

EXTENSIONS OF OPTIMAL FORAGING THEORY FOR INSECTIVOROUS BIRDS: IMPLICATIONS FOR COMMUNITY STRUCTURE

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Abstract. Optimal foraging theory has been successful in developing specific, testable predictions regarding the behavior of a number of organisms. Useful models must include as much relevant biological detail as possible. Two such models are presented here. The multitactical model predicts that organisms will pursue a given prey with a given tactic if the gain exceeds the cost. By assuming that the probability of capture increases as prey encounter rates increase, predicting the prey densities at which switching tactics is profitable is possible. The interference model predicts that if a bird is choosing an optimal diet it will inevitably face increasing interference costs as prey densities increase. A bird should avoid interference whenever possible. If it is assumed that the encounter rate with other birds increases as prey encounter rates increase, it is possible to predict prey encounter rates at which birds will switch foraging tactics to avoid interference. For birds to make foraging decisions, they must be capable of evaluating profitability of prey items, the probability of capture using a tactic, and the amount of time required to capture them. I present suggestions for testing of the models and consider implications of these models for the generation and maintenance of community structure.

Key Words: Community structure; insectivorous birds; interference competition; multitactical foraging; optimal foraging.

For several reasons, ecologists studying insectivorous birds have been slow to use optimal foraging theory as a predictive tool. First, the assumptions underlying optimal foraging theory have been questioned (e.g., see reviews by Maynard Smith 1978, Krebs et al. 1983, Myers 1983, Stephens and Krebs 1986). Second, many optimal foraging models are not constructed of variables that are easily measured in the field. Finally, field biologists often seem resistant to theorizing, perhaps because theoretical formulations often ignore biological properties of the organisms. The debate regarding assumptions will continue, until someone can explain why the models produce successful predictions. Even if the models fail in some respects, they provide powerful tools for developing specific, testable hypotheses regarding foraging behavior (Stephens and Krebs 1986; Stephens, this volume).

In this paper, I attempt to develop simple extensions of a model of optimal foraging that can be applied to insectivorous birds in forest ecosystems. No attempt will be made to deal with all of the complexities of their foraging behavior, but two important observations will be used to extend optimal foraging theory for insectivorous birds. The first extension is based on the observation that insectivorous birds often use several different tactics to secure the same type prey (Robinson and Holmes 1982). For example, lepidopteran larvae can be caught by either gleaning from the surface of a leaf or snatching from leaves while hovering. The second extension recognizes that interference competition among birds regularly occurs (Morse 1976b, Maurer 1984) and

may influence foraging behavior. The models I consider below incorporate both multitactical foraging and the costs of interference.

In this paper I: (1) present several models beginning with the basic optimal foraging model and then add successive considerations for multitactical foraging and interference competition; (2) examine the basic assumptions of the models and describe how model parameters might be estimated in the field; (3) suggest specific experiments to test the models; and (4) consider implications for the maintenance of community structure for forest birds.

THE MODELS

OPTIMAL FORAGING IN A FINE-GRAINED HABITAT

Charnov (1976a) developed a model of optimal foraging that built on work by MacArthur and Pianka (1966), but parameterized the arguments in a way similar to Holling (1959a, b). Stephens and Krebs (1986) demonstrated the generality of the Charnov model and discussed many refinements. The model predicts the choice that a predator will make when it encounters a prey item of given quality. That quality has two components, energy value and handling time. The predator was assumed to maximize the rate of energy intake by behavioral adjustments.

Let E be the rate of energy intake; then, according to Charnov (1976a)

$$R = \frac{E}{T_h + T_s}, \quad (1)$$

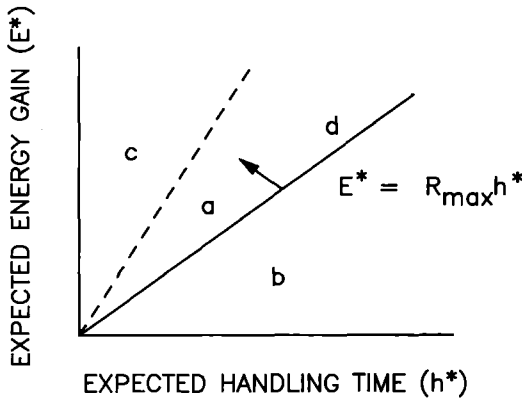


FIGURE 1. In Charnov's (1976a) model of optimal foraging, the solid line indicates the lower limit of the prey acceptability region. A prey type at b would never be selected. If prey become superabundant at c, then the lower limit of the prey acceptability region moves towards the dashed line, so that prey types a and d, which were originally taken, become suboptimal. Under these conditions prey type d is not included because of a greater handling time, even though it has higher energy content.

where R is the long-term rate of energy intake (Stephens and Krebs 1986), T_h is the total amount of time spent in handling the prey, and T_s is the total amount of time spent in searching for prey. Handling time includes the time between when a foraging bird first identifies a prey item until it begins foraging again. It could be further broken down into pursuit time and actual handling time (e.g., Eckhardt 1979).

Charnov (1976a) suggested that if one defined the following quantities: E_i^* = expected energy gain of prey i , h_i^* = expected handling time of prey i , P_i = probability that prey type i is attacked, and λ_i = encounter rate of predator with prey type i , then the individual terms in eq. (1) could be defined as $E = \sum \lambda_i E_i^* T_s P_i$ and $T_h = \sum \lambda_i h_i^* T_s P_i$. These values, upon substitution into eq. (1) give

$$R = \frac{\sum \lambda_i E_i^* P_i}{1 + \sum \lambda_i h_i^* P_i}$$

Charnov (1976a) showed that R is maximized if the following three conditions hold: (1) $P_i = 0$ or $P_i = 1$; that is, the predator always attacks some prey types and never attacks others. (2) If prey types are ranked according to the ratio of expected energy gain to expected handling time (E_i^*/h_i^*), then the inclusion of a prey type in the optimal diet depends only on the density of items of higher ranking. The term E_i^*/h_i^* represents a measure of prey quality, and can be thought of

as the expected energy gain per unit time of effort (exclusive of search time). (3) Those prey items that are eaten are those for which the following inequality holds:

$$\frac{E_i^*}{h_i^*} > R_{max}$$

where R_{max} is the maximized rate of energy intake. These results are presented graphically in Figure 1. Condition (3) can be interpreted by noticing that the long-term rate of energy intake (R) also includes search time (see eq. 1). Thus, for a prey type to be of sufficient quality to be included in the diet, the energy derived from its consumption must allow the predator to compensate for time that must be spent searching.

MULTITACTICAL FORAGING IN A FINE-GRAINED ENVIRONMENT

To extend Charnov's model to the multitactical situation, first note that the rate of energy intake is assumed to be given as in eq. (1). The quantities E_i^* and λ_i remain as before, but the following new quantities are defined: P_{ik} = probability that prey i is pursued with tactic k , C_{ik} = probability that prey i is captured using tactic k , h_{i^*k} = expected handling time of prey i using tactic k . If E_k is the total energy collected using tactic k , then the total energy obtained will be the sum of the energy obtained from each tactic, and the handling time will be the sum of the handling times of each tactic, so:

$$E = \sum \sum \lambda_i E_i^* T_s P_{ik} C_{ik} \tag{2a}$$

$$T_h = \sum \sum \lambda_i h_{i^*k} T_s P_{ik} \tag{2b}$$

This formulation assumes that there are some prey items that are pursued but not captured because the probability of capture, C_{ik} , can be < 1 , but does not appear in the relationship defining total handling time. When these relationships are substituted into eq. (1), then the following relationship is obtained:

$$R = \frac{\sum \sum \lambda_i E_i^* P_{ik} C_{ik}}{1 + \sum \sum \lambda_i h_{i^*k} P_{ik}} \tag{3}$$

A similar set of conditions to Charnov's (1976a) holds when R is maximized in this model. These are: (1) $P_{ik} = 0$ or $P_{ik} = 1$, that is, the predator either always or never attacks some prey items using a given tactic. (2) When prey are ranked according to the ratio of expected energy gain to a tactic's expected handling time multiplied by the probability of capture using that tactic ($[E_i^*/h_{i^*k}] \times C_{ik}$), then the inclusion of a prey type in the optimal diet depends only on the density of items of higher ranking. The value of a prey item is weighted by its expected probability of capture.

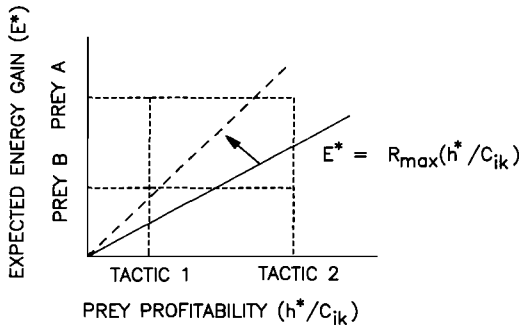


FIGURE 2. In the simplest multitactical model, there are two prey types of differing energy content and two tactics that differ in their profitability. The solid line represents the lower limit of the prey acceptability region. Prey type B is never taken using tactic 2, but is using tactic 1. If prey type B becomes superabundant, then the lower limit of the prey acceptability region moves towards the dashed line. When this occurs, prey type A will not be taken using tactic 2.

(3) Those prey items eaten are those satisfying the following inequality:

$$\frac{E_i^*}{h_i^*/C_{ik}} > R_{\max}$$

The value of a prey type weighted by its probability of capture must exceed the maximal rate of intake. Thus, some items that might otherwise be taken in the diet may not be included if the probability of their capture is too low. These conditions are summarized graphically in Figure 2.

The above argument holds if the probability of capture using a tactic is independent of the density of prey. However, probability of capture may increase as the rate of encounter of prey items increases (Figs. 3A,B). The simplest assumption to make is that there is a linear increase in C_{ik} with λ_i over a certain range of prey encounter rates. If this assumption is made, then prey profitability will be proportional to h_i^*/λ_i (Figs. 3C,D).

Consider two different tactics, each with a different functional relationship of C_{ik} with prey encounter rate. There are two ways for the tactics to be related to encounter rate (Figs. 3A,B). First, one tactic might always be superior to the other, so that the probability of capture using it will always be greater (Fig. 3A). If this condition holds, the less successful tactic will only be used when the prey item has an exceptionally high energy value. Prey items with low energy content will always be taken only with the first tactic (Fig. 3C). However, if one tactic has a lower capture probability at low prey encounter rates, but is

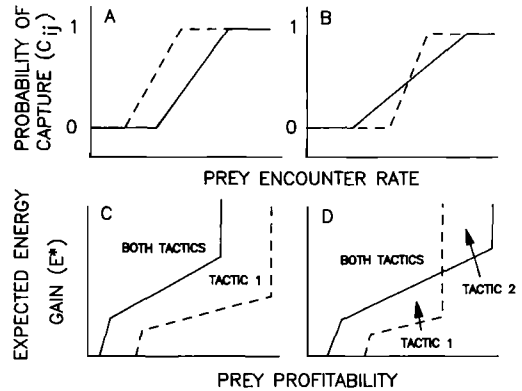


FIGURE 3. Results of the multitactical foraging model when probability of capture is assumed to increase with prey encounter rates. A. An assumed relationship between the probability of capture and prey encounter rate for two tactics. Tactic 1 (dashed line) is always better than tactic 2 (solid line). B. A different relationship where tactic 1 (dashed line) is better than tactic 2 only at higher prey densities. C. The resulting limits for prey acceptability from part A. Tactic 2 is only used for relatively high quality prey, while tactic 1 is the sole tactic used to take prey of low energy content. Note that prey profitability increases to the left on the axis. D. The resulting limits for prey acceptability from part B. Tactic 1 is used exclusively for low quality prey at high prey profitabilities, while tactic 2 is used exclusively for prey of low profitability. Note that prey profitability increases to the left on the axis.

superior at high rates (Fig. 3B), at low encounter rates it will be used exclusively to obtain energy rich prey; energy poor prey will be taken only at high densities by using the first tactic (Fig. 3D).

FORAGING WITH INTERFERENCE

The inclusion of interference interactions into the optimal foraging model described above is accomplished by a redefinition of eq. (1) to include energetic and time costs for interactions. Thus we have

$$R = \frac{E_g - E_c}{T_s + T_h + T_c}, \quad (4)$$

where E_g is the gross energy intake, E_c is the energy lost in interference interactions, and T_c is the time spent in interactions. For simplicity, assume that the bird is foraging on a single homogeneous prey resource with expected energy content E^* , expected handling time h^* , encounter rate λ , and probability of attack P . Then the quantities in eq. (4) can be defined as: $E_g = \lambda E^* P T_s$; $E_c = \eta E_c^* P_c T_s$; $T_h = \lambda h^* P T_s$; and $T_c = \eta t^* P_c T_s$, where η is the encounter rate with other foragers, E_c^* is the expected energy spent in a single interference interaction, P_c is the proba-

bility that an encounter will result in an interference interaction, and t^* is the expected time spent in the interaction. Substituting into eq. (4) gives:

$$R = \frac{\lambda E^*P - \eta E_c^*P_c}{1 + \lambda h^*P + \eta t^*P_c} \quad (5)$$

Eq. (5) indicates that R will be maximized if either η or P_c are equal to 0. If an individual can predict when another individual will be encountered, then the first bird should act to prevent interference. Territoriality can reduce the amount of interference and may be reinforced in species with high encounter rates. Although some birds defend territories against both conspecifics and individuals of different species, territoriality is usually directed at conspecifics. If this is true, then much of the interference birds experience will be due to encounters with other species. If such encounters are random or show no consistent pattern, adaptations to prevent them may not evolve and, consequently, it may not be possible for natural selection to minimize η or P_c .

If avoidance of interference from other species cannot readily evolve, then what is the ecological cost of interference? In eq. 5, the effects may be examined by making some simplifying assumptions. First, assume that the energetic cost for an interference interaction is negligible, then eq. 5 can be rearranged to give:

$$\frac{T_c}{T_s} = \frac{\lambda P(E^* - Rh^*)}{R} - 1 \quad (6)$$

The ratio of time spent in interference to time spent searching is thus a linear function of prey encounter rate. Notice that for the slope to be positive, $E^*/h^* > R$. Thus, if a bird is foraging optimally, that is it meets the condition $E^*/h^* > R$, it must spend more time in interference interactions as prey density increases (Maurer 1984). The threshold prey encounter rate above which interference will be experienced is given by

$$\lambda_0 = \frac{R}{E^* - Rh^*} \quad (7)$$

Second, assume that the time spent in interference interactions is negligible, but each encounter is energetically expensive. In this instance, eq. (5) can be rearranged to give

$$E_c = \lambda P(E^* - Rh^*) - R \quad (8)$$

Again, the cost for interference—this time in energy lost—is a linear function of prey encounter rate, and if the organism is foraging optimally energy lost to interference will increase with prey encounter rates. The threshold prey encounter

rate for this cost to be positive is also given by eq. (7).

This simple model suggests that both the time spent and the total amount of energy expended in interference interactions will increase as prey encounters increase. There are at least two ways for the cost of interference to increase (Maurer 1984). First, as the density of prey increases, birds will encounter other birds attracted to the abundant resource more often. Second, prey encounter rates may also be high if insect prey are clumped, and if birds are attracted to such clumps, the amount of time and energy spent in resolving interference will increase.

COMBINING THE MULTITACTICAL AND INTERFERENCE MODELS

In this section a different approach to the cost of interference is taken by asking, "How does a bird make decisions in foraging if using different tactics exposes it to different intensities of interference competition?" In eq. (4) we can take E_g and T_h as in eqs. (2a) and (2b) and make the simplifying assumption that every predator encounter will result in an interference interaction, so $P_c = 1$. The interference terms become: $E_c = \Sigma \Sigma \eta_{ik} E_c^* T_{k_s}$ and $T_c = \Sigma \Sigma \eta_{ik} t^* T_{k_s}$, where $T_k = \Sigma \lambda_i h_i^* P_{ik} T_{k_s}$. The modified conditions that predict the decision of the predator to pursue a particular item are similar to the conditions for previous models: (1) $P_{ik} = 0$ or $P_{ik} = 1$. (2) Prey items and tactics can be ranked according to their profitabilities, which now are given by the expression:

$$\frac{E_i^* C_{ik} - \eta_{ik} E_c^*}{h_i^* (1 + \eta_{ik} t^*)}$$

(3) The profitability of a prey item as given by condition (2) must exceed R_{\max} in order to be attacked using a given tactic.

In the expression for profitability, there are several factors that affect the profitability of a prey item pursued with a given tactic. Increasing the probability of capture using a given tactic (C_{ik}) increases the value of a prey type and increasing the expected handling time using that tactic decreases the value of a prey item. Increasing the amount of interference decreases the value of a prey item, making it less likely to be included in the optimal diet. This can be seen by rearranging the inequality implied by conditions (2) and (3):

$$\frac{E_i^* C_{ik} - R_{\max} h_{ik}}{R_{\max} h_{ik} t^* + E_c^*} > \eta_{ik} \quad (9)$$

If $\eta_{ik} = 0$, then inequality (9) reduces to the condition that must be met in the multitactical model for a prey item to be included in the diet.

However, if $\eta_{ik} > 0$, then the value of the item has to be greater (i.e., $E_i^* C_{ik} - R_{\max} h_{ik}$ has to be larger) for the item to be included in the diet. Therefore, interference forces the optimally foraging organism to pursue items of greater energetic quality than it would have to if there was no interference.

A final variation of the combined model is obtained by assuming that the predator encounter rate is a positive linear function of prey encounter rate (Figs. 4A,B). Assuming that above a threshold prey encounter rate interference with a predator when using a given tactic for a specific prey type increases, then the predator encounter rate is

$$\eta_{ij} = \frac{\lambda_i - \lambda_{ij}^0}{a_{ij}}, \text{ if } \lambda_i > \lambda_{ij}^0,$$

otherwise

$$\eta_{ij} = 0,$$

where $(1/a_{ij})$ is the slope of the relationship between η_{ij} and λ_i , and λ_{ij}^0 is the threshold prey encounter rate for a tactic j . This model shows that if one tactic is always better than another tactic (Fig. 4A), there will be one set of prey items that will always be taken by the better tactic, and another region where both tactics will be used, but the inferior tactic will never be used exclusively (Fig. 4C). However, if one tactic is inferior at low prey encounter rates but better at high encounter rates (Fig. 4B), then that tactic will be used exclusively at high encounter rates. The other tactic will then be used exclusively to take relatively low quality prey at relatively low encounter rates (Fig. 4D). Further, as prey encounters increase the increased cost of interference induced by high predator encounter rates can allow prey that would be taken at low encounter rates to become suboptimal. Thus, if a prey species can increase its density sufficiently to attract high numbers of predators, it can reduce predation by becoming more costly for individual predators to harvest due to high numbers of interference interactions.

DISCUSSION

VALIDITY OF MODEL ASSUMPTIONS

Optimal foraging models make many implicit and explicit assumptions. Perhaps the most important is that the predator has complete information when deciding whether or not to attack a prey item (Stephens and Krebs 1986). The information needed by a foraging bird in the models above is the energetic content of the prey item (or its average value), the time spent handling the item using different tactics, and the rate of encounter with other birds. It is unlikely that a

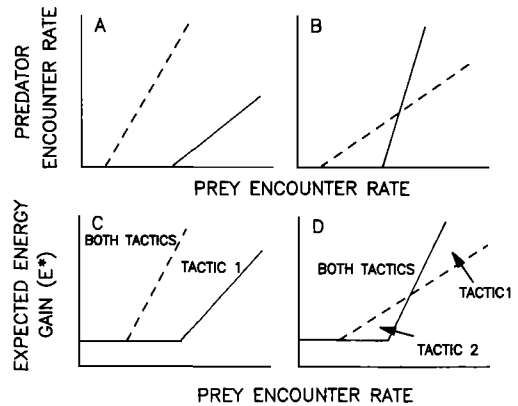


FIGURE 4. Results of the combined model when predator encounter rate is assumed to increase with increasing prey encounter rates. A. Tactic 1 (solid line) is always better than tactic 2 (dashed line) in allowing the predator to avoid other predators. B. Tactic 1 (solid line) is better than tactic 2 (dashed line) only at lower prey encounter rates. C. Prey acceptability lines resulting from conditions specified in A. D. Prey acceptability lines resulting from conditions specified in B.

bird will be able to make fine distinctions between individual prey species. In fact, it will only be profitable to make such distinctions if the energy or time loss for not doing so is larger than the actual value of the prey (Stephens and Krebs 1986:79–80). In making distinctions among edible prey items, birds may estimate energy content by evaluating prey size. To estimate handling time, birds may use the location of a prey item. For example, a lepidopteran larvae under a leaf may be difficult to remove by a perched bird, but more efficiently removed by hovering. Assessment of predator encounter rates can be made visually as the bird forages.

Empirical evidence suggests that birds do discriminate among locations of potential prey items (e.g., Holmes et al. 1979b, Maurer and Whitmore 1981, Robinson and Holmes 1982). Several studies have shown that differences in foraging reflect different prey distribution (Maurer and Whitmore 1981, Franzreb 1983a, Mannan and Meslow 1984). Although insectivorous birds probably make the kinds of distinctions among prey items that are necessary to apply foraging models, it remains to be seen whether field methods of sufficient accuracy can be developed to test model predictions.

TESTING THE MODELS

The multitactical model

This model predicts which of several foraging tactics will be used on different prey. In order to

do so, several quantities must be measured. First, the expected energetic content of prey must be estimated. Usually, only relative content, such as prey size, need be measured, so prey items can be ranked. Next, it is necessary to estimate expected handling times of items for each foraging tactic. For example, capture of a lepidopteran larvae under a leaf may require less than a second while hovering, but take longer if picked from the substrate while perched. Finally, it is necessary to estimate the probability of capture of each prey type using each tactic. Based on these quantities, it should be possible to predict whether a prey will be taken, or equivalently, whether a tactic will be used to obtain prey in a specified location.

Handling times and capture probabilities are likely to vary among bird species. For example, American Redstarts (*Steophaga ruticilla*) may be more proficient at hovering beneath leaves than Scarlet Tanagers (*Piranga olivacea*). Hence, the optimal prey set should reflect species-specific behaviors, resulting in a correlation between foraging maneuvers and the types of prey taken (Robinson and Holmes 1982).

If it is possible to measure prey densities, and thus estimate encounter rates, then the multitactical model in Figure 3 can predict when a bird will switch foraging tactics. To do so, the relationship between prey density and capture probability using different techniques would need to be estimated. For example, suppose over the course of a breeding season, lepidopteran larvae under leaves increased in density. If the probabilities of capture for hovering and gleaning increased at different rates as the larvae became more common, then the multitactical model could be used to predict when birds should switch tactics. It should also be possible to design more rigorous tests of the model using laboratory experiments in which prey encounter rates are manipulated and prey are presented in ways that require different tactics.

The interference model

This model predicts quantitatively a threshold prey encounter rate, above which the costs of interference are greater than 0 (eq. [7]). The critical quantities to be measured are the time and energetic cost of interference interactions, the expected energy content and handling time of prey, the prey encounter rate, and the long term energy intake rate.

Observations of interactions among individuals in foraging flocks might be used to test the model. For such studies, the optimal solution for the model is to avoid interference interactions (see eq. [5]). Flocking species must often balance the disadvantages of flocking (which could be

parameterized in terms of eqs. [6] and [8]) with advantages in minimizing risks of predation or locating rare food items.

The combined model

The most interesting aspect of this model is its prediction of the prey encounter rates at which a foraging bird should switch tactics to avoid interference from other birds. To test this model, it is necessary to estimate the quantities for both the interference and multitactical models, establish a relationship between prey density and the encounter rate with other birds and show how that relationship varies depending on the type of tactic used. The model does not require that a tactic causes a bird to encounter other birds; it simply assumes some correlation exists between the tactic used and the likelihood of encountering another bird. Thus, the foraging bird can expect to alter the amount of interference it experiences by using different prey capture techniques.

IMPLICATIONS FOR COMMUNITY STRUCTURE

How do patterns of foraging behavior influence community structure? In his classic study, MacArthur (1958) showed that five species of paruline warblers foraged in different locations in coniferous trees. This was used as evidence that the species could not outcompete one another and hence could all persist in the same habitat. These ideas led to the widespread acceptance of the idea of niche partitioning: species had to be sufficiently different in their resource use to allow them to coexist. Since that study, many workers have assumed that differences in foraging behavior are adaptations to permit coexistence (Schoener 1974).

The view of foraging behavior in this paper suggests a different emphasis. If insectivorous birds encountered prey of uniform energetic content and ease of capture, there would be no need to make foraging decisions. However, insects have a wide variety of predator avoidance tactics (e.g., Heinrich 1979c) that in effect create a great deal of spatial variation in insect abundance. Presumably, if a bird used only a single prey type, species representing that type would evolve to reduce predation, so that either the predator would have to evolve to use a different prey type, become more efficient, or go extinct. Hence, a predator should diversify its methods of taking prey so that any one set of prey types will not have too great a selection pressure. Spatial variation in insect populations can also result from predation by other species of birds, mammals, and parasitoids, and by variations in the defensive chemistry of host plants (Cates and Rhoades 1977). In the face of such spatial variation in insect prey, a multitactical strategy would allow a bird to vary

its foraging behavior in response to prey dispersion.

If bird species found together have sufficiently variable foraging behaviors, then applying traditional models of community structure to bird communities may be inappropriate (Wiens 1976, 1977; Maurer 1984). In a spatially variable environment, it may be impossible for one species to exclude another. Furthermore, if interference increases with prey density, species may be subjected to many different forms of competition in different ecological settings, each with its own consequences (Maurer 1984, 1985a). Therefore, selection affecting divergence might be variable in intensity and in the phenotypic characters favored (Wiens 1976, 1977). Hence, species may not individually evolve pairwise adaptations, but rather evolve generalized adaptations allowing them to compete effectively with many species. Consequently, communities of insectivorous birds probably are not assemblages of coevolved

species, but collections of species that have the right sets of adaptations that allow them to live together. In this approach to community structure, competition is a transient factor in the habitat that varies spatially and temporally in its effects on individual organisms. Community structure is determined by a hierarchical set of factors operating at different spatial and temporal scales (Maurer 1985b, 1987). At the organismic level, decisions made by individual organisms attempting to maximize their long term net energy intake determine how much energy enters the community and thus determine, in part, how the community responds as a unit to changes in its environment.

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