our understanding of numerous life history characteristics and their population- and community-level consequences. The importance of food availability as a hypothesis to explain various biological patterns is reflected in the large number of studies that deal with this issue. For example, in a perusal of a dozen ecological and ornithological journals published since 1978, I located 155 articles on landbirds that dealt specifically with the relationship between food supply and several ecological patterns, including timing of annual cycles, territoriality, habitat selection and territory placement, diet, mating system, clutch size, reproductive success, population size, geographic distribution, and community structure.

The role of food supply in a few of those cases has become clear, either because of an unusual ability to measure food availability precisely (e.g., territoriality in nectarivores, or use of space by ground-feeding shorebirds and insectivores), or because of the ability to manipulate food supply experimentally (e.g., optimal foraging, or clutch-size experiments). The role of food in other arenas of investigation (e.g., timing or occurrence of various annual cycles) has become dogmati-

cally accepted, despite the lack of careful measurements of food resources. The role of food availability for still other (mostly population- and community-level) phenomena remains unresolved and controversial.

The inability to resolve whether food is important often results from difficulty knowing whether food availability has been measured adequately. Often these measures are of questionable relevance to the organisms involved. For example, several authors reported that food density and habitat use by raptors were not well correlated (Wakeley 1978, Baker and Brooks 1981, Bechard 1982), but vegetation structure was related to habitat use. Therefore, vegetation structure was deemed to be more important than food as a factor influencing habitat use, even though the importance of vegetation lay with its effect on food availability. In fact, after converting rodent density (as estimated from trap data) to rodent “availability” (as estimated by multiplying rodent density by the fraction of incident light at ground level), Bechard (1982) concluded that food availability was related to habitat use. If the researchers had measured prey availability as perceived by hawks at the outset, then the correspondence between food supply and habitat use would have been more readily apparent.

At the population level, Pulliam and Dunning (1987) argued that local population density of sparrows over a series of years was independent of food abundance, when abundance exceeded some threshold level. They based their conclusion on a lack of correlation between sparrow density and seed availability, as estimated by counting seeds that fell into small traps. How-

ever, seed traps may not accurately reflect food available to sparrows (especially in view of the unmeasured seed stores that must have been present in the soil). As these two examples suggest, measures of food availability undoubtedly have contributed to the conflicting results and disagreements that surround the more controversial arenas of investigation. Such conflicts have, consequently, led to pleas for greater care in the measurement of food availability (Wiens and Rotenberry 1979, Wiens 1983, Morrison et al. 1987b).

But how can we measure food availability in a biologically meaningful manner? Even if one samples selected prey types from a single microhabitat, the relative prey abundance between sites can differ significantly among sampling methods (Majer et al., this volume). To learn more about the factors that should be considered when measuring food availability, I searched through the current literature for patterns in the way biologists justify their sampling methods. In this paper, I synthesize results of this search, and suggest how we might begin to test whether our measures of food availability are appropriate.

## METHODS

After cataloguing the ways by which biologists measure food availability in the field, I chose to concentrate on the arguments given to justify use of a given measure. In addition to including some references published prior to 1978, I searched through all issues of *American Naturalist*, *Animal Behaviour*, *Auk*, *Behavioral Ecology and Sociobiology*, *Condor*, *Ecology*, *Ecological Monographs*, *Ibis*, *Journal of Animal Ecology*, *Journal of Field Ornithology*, and *Wilson Bulletin* published after 1978 for articles involving the impact of food availability on biology of landbirds and shorebirds.

I conducted field studies on the relationship between food availability and bird behavior in western Montana Douglas-fir (*Pseudotsuga menziesii*) forests in 1985 and 1986. In most coniferous forests of the western United States, the western spruce budworm (*Choristoneura occidentalis*) is the most widely distributed and destructive defoliator (Carolin and Honing 1972, Felin and Dewey 1982). It is also an important prey species for forest birds during the nesting season. The use of systemic insecticide implants (Reardon 1984) was tested in northwestern Montana in 1985 by USDA Forest Service personnel as a method to reduce foliage and cone crop loss. I watched groups of trees that contained both experimentally treated and adjacent untreated trees to discover whether artificially reduced budworm levels on treated trees would affect the probability of a bird visiting a tree, the length of a given visit, or a bird's feeding rate.

Thirty Douglas-fir trees were selected for experimentation by Forest Service personnel associated with the Northern Region Cooperative Forestry and Pest Management Division, and 15 of those trees were randomly chosen for treatment with insecticide implants

(Reardon 1984). I used 14 of their treated trees, their 15 control trees, and an additional 20 trees as controls, so that I sampled nine groups of five to seven trees. Each group had at least one, but no more than two treated trees. Three groups of trees were in Lubrecht Experimental Forest of the University of Montana [46°52'N, 113°27'W] within a mixed conifer forest that was dominated by Douglas-fir, and six groups were on Champion International Paper Co. land [46°48'N, 113°33'W] on a pure Douglas-fir site that was commercially thinned in 1980.

Trees were treated with implants on 18 April 1985, and I sampled late-instar budworm larvae on 29 June 1985 by clipping two or three 45-cm terminal branch tips from the lower to middle crown of each tree using a 9-m pole pruner affixed with a collecting bag. Contents were emptied into plastic bags and transported to the laboratory where I sprayed them with a pyrethrin-based insecticide to reduce the activity of budworm larvae. Branch samples were then placed on white cardboard, and foliage surface area was estimated by compacting foliage into the smallest single-layered space possible and measuring length and width of the area to the nearest cm. Each branch sample was searched carefully for budworm larvae and other arthropods, which were then removed and "rinsed" of debris in a wash bowl containing 70% alcohol before being dried through contact with a paper towel and weighed on an electronic balance to the nearest 0.01 g.

From one observation point, each group of focal trees formed a slight semicircle (concave toward the observer) and fell within a 120° arc. Consequently, all trees could be watched simultaneously for bird activity. The observer (myself or an assistant) observed for 90 min before moving to another group of trees. From 18 June to 1 July 1985, we recorded bird activity between 07:30 and 11:00. Observation times were rotated so that each group of trees was watched for 180 min during each half of the morning.

When a bird landed in an experimental tree, we recorded the tree number, time of day, bird species, duration of its stay in the tree (in sec), its activity (feeding, singing, or perching), and when possible, its foraging attack rate (recorded as number of pecks/sec of observation). On rare occasions, when several birds were present at the same time in a group of trees, we noted the identity of each visitor, and estimated the duration of stay for each bird.

In 1986, we studied avian foraging behavior in a Douglas-fir stand 5 km southeast of Missoula, Montana [46°50'N, 113°56'W]. The 5-ha site was traversed in a systematic fashion on a daily basis from mid-June through mid-July. An observer recorded the identity and height of every bird encountered.

## RESULTS AND DISCUSSION

### *Literature review*

*Food not measured directly.* Twenty percent of the authors did not attempt to measure food because their comparison obviously involved relatively food-rich vs. relatively food-poor conditions. For example, Tryon and MacLean (1980) interpreted the use of space by Lapland Longspurs (*Calcarius lapponicus*) in terms of food

availability, which was assumed to be greater at times of "cranefly pupation" and when "the tundra was aswarm with adult Diptera." Strehl and White (1986) studied reproduction of Red-winged Blackbirds (*Agelaius phoeniceus*) during years that had and years that did not have a periodical cicada outbreak.

*Food measured directly but relevance not addressed.* Forty-seven percent of the authors measured food density but made no explicit assumptions about relevance of their measures in terms of food availability. Their implicit assumptions were so reasonable that most of us would not think to question the measures. For example, Baird (1980) and McPherson (1987) measured fruit availability to frugivorous birds by counting fruits on trees in their study areas. Similarly, biologists who have studied nectar-feeding birds generally counted flowers but did not explicitly assume that such samples adequately reflected food available to birds (e.g., Carpenter and MacMillan 1976, Kodric-Brown and Brown 1978, Feinsinger and Swam 1982).

*Food measured directly and relevance addressed.* Twenty-four percent of authors took a simple measure and explicitly assumed that it was correlated with food availability. For example, after describing a vacuum sampling technique, K. G. Smith (1982) stated that his "meadow samples reflect actual abundances available to birds." Or, Blancher and Robertson (1987) trapped "flying insects between ground level and 1 m" because that height range represented food availability for Western Kingbirds (*Tyrannus verticalis*). Conner et al. (1986) stated that their sweep samples were not a direct measure of food for Northern Cardinals (*Cardinalis cardinalis*) but that they would "give a relative index of overall food availability." Dunning and Brown (1982) assumed that food resources available to wintering sparrows were "closely and positively correlated" with what they chose to measure: the quantity of precipitation during the previous summer.

*Food measured, then adjusted to be more relevant.* In still other instances (9% of the studies reviewed), researchers "adjusted" their measures of food density on the basis of some intuitive argument before making the explicit assumption that their adjusted measure accurately reflected food availability. Hutto (1980, 1985a), for example, derived an "adjusted insect density" by multiplying number of insects trapped on sticky boards by a measure of vegetation density. Adjusted density was assumed to be better correlated with food availability to foliage-gleaning insectivorous birds than was either flying insect density or vegetation density alone. Greenlaw

and Post (1985) determined the "food value" of Seaside Sparrow (*Ammodramus maritimus*) territories by multiplying volume of potential prey in each of several patch types by a factor that accounted for both relative use and relative abundance of that patch type within the territory. The most common adjustment, however, involved a refinement of food types considered on the basis of stomach contents of the bird species. For example, Bryant (1975a), Zach and Falls (1979), Smith and Anderson (1982), and Smith and Shugart (1987) eliminated prey types from the sample if they were not present in stomachs.

#### *Problems with current methods*

I cannot judge the accuracy of any of these methods but, clearly, no current method of measuring food *abundance* is immune to the criticism that it may be an unreliable measure of food *availability*. Baker and Baker (1973) warned that "the food density for shorebirds as revealed by ordinary sampling techniques is related to the food density experienced by the bird by some often complex functions or may be entirely unrelated." Their warning applies equally to forest birds (see Martin 1986, and Wolda, this volume). At least three categories of potential problems would apply to any of the sampling methods outlined above, as discussed next.

*We lack the bird's perception and do not know its feeding constraints.* Even for relatively simple fruit and nectar systems, all fruits or flowers may not be equally available (as assumed by simple counts). In general, sampling the "kind" of food a bird eats probably falls short of a meaningful measure because the animal's perception screens items in a manner that differs from that of a sticky board (Seastadt and MacLean 1979; Hutto 1980, 1985; Cody 1981), sweep net (Wilson 1978; Wittenberger 1980; Fischer 1981, 1983; Folse 1982; Laurenzi et al. 1982), vacuum cleaner (Craig 1978, K. G. Smith 1982, Smith and Anderson 1982, Ault and Stormer 1983), suction trap (Bryant 1975a, Holmes et al. 1978, Turner 1982), snap trap (Wakeley 1978, Baker and Brooks 1981, Bechard 1982), or visual count (Salomonson and Balda 1977; Holmes and Robinson 1981; Schluter 1982a, b; McFarland 1986a). Items will be sampled differentially because of mechanical and perceptual differences between a given sampling technique and a bird (Robinson and Holmes 1982, Heinrich and Collins 1983, Sherry 1984). Moreover, lacking a bird's perception, we do not know which prey items it would ignore because of the prey's crypticity (Janzen 1980a), inaccessibility (Kantak 1979, Moermond and Denslow 1983, Avery and Krebs 1984), difficulty of capture (Hespenheide 1973a),

mechanical defenses (Davies 1977b, Sherry and McDade 1982, Heinrich and Collins 1983) or chemical defenses (Eisner 1970, Janzen 1980a).

Some believe that these perceptual problems can be solved by adjusting sampling methods to match stomach contents. They reason that if the sample has the same prey types as stomach contents, the sample will be relevant. Although stomach contents can help refine one's definition of available prey types, differential digestibilities among prey types (Custer and Pitelka 1975), variation in times of collection, and differences between diets of adults and the young they feed will cause biases in the estimate of what the bird actually takes from the field. It is not a simple matter to determine a bird's diet. That issue aside, a mere listing of the contents of both stomachs and field samples to show that they are "more or less the same" (Terrill and Ohmart 1984, Blancher and Robertson 1987), or adjusting the measure of food availability by eliminating what is not in stomachs (Feinsinger et al. 1985, Smith and Shugart 1987), does not necessarily solve the perception problem. Unless diet and field samples have the same proportions of item types, they are not likely to have been sampled with the same perceptual "filter." Even if fruit species A were the only prey type sampled from the environment and the only prey type found in stomachs, not all fruits are equally accessible; a mere tally of the appropriate food type may be an inadequate representation of food availability. In short, without accounting for a bird's perception, simple biomass measures (even "adjusted" ones) are probably poor reflections of actual food abundance available to birds (see also Moermond, this volume).

*We ignore scale-of-measurement problems.* Scale problems of tremendous magnitude occur when determining food availability, and these seem to be routinely ignored by researchers. Consider the following hypothetical problem. Suppose we want to test whether number of feeding trips/nestling/hour is related to food availability. Food availability would have to be measured and averaged over a unit at least as large as a territory—the unit searched by the bird for food. One could not use a single trap on each territory to represent conditions over the whole territory unless variation among traps within a territory was known to be less than variation between territories. Similarly, imagine a system where the ranking of areas by food density (measured as amount of food per branch) differs markedly from a ranking of those same areas when food density is measured as amount of food/leaf, or food/tree (Fig. 1). Holmes and Robinson (1981) measured food availability in terms of numbers of arthro-

pods per cm<sup>2</sup> of leaf area after counting 400 leaves. Would number/leaf be a better indication of value of the tree to the bird, or perhaps number/tree? Such problems are not trivial because number/leaf cannot be extrapolated to number/study area (and vice versa) unless food is distributed uniformly throughout. Since food is not so distributed, one's density estimate will vary with the scale of measurement. So which scale of measurement is correct?

*We measure standing crop only.* Most of our measures of food availability are equated with standing crop volume, number, or biomass (Carpenter 1987), even though bird behavior can depend on whether a patch of food is depletable (Kamil and Yoerg 1985). With the exception of nectar resources (Gill and Wolf 1979, van Riper 1984, Feinsinger et al. 1985), attempts to measure (or even discuss the effects of) renewal rates for continuously renewing food resources are rare (notable exceptions include Zach and Falls 1976b, 1979; Davies 1977a; Davies and Houston 1981, 1983). Yet, an area with two food items/m<sup>2</sup> that is restored to the same density within a second after removal of an item has much greater food availability than another with 20 items/m<sup>2</sup> and no renewal. Furthermore, a place with greater food density at the time of sampling is assumed to have more later, even though some food resources (e.g., fruit and seeds) are not continuously renewing.

#### *Toward the validation of food availability measures*

Given the potential problems, do authors ever attempt to confirm the appropriateness of their chosen method, beyond the use of intuitively logical assumptions and adjustments? They generally do not, based on my literature search. Occasionally authors will compare two methods of sampling food and presume that agreement between the two means that either is valid. For example, Ault and Stormer (1983) vacuumed the soil and got the same seed types that scraped samples produced, so they concluded that any dietary deviation from the sample would reflect a food "preference" by birds. A correlation between the abundance measure of two samples does not, however, validate either as an adequate measure of food availability. Not only has the animals' perception been ignored but, also, identical sample contents from two methods do not guarantee the correctness of either.

Most of us would consider stomach contents to be one way to validate sampling methods, but stomach contents can only guide one's "adjustment" of a measure to be closer to what the bird actually experiences. Samples that match stom-

IS FOOD AVAILABILITY GREATER FOR THE INDIVIDUAL ON TERRITORY A OR TERRITORY B ?

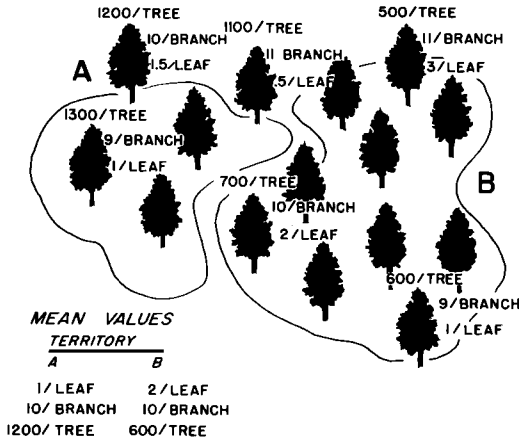


FIGURE 1. Hypothetical examination of the relative availability of food in two areas. Results depend on whether the unit area used to estimate food density is a single leaf, a branch, or a tree.

ach contents still do not address the perception problem or the other two classes of problems outlined earlier. Is it possible, then, to confirm that one's sampling method is meaningful? How do we know when we have measured actual food availability? At least one possibility deserves consideration.

Why not use patterns of bird behavior to confirm that our measures of food availability are appropriate? In fact, because conditions good for one individual may be poor for another, we cannot afford to measure food availability independently from bird behavior. Even the same food abundance can change in "availability," for example, as the thermal load of a bird changes (Clark 1987). If variation in some behavioral act were necessarily correlated with food availability, we might be able to use that behavior to "check" the validity of a food availability measurement made for some other purpose. Figure 2 depicts the essence of this argument. Normally, to understand whether food availability affects some biological phenomenon, we measure food by one of the four approaches categorized earlier, and then interpret results. I suggest that we simultaneously monitor a behavioral act, the rate of which is known to be influenced by food availability, and check the (partial) correlation between our food measure and the behavior. A significant correlation between our chosen measure and an act that is known to be related to food availability would strengthen the argument that we have measured food availability adequately.

Food availability surely affects some aspects of foraging behavior in predictable ways (Robinson and Holmes 1982, 1984). Indeed, birds can rapidly adjust their foraging behavior in response to prey availability (Paszkowski 1982, Pienkowski 1983). But which behaviors have been shown to be universally correlated with variation in food abundance under well-controlled experiments, such that we might use them to find a meaningful sampling method?

To find such a behavior, we must look at systems in which food availability can be undeniably ranked independently from bird behavior. Laboratory systems and field systems in which vegetation structure is relatively simple and available prey types are limited in number should allow one to measure food availability as accurately as possible. For example, in western Montana, Douglas-fir often occurs in homogeneous, nearly monospecific stands. Little other than western spruce budworm is available as a food source in early summer. On the basis of foliage samples taken from a series of 48 trees in June 1985, spruce budworm larvae comprised 72% of the 1035 arthropods that I collected. The predominance of spruce budworm larvae was most evident in the biomass measurements, however, where they comprised 96% of the total. Analyses of stomach contents from mixed-conifer forests in both Washington and Montana confirm that most forest passerines depend heavily, if not exclusively, upon budworm larvae for food from May through July (DeWeese et al. 1979). Remarkably, species that are known to feed on the ground during most other times of the year [American Robin (*Turdus migratorius*), Chipping Sparrow (*Spizella passerina*), and Dark-eyed Junco (*Junco hyemalis*)] fed extensively on larvae in trees from mid-June to mid-July; the entire insectivorous bird community appeared to rely on this single food source during the breeding season. Recognition that forest birds depend heavily upon lepidopteran larvae at this time is nothing new (MacArthur 1959, Robinson and Holmes 1982), but the preponderance of western spruce budworm larvae in both field samples and diets means that food availability should be exceptionally easy to estimate in that habitat type at that time of year.

The mean density of late-instar budworm larvae was significantly less on trees treated with systemic pesticide implants than on control trees during the year of treatment (Table 1). Twelve bird species visited the experimental control tree groups, and individuals of each species were observed eating or gathering budworm larvae. Limited sample sizes prohibited a meaningful species-by-species analysis, but results pooled across species showed that neither the probability of a

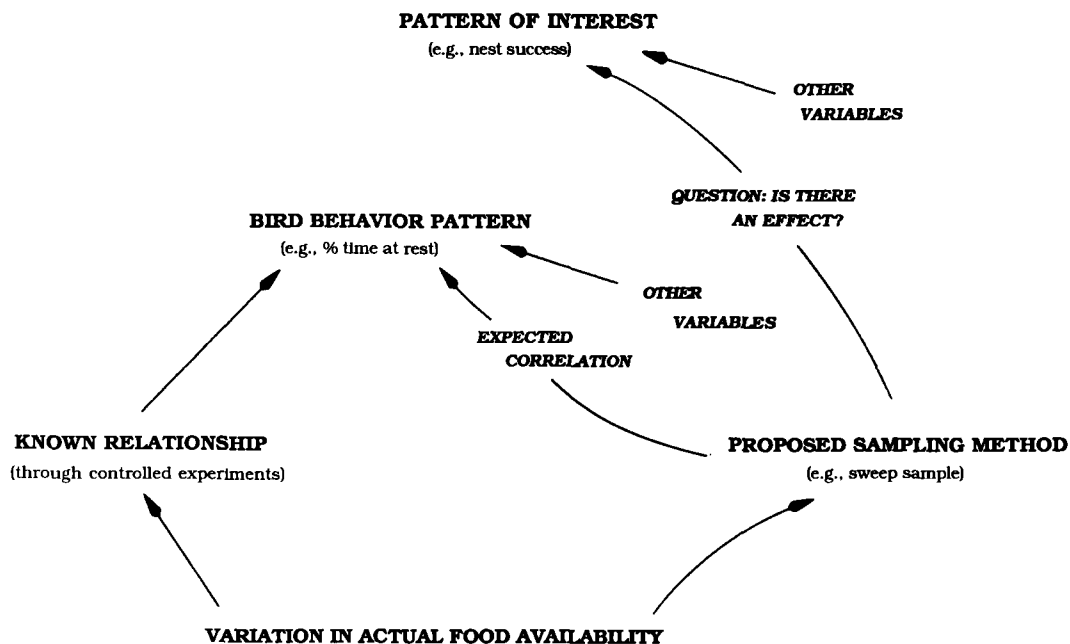


FIGURE 2. Diagrammatic illustration of the way bird behavior might be used to “screen” possible sampling methods, so that an appropriate measure of food availability is selected.

bird entering a tree (visits/hour) nor the mean duration of a bird’s stay was significantly greater in trees that harbored more food. The same held true if I considered feeding observations only, although the trend in all cases was to spend more time in trees with higher food densities. In contrast, mean attack rate of birds that foraged in systemically treated trees was significantly less than mean attack rate in control trees.

In an effort to uncover a series of easily quantified behavioral variables (such as attack rate) that might be unquestionably related to food availability, I searched through the literature for additional laboratory or field studies that bore

on the relationship between behavior and food availability. I found information on the following behavioral acts:

*Temporal attack rate (number of attacks/unit time).* Based on the well-studied functional responses of animals to prey density (Holling 1965, 1966), feeding rate of a predator should be proportional to food density until it can increase no further because of satiation or handling limitations. Linear (Type I) and exponential (Type II) responses have been shown to exist for birds that feed, respectively, on invertebrate or seed resources in the wild (Schluter 1984). Therefore, providing that we record foraging observations

TABLE 1. A COMPARISON OF MEAN VALUES OF BIRD USE BETWEEN SYSTEMICALLY TREATED AND CONTROL TREES

Measure	Untreated trees			Treated trees			U*	P
	N	$\bar{X}$	SE	N	$\bar{X}$	SE		
<b>Budworm density</b>								
No. budworms/m <sup>2</sup>	34	135.50	14.3	14	36.70	6.9	58	0.000
No. budworms/tip (×100)	33	7.87	0.7	14	3.13	0.6	82	0.000
No. budworms/g (×100)	33	6.19	1.3	14	2.04	0.7	59	0.000
<b>Bird use</b>								
No. visits/hr	37	0.78	0.2	14	0.74	0.2	256	0.950
Duration of visit (sec)	160	58.24	6.4	58	48.10	7.2	4275	0.373
No. pecks/sec (×100)	30	4.80	0.8	13	1.90	0.6	106	0.016

\* Mann-Whitney U-statistic.

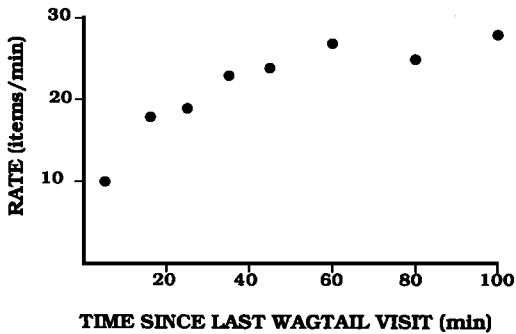


FIGURE 3. Pied Wagtails (*Motacilla alba*) exploit a renewing food supply. The feeding rate of an individual within a patch depends on the time since that patch was last depleted by the same or another wagtail. Foraging attack rate is clearly related to food availability to the birds (redrawn from Davies and Houston 1981).

during periods of active feeding prior to satiation, we should expect a more or less linear relationship between food density and feeding rate.

My experimental decreases in spruce budworm density on selected trees produced decreased attack rates by foliage-gleaning birds. Many other studies have produced similar results (Goss-Custard 1977a, Greenwood and Harvey 1978, Tinbergen 1981, Paszkowski 1982, Pienkowski 1983, Robinson and Holmes 1984, Schluter 1984, Maron and Myers 1985, Marcotullio and Gill 1985). Perhaps the strongest field study of this sort is that of Davies and Houston (1981), who worked with a relatively simple two-dimensional system. They found a Type II relationship between peck rate of ground-feeding wagtails on a patch and the time since last visit to the patch (Fig. 3). The relationship between prey availability and feeding rate seems irrefutable in this instance.

Neither Davies (1977a), Morse (1981), Møller (1983), nor Roland et al. (1986) found correlations between their measures of food availability and feeding rate. Careful examination of methods, however, revealed that food availability was not measured well or was not the only variable likely to have influenced feeding rate. Specifically, Davies measured prey availability by using a cumulative-total trap method, which may not have reflected food availability accurately over a smaller portion of the day. Morse did not measure food directly. Møller compared attack rates among seasons, over which time period the food types changed dramatically. And Roland et al. used number of larvae per cluster as a measure of food availability, which may not have been the best scale of measurement for determining

food availability because a tree could have only a few leaf clusters despite a high density of larvae per cluster.

*Spatial attack rate (number of pecks/unit distance).* Intuitively, it seems that number of items taken per unit distance traveled should be greater in relatively food-rich areas. Goss-Custard (1977c) showed such a response for Redshanks (*Tringa totanus*) feeding on large worms in the mud, and Hendricks (1987) used this measure after assuming it to be well correlated with food available to Water Pipits (*Anthus spinoletta*). The relationship deserves further study.

*Rate of progression (distance/unit time).* The number of steps that a shorebird takes following a successful capture is generally less than the number following an unsuccessful capture (Baker 1974). Thus, movement rate might decrease when a bird is in a relatively food-rich area. Area-restricted searching would also predict a slower rate of beeline progression with an increase in prey availability. In apparent contrast with these expectations, Baker and Baker (1973), Baker (1974), and Zach and Falls (1976c) found that movement rate was positively correlated with temporal attack rate (= food availability?). Goss-Custard (1970) found no relationship between the number of paces/min and prey density, whereas Zach and Falls (1979) found rate of progression (based on beeline distances) to be positively related to food supply.

*Search velocity (hops or perch changes/unit time).* Search velocity has been shown to be well correlated with temporal attack rate (Robinson and Holmes 1982). Because it may be easier to measure than attack rate for birds that forage in dense vegetation, search velocity might be more useful.

*Average stop-to-stop movement length (hops/unit distance).* We might expect a greater number of hops per unit distance in relatively food-rich areas because of area-restricted searching, which has been shown to occur after a successful capture (Croze 1970; Krebs 1973; Smith 1974b; Zach and Falls 1976b, c). Smith (1974b), in fact, showed that average move length by a foraging thrush decreased after a prey capture.

*Search tactics.* Birds may change search tactics with variation in prey availability. For example, several species have been shown to perform proportionately more aerial flycatching maneuvers as flying insects become more abundant (Davies 1976, 1977b; Davies and Green 1976; Greenwood and Harvey 1978; Holmes et al. 1978; Robinson and Holmes 1984). These changes probably reflect shifts in relative availability of one prey type over another, however, and not necessarily a change in overall prey availability.

TABLE 2. SOME FORAGING BEHAVIORS LIKELY TO BE INFLUENCED BY FOOD AVAILABILITY LEVELS

Behavior	Expected relationship with food availability	No. studies consistent with trend <sup>a</sup>	No. studies inconsistent with trend <sup>a</sup>	Other variables to control <sup>b</sup>
Temporal attack rate (No. pecks/sec)	Positive	11	4	1-7
Spatial attack rate (No. pecks/m)	Positive	2	0	11
Rate of progression (cm/sec)	Negative	0	5	9
Search velocity (No. hops/sec)	Positive	1	0	7
Mean move length (No. hops/m)	Negative	6	0	11
Search tactic change (glean, sally . . .)	Change	0	6	1, 7, 8
Food delivery rate (No. trips/hr)	Positive	3	1	10
Rate of aggression (No. attacks/hr)	Positive	3	0	8
Percent time feeding/resting (daily time budget)	Negative/positive	6	0	6, 8, 9

<sup>a</sup> Specific references are cited in the text.

<sup>b</sup> The other variables are: (1) time of day or season; (2) quality or quantity of food per peck; (3) prey type consumed; (4) foraging tactic used; (5) success rate; (6) physiological condition of bird; (7) foraging microhabitat; (8) sex, individual identity; (9) weather; (10) clutch size; and (11) none reported yet.

Therefore, this is not likely to be a measure that accurately reflects changes in food availability.

*Nestling food delivery rate (trips/unit time).* In several instances, food delivery rates by aerial foragers have been positively correlated with food density (Zammuto et al. 1981, Turner 1982, Blancher and Robertson 1987). Strehl and White (1986), however, recorded fewer trips/hour by Red-winged Blackbirds during times of high food (periodical cicada) density. The latter result was a consequence not only of a change in prey types available but also of a change in foraging locations used by adults. Therefore, the positive relationship between food availability and delivery rate seems to be consistent among recent studies.

*Rate of aggression (number of supplanting attacks/unit time).* Rates of aggression may increase when food availability decreases, as Hinde (1952), Gibb (1954), and McFarland (1986a) have reported for forest tits and honeyeaters. Although results are consistent, the difficulty associated with obtaining large sample sizes in most instances will almost certainly render this measure useless as an index of food availability.

*Percent time feeding (from time budget information).* We might expect a bird in a food-poor area to spend more time feeding and less time resting, relative to a bird in an area of high food availability. Davies and Lundberg (1985) added food to Dunnock (*Prunella modularis*) territories three months prior to the breeding period. The birds not only bred earlier, but spent significantly more time perching (resting) (20% vs. 7%) and interacting (9% vs. 1%), and less time feeding (62% vs. 89%) than control females that were without supplemental food. Similar patterns have been shown nonexperimentally for tits (Gibb 1954), hummingbirds (Gill and Wolf 1979), ducks (Hill and Ellis 1984), shorebirds (Maron and

Myers 1985), and honeyeaters (McFarland 1986a).

## CONCLUSIONS

By using bird behavior to confirm that a measure of food availability is biologically meaningful, we can probably avoid the three major problems discussed earlier. The bird's perception of food availability is no longer ignored, scale-of-measurement questions are automatically resolved, and renewal rates are also automatically integrated. Nonetheless, potential problems remain. In particular, search tactics (behavioral acts), patterns of locomotion (rates), and time budgets may change independently of food availability because of changes in (micro)habitat (Robinson and Holmes 1984), time of day (Davies and Green 1976, Holmes et al. 1978), season (Root 1967), weather (Grubb 1978), and physiological condition of the bird (Moore and Simm 1985, Clark 1987). Many of these aspects of foraging behavior are also sex-specific (Holmes et al. 1978; Smith 1974a, b).

As an example, foraging attack rate should vary not only with food availability but also with quality and quantity of food/peck (McFarland 1986a), prey type or size consumed (Goss-Custard 1977a, b; Paszkowski and Moermond 1984; Robinson 1986), foraging tactic used to acquire food (Baker and Baker 1973), probability of success for a given attack (Goss-Custard 1970, Baker and Baker 1973), and physiological condition of the bird (Paszkowski and Moermond 1984, Moore and Simm 1985). Thus, one would need to control those additional variables before using attack rate as an index of food availability. That can be accomplished by restricting comparisons to time periods and locations in which such changes should be minimal, and by recording only num-



ber of successful captures/sec. Even in the absence of control for those variables, however, they will only add variance to the relationship between attack rate and food availability and decrease the chance of observing a significant correlation. Finding a significant correlation in the face of such scatter would only strengthen the argument that the measure is a reliable estimate of food availability.

For each of the foraging behaviors considered here, I have summarized (Table 2) whether the behavioral act is likely to be reliable as an indicator of food availability (based on the consistency of published results where both the behavior and prey density were measured). I have also included a list of nonfood-related variables found to affect a given behavior, so that they might be controlled as much as possible.

It is important to note that the behavioral acts outlined here are those for which published information exists. Undoubtedly, other behavioral measures (e.g., pecks/stop) might be sensitive to variations in food supply. Researchers working with systems that afford accurate measurement of food availability could record bird behaviors to test the usefulness of those measures. Meanwhile, temporal and spatial attack rates, mean stop-to-stop movement length, and percent time feeding are probably the most promising behaviors to record.

Finally, it may be practical to use foraging behavior to validate a measure of food availability when one's goal is to determine whether food availability is important in explaining observed biological differences among individuals. Indeed, behavior alone might be an adequate index of food availability in such instances. If, on the other hand, one wishes to determine whether food supply is important in explaining why some parcels of land are used and others are not used by individuals of a given species, the problem is

more difficult. Even if sweep net samples provide a perfect measure of food availability (as evidenced by a perfect correlation with variation in some behavioral act), one cannot assume that sweep samples from occupied and unoccupied areas will be comparable because the correlation between bird behavior and food abundance will have been based entirely on data taken from occupied areas. Occupied and unoccupied areas may differ significantly in physical structure such that food might not be perceived the same way in those locations. Another possibility is that predators or competitors may occur in areas that are avoided by the subject species. Thus, measures of food abundance could be similar between occupied and unoccupied areas, but food could still be less available in the unoccupied areas.

To compare food availability between occupied and unoccupied areas, we must know the constraints on what is *possible* for the bird to use. Just as we must know about the subset of prey types and sizes that should be excluded from estimates of food availability, we need to know the subset of (micro)habitats that should be excluded for comparisons of occupied and unoccupied areas. This problem will stand as a fundamental obstacle to our eventual understanding of the relationship between habitat use and food availability.

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