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FORAGING STRATEGIES OF INSECTS

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INTRODUCTION

The evolutionary fitness of an animal depends significantly upon an optimal diet in both quantity and quality. Foraging strategies are therefore rigorously shaped by natural selection and should be considered in terms of the degree to which they maximize the net nutrient gain from feeding, and to which they minimize the risks to survival.

Any discussion of foraging behavior is complicated by the forager's perceiving the environment at several hierarchical levels. We endeavor to categorize these, being fully aware that any such framework is bound to be plagued with exceptions and examples of blurred boundaries.

Our classification includes three such levels: the habitat, the patch, and the food item. Of these, the food items are generally the easiest to define. They are the prey of predators, the hosts of parasitoids, the leaves for caterpillars, the feeding sites for mosquitoes, the nectaries and anthers for bees, and so on. Such items are almost invariably heterogeneous in their spatial distribution, which makes it appropriate for us to identify an aggregation of food items—a "patch"—as the next level in the hierarchy. The definitions of what should and should not constitute a patch have been various (174, 179). We look upon patches as spatial subunits of the foraging area in which aggregations of food items occur. A patch is most readily identified when the food items are distributed among discrete natural units, as are, for example, prey on leaves. But we must beware of identifying a patch solely by what we perceive or consider reasonable. The forager itself defines the patch, and we should look to changes in the forager's behavior to identify patch boundaries. A patch in these terms is therefore an area containing a stimulus or stimuli that at the proper intensity elicit a characteristic foraging activity in a responsive forager (174). Such a definition, rather than one based on the forager's response itself, avoids attributing more patches to the environment of a responsive forager than to that of an unresponsive one.

Patches themselves are not uniformly distributed in the environment. Like food items, they tend to be clustered, so that a "habitat"—a collection of patches—becomes a convenient third and final level to be considered in relation to foraging. The jump from "patch" to "habitat" is a bold one and will often conceal the existence of different levels of patchiness. Consider a coccinellid foraging for aphids in a field of cabbage plants. We can readily identify the field as the habitat, but at least two levels of patchiness occur within this. At one level there is the plant and at the other the individual leaves upon which the aphids aggregate.

Students of insect dispersal generally distinguish between trivial movement within the habitat and migratory movements outside it (35, 94, 97, 98, 158, 159). These types of movement have their own behavioral characteristics; within the habitat, the forager is frequently exposed to vegetative, or "trophic" signals [and hence the term "milieu trophic" of Labeyrie (105)] and during trivial movement its thresholds for response to these signals are low (97). These differences between intra- and inter-habitat behavior have seldom been considered in relation to foraging strategies, and yet are a crucial component in the first phase of foraging—the "habitat finding" of Laing (106) and Doult (37).

Such a classification of the environmental levels apparent to a forager (shown schematically in Figure 1) is important if we are to consider the components of foraging and place them within a general framework. It is also important to the testing of current foraging theories, such as the Marginal Value Theorem (26), which assumes that the forager perceives as discrete units both habitats and the patches that comprise them.

Since the foragers considered here include predators, herbivores, and bloodsucking insects, the range of habitat, patch, and food types involved is considerable. For a herbivore such as a butterfly, for example, the gross vegetation type—perhaps a woodland or field—constitutes the habitat. The patch is then the clump of vegetation that provides either the larval or adult food, and the food item is present at the particular feeding sites [e.g. the young growth of *Passiflora* for some *Heliconius* species (57, 58)]. The habitat for aquatic insects is the particular type of water body, and within this some degree of patchiness will occur. Thus for the dragonfly *Cordulegaster boltoni*, whose larval habitat is a fast stream, the patch is an area of relatively tranquil water with a sandy substrate in which the predatory larva submerges itself. The food items are the prey (such as chironomid larvae, although these are neglected by later predator instars), and these are detected by a combination of tactile and visual cues (19). The habitat for honey bees is likely to be a rather loosely defined area depending on the vegetation type. Within its habitat, the bee recognizes the patch of flowers by color, shape, and odor; whether or not a particular flower will provide suitable food, and the exact position of this (the nectary or anthers), is determined at very close range, often after settling (50, 140). As a final example, we turn to bloodsucking insects. Their habitats, whether they be savannah, cultivated areas, or woodlands ("sylvan species"), are recognized by visual signals, as well as by light intensity and humidity (10, 11). Within these habitats the host animal is the patch and is found by odor, output of carbon dioxide, and possibly convection currents (60, 82). At the finest level, the food item is the actual feeding

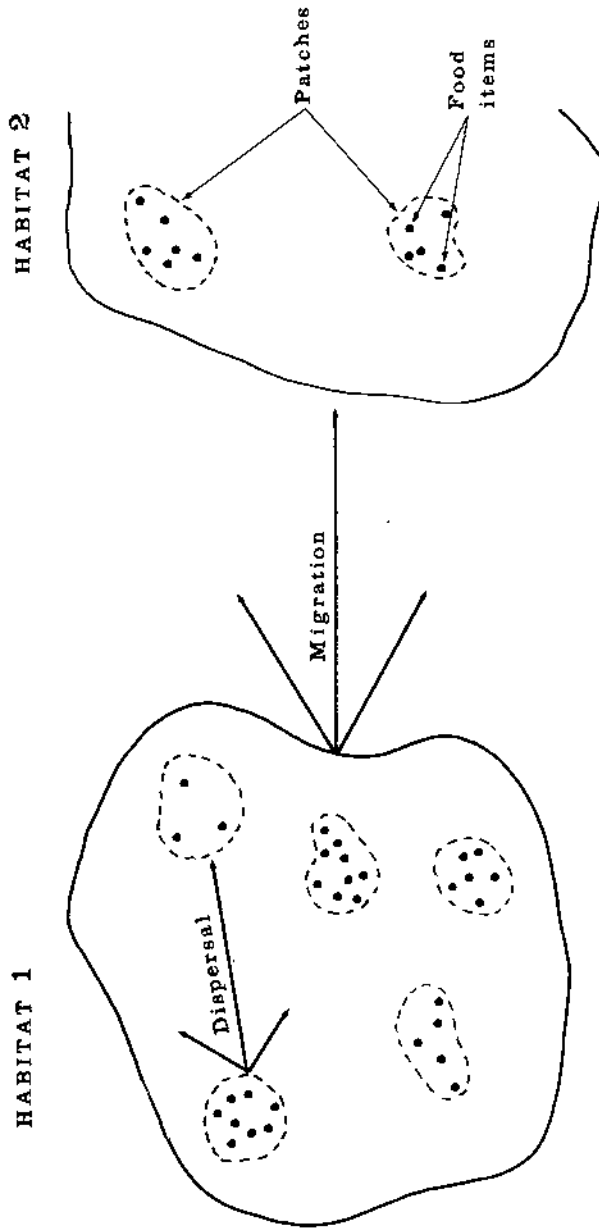


Figure 1 Diagram illustrating the divisions of habitat, patch, and food item. Bold arrows indicate migratory movements between habitats and dispersal between patches.

site, and there is some evidence that other signals, such as the level of ATP, may be used in the location of such items (52). These examples emphasize the existence of a hierarchy of levels in the environment of a forager, each one recognized by characteristic signals that differ if not in their nature, at least in their frequency and intensity.

We turn first to the general components of insect foraging—the encountering of habitat, patch, and food item—and thence to the need to minimize risks while foraging. We then consider polyphagous insects and comment on preference and switching between different food types. Finally, we comment on the categories into which an animal's foraging time may be partitioned.

We have striven to draw parallels between the work on insect predators and parasitoids that already figures prominently in the foraging literature, and that on herbivores (including pollen and nectar feeders) and bloodsuckers. We believe that all such examples may be described within the same framework, although the relative importance of the various components of foraging may differ from one group to another.

ENCOUNTERING THE HABITAT

The identification of specific attractants to which a forager responds is often difficult at the habitat level; it is somewhat easier at the level of the food item or the patch. This may arise because the boundaries of the habitat are the vaguest of the three levels in our hierarchy; or it may be due to the complexity of the habitat and the difficulty in sorting out the significant signals. The usefulness of including the habitat as a level above the patch arises when we distinguish between migration on the one hand, and local dispersal among patches on the other. Migration is by definition a process that causes a forager to leave one habitat with the chance of encountering another, and must, at least at times, be an important aspect of the overall foraging process. Migration has been the subject of several reviews (e.g. 35, 94). Two aspects are of particular importance to this review because they represent the junctions between foraging and migration: (*a*) the factors that stimulate facultative migration, and (*b*) the mechanisms that increase the probability of encountering a new habitat.

Although the general level of migratory activity of a species is an evolved adaptation (93, 155, 158), its actual extent in any population is often (34), and perhaps always (165), related to the density of that population. In aphids, for example, crowding leads to the production of alates (88); the stimulus involved, the frequency of contact between individuals (108), is much the same as that which leads to interference in adult parasitoid Hymenoptera (70). Another "trigger" for migration is deterioration in the food supply (29), which leads to an inadequate rate of food-gathering.

There is evidence that the behavior during migration has evolved to maximize the expectancy of arriving in a new habitat. For example, desert locusts' flight is such that they are carried towards the inter-tropical convergence zone, where rain is likely to occur (94, 137). The coccinellid *Hippodamia convergens* makes use of the 55°F thermocline as a "guide" on its migration in May and June from the San

Joaquin valley in California to the Sierra Nevada and also in February and March on its return flight to the San Joaquin valley (66). On a smaller scale, the first instar nymphs of the salt marsh aphid, *Pemphigus trehernei*, float on the water surface of high tides and in this way are likely to be deposited along the edges of gulleys where their host plant, the sea aster, grows (48).

Sometimes the patch attractants may themselves be responsible for the attraction to the habitat. For example, Finch (45) has shown that the cabbage root fly, *Erioischia brassicae*, is attracted over considerable distances by the mustard oil glucosides emanating from Cruciferae. These mustard oils may also play an important role in habitat location for other crucifer-eating insects, since they have been shown to be important for host plant selection by various Lepidoptera (86, 168), Coleoptera (44, 163, 164), and hymenopterous parasitoids (87, 138).

ENCOUNTERING THE PATCH

The range of behavior displayed by foragers in locating patches is considerable. Some respond directly to patch-specific stimuli while others may be remotely attracted by the food item itself and thus encounter the patch almost incidentally. This is particularly the case among predators and parasitoids where the food item is totally different from the patch. The food item for a herbivore, being a small part of the patch itself, is less likely to be chemically distinguishable at a distance.

In general, patch-specific attractants carry little information about the density of food items and thus would not contribute to the aggregation of foragers in the most profitable patches. Thus the parasitoids *Alysia manducator* and *Nasonia vitripennis* are known to be attracted to the odor of carrion, whether or not their hosts are present in the meat. There are also several examples of parasitoid females being attracted to the food plant of their phytophagous hosts rather than to the hosts themselves. Thus both *Apanteles glomeratus* and *Diaeretiella rapae* locate cruciferous plants upon which their hosts feed by response to the volatile mustard oils referred to above (87, 138). Furthermore, van Emden (40) has recently shown that there is less parasitism of the aphid *Brevicoryne brassicae* by *D. rapae* on cabbage varieties low in these oils. A similar example of a partially protected host population is provided by *Lygus lineolaris*, which is attacked by the parasitoid, *Leiophron pallipes* (162). The host is found on several species of grasses and herbs, but significant parasitism only occurs on host plants in the genus *Erigeron*. An odor from *Erigeron* is presumably particularly attractive to *Leiophron*. A further example in a similar vein is provided by the wheat bulb fly, *Hylemyia coarctata*, whose larvae locate wheat plants in the soil by means of an exudate from the base of the stem and roots that acts as an arrestant for the roving larvae (154). Interestingly, oats are immune from attack by this species and this is thought to be due to another specific chemical, which in this case acts as an anti-arrestant.

Sometimes the release of the patch stimulus is a function of the presence of the prey within. The parasitoid *Heydenia unica*, for example, responds directly to a volatile terpene released as a result of feeding by its bark beetle host (21). Similarly, the parasitoid *Itoplectis conquisitor* is attracted more to the red shoots of *Pinus*

sylvestris than to the green ones, the reddening being due to infestations of its host, the moth *Rhyacionia buoliana* (3). Other examples have been provided by Monteith (121) and Bragg (16).

Signals arising directly from the food item also attract insect foragers. There are, for instance, clear examples in which parasitoids are attracted by their host's sex pheromones (119, 161). More recently, examples of acoustical orientation to hosts have been reported. The tachinid, *Euphasiopteryx ochracea*, which parasitizes the cricket, *Gryllus integer*, is attracted by the male cricket's song (18); and the sarcophagid parasitoid, *Colcondamyia auditrix*, responds to the mating song of its cicada hosts (157). In both instances parasitized males are incapable of producing songs, an interesting means of preventing superparasitism.

Comparable mechanisms for patch-location are widespread in insects other than predators and parasitoids. Bloodsucking insects, for example, respond to such general cues as the carbon dioxide output and the visual signals of a moving animal, which in tsetse flies (*Glossina* spp.) lead to the formation of a "following swarm" associated with herds of grazing ungulates (47, 55). However, as with parasitoids and predators, the specific host odor is often an essential component of the signal (8). Gillies & Wilkes (61-63) found that most mosquitoes were attracted over a larger distance by the odor of the host, than by carbon dioxide alone. *Aedes* species, for example, responded to bait calves from a distance of 22.5 m to 30 m, but with carbon dioxide alone a response was not detected beyond 15 m. Herbivores are likewise attracted to the patch of their food plants by combinations of scent (25, 100, 116) and visual clues (99, 120, 135). Madden's (115, 116) observations on the wood-wasp, *Sirex noctilio*, suggest that it is the concentration of the scent that is critical: shocked or stressed trees transpire more and so liberate greater quantities of the monoterpenes and other volatiles to which the insects are attracted. The rate of release from healthy trees is too low to stimulate *Sirex*.

ENCOUNTERING THE FOOD ITEM

Once within a patch, a forager is subjected to specific patch stimuli as well as to any stimuli that arise from encountering the food item. Patch-localized behavior is therefore a combination of the response to patch stimuli and to prey-contact stimuli (174). In addition, among parasitoids there are instances where chemical "trail markers" are deposited by a forager as areas are searched, presumably to discourage re-searching of the same areas (64, 134). It is noteworthy that "pheromone trails" can have the opposite action within the same order (Hymenoptera), notably those in ants that serve to encourage other individuals to visit the same food source (22).

Prey-contact stimuli strongly influence the ability of foragers to spend longer periods of time in those patches where the rate of encounter with food items is highest [i.e. their aggregative response (70, 71, 73)]. The arrestant stimuli responsible for this are various and have been thoroughly discussed by Waage (174). There may, for example, be a threshold rate of prey encounters, probably influenced by hunger level, below which the predator leaves the patch. Thus, Lindley (109) found that immature lyniphid spiders tend to disperse on gossamer threads from an area

where no prey had been recently captured. Similarly, Turnbull (173) showed that web-spinning spiders abandoned sites that were unprofitable; this led to the accumulation of spiders in regions of higher prey density. A different mechanism, shown by several predators, involves a change in searching pattern following feeding. This is well shown by a "pseudopredator," a housefly, searching for sugar droplets distributed in clumps on the floor of an arena (124). There is a pronounced increase in turning rate (klinokinesis) and a reduction in speed of movement (orthokinesis) when search is resumed after each feed. This behavior then decays to the prefeeding pattern within approximately 30 seconds if it is not reinforced by the location of further droplets. A similar sequence was observed for the anthocorid predator *Anthocoris confusus* feeding on aphids (43), but here the turning behavior lasted for approximately 8 minutes, a difference probably related to the predator's search rate and the average patch size of its prey. Other examples of increased turning behavior are particularly plentiful among insects and mites (e.g. 6, 7, 24, 46, 72, 106, 141).

Plant-feeding insects commonly detect food items by gustatory signals (150-152). The Hemiptera probe plants with their rostra; this probing is clearly the final stage in foraging, involving both selection and acceptance (89, 122, 133). In the cabbage aphid, *Brevicoryne brassicae*, the frequency and duration of both probing and walking have been shown to vary according to the plant: On the favored host, feeding periods were longer and searching periods shorter and less frequent (see Table 1). Such examples show the parallels between the behavior of predators and herbivores.

The proportion of an animal's life spent searching for food items varies greatly, and depends on the ratio of the size of the items to the total resources required (Figure 2). Predators such as coccinellids and the Odonata tend to occur toward the lefthand side of the Figure; they spend much of their total life searching for individual food items. (Because of their size and hence large resource requirements, most vertebrates also fall in this region). Pollen and nectar feeders are similar to predators in this respect. Herbivores, on the other hand, tend to fall toward the right of the Figure; the extreme is represented by leaf-miners and gall-dwellers, which consume only one food item in their lifetimes. In this they are similar to insect parasitoids,

Table 1 Time allocation by apterous cabbage aphids (*Brevicoryne brassicae*) on cabbage and bean plants. Symbols as in Table 2. [After Tjallingii (169)]

	Cabbage	Bean
Average duration (in sec) each probe (t_h)	350	60
Average walking time (in sec) up to first probe	40	60
Percentage of time spent feeding $\left(\frac{100 \cdot t_h N_a}{T_{pi}} \right)$	70	25

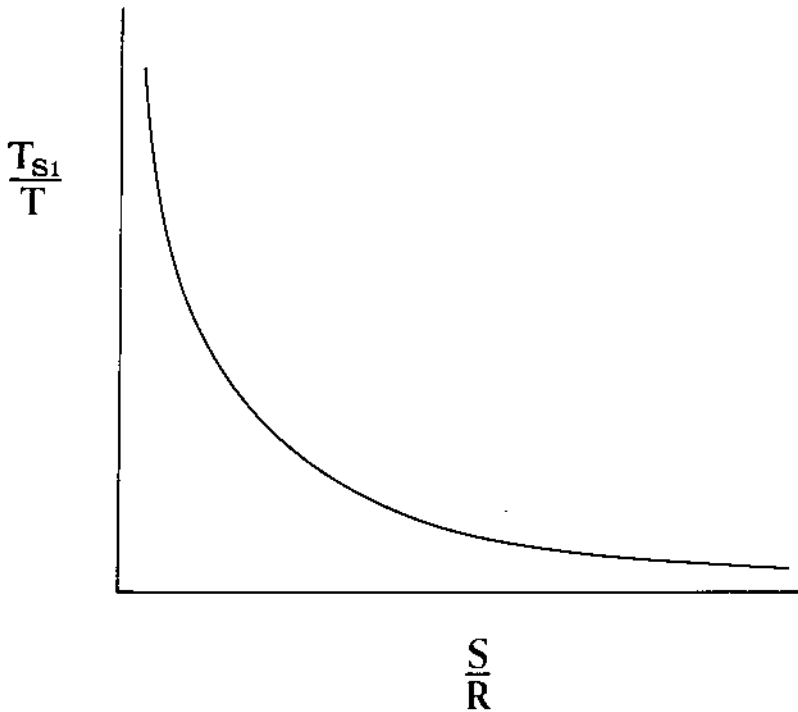


Figure 2 The supposed relationship between the proportion of an animal's life spent searching for a single food item (T_{S1}/T) and the size of the item in relation to the total resources required in its life (S/R).

whose larvae normally feed on a single food item that has been procured by the adult. This separation of the searching and feeding stages is a particular feature of the insects and has allowed larvae and adults to become markedly specialized for their different ways of life (105, 160). Interestingly, some insects regularly leave large food items, presumably because the risks of remaining on them outweigh the difficulties in obtaining another meal: bloodsuckers such as the bed bug, *Cimex lectularius* (93), and herbivores such as the weevil, *Otiorrhynchus* sp. (31), illustrate this behavior.

NONRANDOM SEARCH

The responses to host-mediated patch attractants, to host attractants themselves, and to arrestant stimuli following the encounter of a host or prey, combine to make it unlikely that the allocation of searching time among patches will be at random. Random search implies that the same number of foragers spend on the average the same period of time in each patch. This is a convenient assumption to make mathe-

matically, since the zero term of the Poisson distribution then becomes the basis for population models, but it is undoubtedly a poor assumption biologically. Prudent foragers, those that spend more of their searching time where food is plentiful rather than where it is scarce, should be at a selective advantage.

The question of the efficiency of patch-time allocation has prompted the development of several optimal foraging models for predators (26, 32, 42, 111, 146, 147), all of which attempt to compute the ideal allocation of foraging time to maximize prey capture rate and hence fitness. The tendency in all these models is towards the reduction of all patches to the same rate of prey capture. Excellent reviews of this body of work have recently appeared (103, 136) and we therefore make no attempt to emulate them here. That of Cook & Hubbard (32), however, deserves brief mention since it is aimed specifically at insect parasitoids. Their predictions are based on the parasitoid attack model of Rogers (144) and take the form of an optimal distribution of time between the set of host patches to be visited. The crucial parameters that influence the time budget are the total time available, the search rate within a patch, the handling time, and the transit time between patches. Using data from the ichneumonid parasitoid *Nemeritis canescens* (68), Cook & Hubbard found a broad qualitative agreement between the observed and predicted time budgets.

Since foragers are unlikely to be aware of the profitability of a patch before it is sampled, the manner in which time is allocated among patches depends crucially upon the criterion adopted for leaving a patch. In this context, Waage (174) lists four different behavioral mechanisms that could determine the duration of a patch visit. (a) *Fixed Number* mechanisms: The forager leaves a patch after a fixed number of food items have been captured. This is the "hunting by expectation" hypothesis of Gibb (56). (b) *Fixed Time* mechanisms: The forager leaves after a fixed amount of time has been spent in a patch. This is the "hunting by time expectation" hypothesis of Krebs (102). (c) *Fixed Searching Time* mechanisms. The forager leaves after a constant *searching* time per patch. (d) *Fixed Rate* mechanisms. The forager leaves when the capture of food items falls below a fixed threshold rate.

Among these, the fixed rate mechanism is at the heart of most optimal foraging models. In contrast to the population models of Hassell & May (73) and Murdoch & Oaten (129) where the threshold capture rate was assumed to be constant, optimal foraging models such as that of Charnov (26) assume that the giving-up threshold depends upon the average prey density in that particular habitat. The predators should tend therefore to reduce all patches to the same "marginal value," which is the predators' expected rate of intake for that particular habitat.

A most detailed study of the criteria for leaving a patch is that of Waage (174) on the ichneumonid *N. canescens* parasitizing flour moth caterpillars within circular dishes serving as patches. On the basis of his experimental observations, Waage proposed a more complex behavioral model than those listed above (Figure 3). Patch time is now determined primarily by two factors acting together. First, the amount of patch odor (due to hosts) sets a level of responsiveness, which then decays with time on the patch. Second, any oviposition serves to increase this responsiveness by a set amount and so prolongs time on the patch. The parasitoid finally leaves the

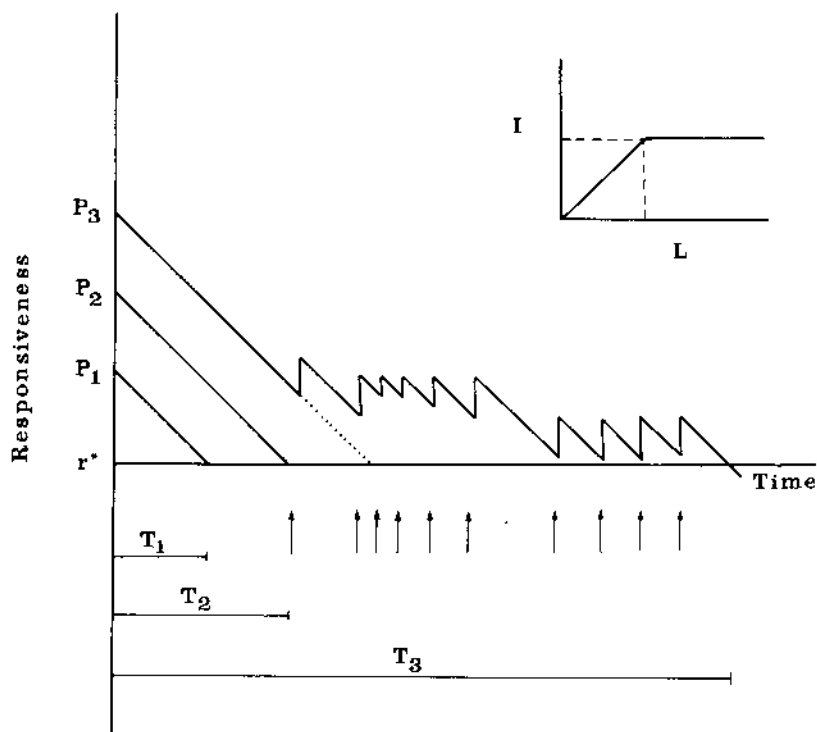


Figure 3 Graphical representation of a patch-time model based on experiments with *Nemeritis canescens* searching for *Plodia interpunctella* larvae. P_1 , P_2 , and P_3 represent different levels of responsiveness set by patch odor from three patches of different host density. r^* is the threshold level of responsiveness below which the parasitoid leaves the patch. The arrows indicate an assumed distribution of ovipositions along the time axis. Each oviposition leads to an increase in responsiveness as defined by the relationship in the inset, which shows the effect (I) of an oviposition in relation to the time since the previous oviposition (L). T_1 , T_2 , and T_3 are the total times spent in each patch. [From Waage (174)]

patch when this responsiveness decays below a threshold level (r^*). Many refinements could be added to this model. For instance, the level of responsiveness set by host odor, the extent of the increment in responsiveness after each oviposition, and the threshold level are all likely to be influenced by the parasitoid's "ovipositional drive," which is largely set by the number of eggs in the oviducts.

Honey bees are excellent subjects for the study of foraging behavior. Their foraging has excited the attention of biologists since the time of Aristotle, and observations on their foraging area and flower selection go back for over 100 years (50, 140). One of the most detailed studies is that of Ribbands (139), whose data clearly show that bees move nonrandomly from flower to flower. In one of his experiments, for example, a bee was observed foraging in a bed of *Eschscholtzia*. Random flower

selection would have led to an equal tendency for successive flower visits to be "higher up" or "lower down" the bed than the previous one. In fact, out of a total of 187 flowers visited, the bee was seen to continue in her previous direction of travel on 155 occasions. Normally the bee moved only short distances between flowers (food items), sometimes even revisiting the same flower. However, when the blossoms started to close in late afternoon, she had a marked tendency to move long distances from one portion of the foraging area to another (i.e. as the profitability of the patch fell there was a tendency to change patches). From several quantitative studies, Ribbands concluded that the tendency to change patch was determined by "memory of the relative yields" from various flowers in the immediate past. He also found that the number of flowers visited per trip was inversely related to the likely pollen or nectar yields of the flowers. Pollen gatherers averaged from 7 to 120 flowers visited per load depending upon the pollen content per flower, while nectar gatherers averaged from 250 to 1446 flowers visited. Thus, although bees probably have a fixed rate mechanism for leaving a patch, the threshold is adjusted in relation to experience of the yield from that type of flower.

THE INFLUENCE OF RISKS WHILE FORAGING

The optimal foraging models mentioned above have suggested testable hypotheses and focussed research on the way that foragers exploit a patchy environment. However, factors other than those maximizing food intake may be crucial in shaping the allocation of searching time. Foremost among these in many insects is the need to minimize the forager's risk of death.

Observations on vertebrates frequently show that the presence of a predator inhibits foraging. Although less dramatic, similar observations are widespread among insects. The most frequent adaptation is to forage when natural enemies are inactive. Thus many plant-feeding insects are inactive during the day and adopt positions to enhance their crypsis (78). This reduces their vulnerability to insect predators such as ants (*Formica* spp.), which often overlook immobile prey (4), and to parasitoids (77), as well as to birds. Such adaptations, however, only affect the periods of foraging activity; they do not alter the time allocation per patch during foraging. But examples also occur of actual foraging behavior that reflects the need to minimize the risks from predation. Green & de Freitas (65) found that the frass-drop rate of sawfly larvae, which is related to their feeding rate, fell in the presence of certain parasitoids. The various types of the forest tent caterpillar, *Malacosoma disstria*, adopt different foraging tactics that have been shown to alter their susceptibility to attack by certain parasitoids (91). Charnov (27), in analyzing C. S. Holling's data on mantid predation of houseflies offered at different distances, concluded that the experiments support the optimal diet prediction (see below) that flies at increasing distances (the less profitable ones) should only be included in the diet as the food abundance declines. He also points out, however, that an alternative plausible explanation is that a moving mantid is more susceptible to predation, than a still one and hence is unlikely to stalk prey (i.e. take the more distant flies) unless the food level is low and the mantid hungry. Perhaps the extremes of a risk-averse

foraging strategy are to be found among such "sit-and-wait" predators as the damselfly larva, *Ischnura elegans*. When moving, and particularly swimming, they are in great danger from fish predation. It is tempting to conclude that this explains their great reluctance to leave a "fishing perch," even when threatened by starvation (J. H. Lawton, personal communication).

Foraging may also increase the exposure to physical risks. By leaving shelter, the insect can become susceptible to desiccation, thermal shock, or drowning (81); for plant-dwelling species there is always the danger of dislodgement. The change in the diel foraging pattern between wet and dry seasons in the leaf-cutting ant, *Atta* spp., is believed to minimize the risks due to weather (142).

In general, therefore, risk-averse behavior should prolong the time spent in a patch over that predicted from a simple optimal foraging model, provided that the patches tend to act as refuges from mortality.

The risks from predation may sometimes be minimized by group foraging (67, 156, 166, 167, 171, 172) as seen in several aphid species. This depends, however, on a delicate balance between the benefits of cooperative defence (either active or passive) and the possible costs of either increased intraspecific competition or high mortality once the aggregation is discovered by a voracious predator (123, 180). Aggregation as a defence against predators or other natural enemies is only effective if a significant proportion of the individuals are thereby protected from mortality. This refuge effect may result from the predator becoming quickly satiated on encountering the prey so that the colony as a whole is not significantly exploited. Alternatively, the refuge of large aggregates may be a physical one—for example, when only the outermost individuals are at risk. This is the case for the tightly packed colonies of the cabbage aphid, *Brevicoryne brassicae*. Those at the periphery are more susceptible to parasitism by the braconid, *Diaeretiella rapae*, than those toward the center (1). A similar observation has been made on a scelionid parasitizing the egg masses of the cacao stink bug (20). A further defence against predation can be the scattering of the prey on attack as observed for larvae of the coreid bug, *Acanthocoris sordidus* (53), and for some aphids (17, 36), although such dispersal can also lead to appreciable mortality from other causes (130).

We should also note here that gregariousness during foraging may serve purposes other than protection from natural enemies. In some aphids, for example, the combined feeding of a colony acts as a "sink" that diverts plant nutrients to the feeding area (176). In social insects, the efficiency of harvesting can be enhanced by group foraging. This has been analyzed for eusocial bees (*Trigona* spp.) by Johnson & Hubbell (95) and for harvester ants by Davidson (33). Their analyses suggest that group-foraging species have the advantage when resources are clumped or abundant, while individual foragers are more efficient when food items are scattered and sparse (Figure 4). Group foraging and trail laying are, of course, widespread among ants (5, 22, 54).

FOOD SELECTION BY POLYPHAGOUS FORAGERS

Some degree of preference is widespread among all groups of polyphagous animals. The preference is usually a species-specific characteristic, although it may in some

cases be modified by experience. Sometimes individuals of the same species exhibit different preferences under identical conditions, and in bees (51, 112), butterflies (85), and mosquitoes (59, 148), this polymorphism has been shown to have, at least in part, a genetic basis.

Preference for a particular food item is normally measured in terms of the deviation of the proportion of that food type eaten from the proportion available in the environment. Such a simple definition belies the complex behavior upon which it may depend. For example, apparent preference may result from differential searching rates, from different times spent in different patch or habitat types, from active rejection of some food types following their encounter and, in the case of predators, from differing abilities of their prey to escape. A variety of indexes of preference have accumulated in the literature, many of which emerge as the same index in different guises. Their evolution, from the work of Scott (153) to that of Jacobs (92), is well reviewed in Cock (30).

Various degrees of preference have been identified in a variety of insects. Host-preference in free-moving bloodsucking insects such as mosquitoes, tsetse flies, and midges has been widely demonstrated (15, 38, 79, 80, 114, 175, 177). The exact definition of preference in these cases has posed difficulties. Certainly, the data on numbers of insects feeding on a certain host must be corrected for the relative abundance of the different hosts (to give a "forage ratio"). The size of the host must

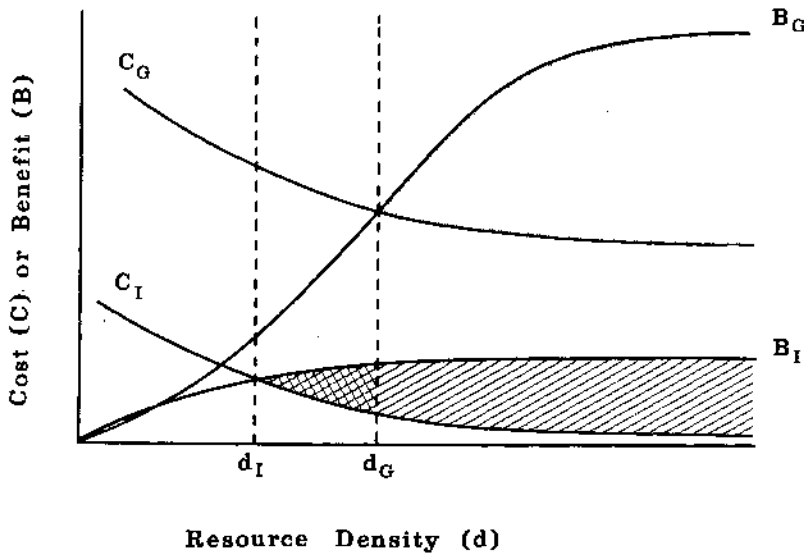


Figure 4 Hypothetical relationships between cost (C) and benefit (B) for group-foraging (G) and individual foraging (I) species. The group forager is more efficient at high resource densities ($d > d_G$; shaded area), but only the individual forager can harvest with net gain when $d_I < d < d_G$ (cross-hatched area.) [After Davidson (33); modified from Johnson and Hubbell (95)]

also be considered; large hosts offer larger targets and presumably emit more odor and carbon dioxide than smaller hosts. The habits of the host and the insect will also make some hosts more available than others (39). Attempts to include all these factors in an index are fraught with difficulties (38), but the application of Cock's (30) method (see below) to bloodsuckers poses even more problems. Comparisons may most reasonably be made between hosts of similar size and habits. For example, Edman's (38) data for seven common species of mosquito feeding on armadillos and rabbits in one area show changes in feeding frequency that follow the changes in abundance of the hosts over four years. In the first two years, armadillos were most abundant; in the next two years, rabbits were most numerous. The pattern of feeding on both hosts showed comparable trends, with a decline in the percentage feeding on armadillos and an increase in that on rabbits in the second two years. (At the same time, the mosquitoes often fed on other animals, especially cattle, whose numbers remained fairly constant.) The pattern was similar in those species that seemed to "prefer" rabbits (e.g. *Anopheles crucians*) and those that fed most on armadillos (e.g. *Coquilletidea perturbans*), suggesting that it is the comparative abundance of the hosts that determines the feeding patterns.

Bees commonly show preferences for one or a few related plant species. Honey and bumble bees tend to show a constant preference for a particular flower type during a day, but this will change over a period of one or two days if flower abundance changes markedly (49, 50, 96, 113). Thus Free (49) found that after one day, 70–90% of pollen gatherers collected pollen from their original source, but after a week only 40–60% did so. The most consistent bees were those that collected the most common pollen, presumably reflecting an adequate rate of food discovery within "their patch." Mixed pollen loads frequently indicated a bee in transition between patches or habitats since the next load would contain only one of the types of pollen.

A more rigorous analysis of preference, one that requires detailed knowledge of the feeding behavior on each food type separately and in various combinations, has been recommended for use with polyphagous predators and insect parasitoids (30, 107, 126). It leads to the following recipe (30):

1. Carry out functional response experiments (71, 83) using each prey type separately. This enables estimates of searching efficiency and handling time for each prey type to be estimated. Any preference resulting from differences in the functional response parameters can now be displayed in terms of the ratios of the prey types eaten plotted against the ratio of their availabilities. Any innate preference will then be detected by a deviation from a slope of unity passing through the origin.

2. Carry out further experiments in which various ratios of the two (or more) prey types are presented together. Ideally, this procedure should be repeated for a range of total prey densities that encompasses those used in the functional response experiments. Any differences between the predicted preference arising from the rates of search and consumption in the separate feeding experiments and that observed from the mixtures will now be due either to an active rejection of one of the food types or to some change in the functional response parameters as a result of the forager's experiencing two food types together.

The value of such an analysis lies in the breaking down of preference into an innate component (i.e. different search rates, handling times, etc for each food type) and a component deriving from any behavioral changes that arise when food types are mixed. Its fault lies once again in ignoring the fact that different prey may exist in somewhat different habitats, which makes preference, like switching (see below), also a matter of differential patch or habitat selection. We should expect, therefore, that preference and switching studies conducted under laboratory conditions will often bear little relation to the natural situation. Many examples indicate this. The nymphs of *Anthocoris gallarum-ulmi* feed readily and develop well on the apple psyllid (*Psylla mali*) in the laboratory, but in the field are confined to aphid galls on elm (2). Many species of adult Coccinellidae show little if any preference when various aphids are presented together in the laboratory (12-14, 90), and yet show a strong preference for a given patch type (90). This, more than any other feature of their behavior, has a marked effect on their specificity. Similar studies have been carried out on aphidophagous syrphids, in particular in relation to the height preferences evinced by ovipositing females (23, 132). These preferences inevitably influence the diets of the feeding larvae. Similar examples abound in phytophagous insects. In Lepidoptera, for example, larvae can survive and develop on a wide range of plants on which eggs are not normally laid (101).

The optimal diet of polyphagous predators has been the subject of considerable theoretical attention (e.g. 26, 41, 110, 149, 178) and the topic as a whole has been excellently reviewed by Pyke et al (136) and Krebs (103). The common conclusion to these studies has been succinctly stated by Krebs (103): "... the models predict that predators should be more selective when food availability (more precisely availability of high quality prey) is high, than when food is scarce. Rather more surprising is the prediction that whether or not low ranking prey should be included in the diet depends only on the availability of high ranking types, and not on the encounter rate with the low ranking prey themselves. In other words, if good quality prey are common enough, the predator should never 'take time out' to eat unprofitable prey, even if they are very abundant." Considerable support for this conclusion has accrued from studies on vertebrates. From invertebrates some support comes from the reanalysis of Holling's (84) mantid data by Charnov (27), who showed that the mantids became decreasingly selective when they are hungrier, although (as mentioned earlier) an alternative explanation involving the risks of movement is plausible.

An important defect in optimum diet models lies in their assumption that prey exist in a homogeneous environment. In this they stand well apart from models for optimal time allocation in a patchy environment. A significant advance will be made when optimum diet theory is based on the same heterogeneous distribution of prey as are other optimum foraging models. A starting point would be the situation where the different food types occur in somewhat disparate patches, with the foragers allocating the greatest fraction of their searching time to whichever patch is the more profitable (145). Under such situations "switching" [*sensu* Murdoch (125)] is to be expected, much as found by Murdoch et al (128) for guppies fed on a mixture of limbless, wingless *Drosophila* adults floating on the water surface with tubificid

worms on the aquarium bottom. The guppies fed disproportionately on whichever prey was most abundant, spending increasing periods of time at the surface as the abundance of *Drosophila* relative to worms increased. An example from insects is provided by the predatory bug *Notonecta glauca* feeding on both mayflies, *Cloen dipterum*, and the isopod, *Asellus aquaticus* (107). Other vertebrate and invertebrate examples are reviewed in (28, 127–129). These examples, and the existing information on free-flying bloodsucking insects and on pollen and nectar gathering social bees (referred to above), conflict with the prediction from optimal diet models that the relative abundance of the different food types should not affect their inclusion in the diet (28).

A further problem with optimal diet models in general is their assumption that a forager can unfailingly rank different prey types. Such omniscience, in fact, is a problem with most optimum foraging models, which make no allowance for the forager's need to sample its environment. An exception to this is Oster & Heinrich's (131) theoretical discussion of sampling by a foraging animal, showing that in an unpredictable environment a strategy of foraging only on the most profitable food without sampling food types becomes suboptimal. Support for their model comes from Heinrich's (76) observations on individual bumblebees that tend to specialize in gathering nectar from one of a range of flower species. The bumblebees are most efficient at foraging on their specialist flower, but nevertheless consistently visit some flowers of alternative species. ["Scouts" and "wanderers" have long been recognized in honeybees (140)]. This would not be the optimum strategy for an omniscient bumblebee in a deterministic environment. In a somewhat similar vein are several other examples: Leaf-cutting ants (*Atta* spp.) sample a wide range of plants, but concentrate their foraging on a small range of preferred species, especially when young leaves are available (143); grasshoppers have been found to ingest only one third of the vegetation chewed (118); lastly, on a larger spatial scale, *Heliconius* butterflies perform "trap lining" flights in which they regularly visit, and so sample, potential oviposition and feeding sites (57, 58).

CONCLUSION

The spatial structure of the environment strongly affects the foraging strategies of animals. This is especially true for insects. Their great mobility enables them to forage on virtually contiguous food items within a patch and also to move between patches or habitats that may be widely dispersed. With habitat, patch, and food item as our framework, the range of behavior to be considered is enormous, from migratory behavior, to inter-patch dispersal, to the various types of patch-specific behavior and how these are affected by the food items themselves.

A conceptual model of insect foraging must therefore be based upon a spatial hierarchy of at least this complexity and should strive to describe how foraging time is divided between the different levels of habitat and patch, and between different activities *within* each of these levels. A simple breakdown of this is shown in Table 2. A forager has a time T available for foraging (here we neglect other time-

consuming activities such as seeking mates, nest building, etc). This time T is made up of the total time spent in all the n habitats visited, and the total migration time between habitats (t_m) (row A of Table 2). Row B shows the time in each j th habitat to be the sum of the total time in all the x patches visited, the total transit (or dispersal) time between patches (t_p), and a further time which we shall call "resting time" (t_r) that is spent outside patches when foraging activity ceases due to insufficient stimulation, or to satiation, or as the result of circadian or other rhythms. Finally, in row C we have the time spent in an i th patch, which is the sum of the searching time there (t_s), the total handling time for all food items eaten in the patch ($t_h N_a$) and once again a resting time (t_r).

One of the contributors to the "resting time" within a patch may be intraspecific encounters between foragers. This is the "mutual interference" that has been noticed particularly in laboratory experiments with insect parasitoids and predators (9, 68, 69, 74, 75). Such encounters lead to an increased probability that one or both foragers involved will interrupt their searching activity for a period of time. More adaptive than such interruption is the outcome that one or both foragers leave the patch as a result of their encounter (68, 69, 104, 117). This will then contribute to dispersal time (t_p) and thus to the possibility of locating a different patch or, perhaps, to departure from the habitat and hence to migration (t_m). It is tempting to think that the very high rates of dispersal of parasitoids introduced for biological control

Table 2 A schematic view of the allocation of potential foraging time between habitats and the patches contained therein

Row	Description
A	$T = \sum_{j=1}^n T_{Hj} + t_m$ <p>where T = potential foraging time, n = number of habitats visited, T_{Hj} = time spent in habitat j, and t_m = total migration time between all habitats visited.</p>
B	$T_{Hj} = \sum_{i=1}^x T_{Pi} + t_p + t_r$ <p>where x = number of patches visited, T_{Pi} = time spent in patch i, t_p = total transit time between patches, and t_r = total "resting time" spent within the habitat but outside patches.</p>
C	$T_{Pi} = t_s + t_h N_a + t_r$ <p>where t_s = time spent searching in patch i, t_h = handling time for each food item eaten, N_a = number of food items eaten within the patch, and t_r = "resting time" within the patch.</p>

[mentioned by Townes (170)] are the result of such a mechanism. In any event, foragers are more likely to leave patches that are, or are likely to become, heavily exploited, and will thus have the chance of finding richer pastures elsewhere.

The spatial heterogeneity discussed in this review is central not only to the understanding of foraging strategies, but also to the population dynamics of predator-prey, parasitoid-host, and probably also plant-herbivore interactions. We feel that links should now be forged between what is known of the population dynamics of foragers in a patchy environment and the burgeoning literature on optimal foraging theory. In particular, it should now be possible to explore predator-prey population models in which the predators' aggregative response to the density of prey per patch is described in the more realistic vein of optimal foraging models.

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