

# SEARCHING BEHAVIOR PATTERNS IN INSECTS

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## INTRODUCTION

Searching behavior is an active movement by which insects seek resources. It is an important kind of behavior because insects thereby acquire food, mates, oviposition and nesting sites, and refugia. Since these resources are absolutely essential for the growth, development, and maintenance of the individual, and for ensuring the success of future generations, efficient searching mechanisms and accurate assessment mechanisms are crucial for an individual's chances of survival and reproduction. Searching behavior incurs costs in addition to the energy used for locomotion. These costs include the risks of predation while engaged in searching, and the time taken away from other activities such as holding territory or protecting nests. Natural selection, presumed to be the driving force for morphological and physiological adaptations, would also be expected to favor searching mechanisms that maximize the difference between searching costs and benefits and that reduce various types of risks incurred while searching.

Searching behavior represents the confluence of three kinds of factors: (i) the biological characteristics and abilities of an insect, including locomotory patterns and perception of sensory information, (ii) external environmental factors determining the resources available and the risks inherent in their quest; and (iii) internal factors, such as deprivation or sexual receptivity, determining what an individual needs at a particular time.

## ENVIRONMENTAL STRUCTURE AND RESOURCE DISTRIBUTIONS

It is difficult to know how animals perceive their environment, but it is likely a hierarchical system with resource items (individual mates, prey, food,

shelter, or hosts), patches (aggregations of resource items or spatial subunits of the foraging area in which aggregations of food items occur), and habitats (clusters of patches) (42).

How are spatial and temporal distributions of resources manifested as constraints on searching activity and searching success? In four ways: (i) Because of the hierarchical nature of spatial distributions of resources we would expect insects initially to use gross cues, indicative of certain habitats, then to home in further using patch cues, and finally to seek individual resources. Hence, search behavior at the habitat level can affect search at the patch, and search at the patch can affect search for individual resources. For example, the success and experiences of apple maggot flies, *Rhagoletis pomonella*, in a tree can have a marked effect on the behavior of the fly when it finds a fruit cluster (70). (ii) The periodic nature of temporal distributions means that animals must be able to restrict search to the most productive times if they are to locate resources efficiently. The temporal nature of search activity often depends on endogenous timing mechanisms or on behavioral mechanisms such as following other individuals that are finding resources. For example, pollen is shed and nectar is produced by *Anguria umbrosa* early in the morning and by *A. triphylla* in the afternoon. *Heliconius* butterflies adjust their foraging by visiting *A. umbrosa* in the morning and *A. triphylla* in the afternoon, thus reducing uncertainty and ensuring against periods without resources (33). (iii) Movements between and movements within resource units (i.e. resource, patch, habitat) can be distinguished. An insect's movements between all of these units have similar characteristics, such as that the insect relies upon environmental cues or topographical contours to move in a relatively straight path. Movements within the units may also be quite similar and can usually be characterized as mechanisms for restricting search to the unit. The term *local search* applies to locomotory movements and scanning within a patch; when an animal leaves a patch or a resource and seeks others, regardless of its orientation mechanism, it is *ranging* (51). (iv) When resources decline below required quantities or quality because of changes in seasons or for other reasons, animals have alternative strategies. Thus, animals *migrate* between habitats, or they may diapause or hibernate under extremely impoverished conditions.

## INFORMATION AND ORIENTATION

### *Information for Locating Resources*

The types of information used by insects to guide search orientation are: sensory information, perceived from the external environment as an animal searches, and internally derived proprioceptive or internally stored genetic information (9, 10, 49, 51, 76).

**NONDIRECTIONAL SENSORY CUES** A nondirectional cue, such as a puff of pheromone, may "alert" or "arouse" an insect to the presence of a resource or to a nearby predator, but the source of the cue cannot be localized. The following principles apply: (i) A nondirectional cue of one modality may change a sensory threshold or input template of another modality (e.g. visual pattern recognition), a process called "cross-channel potentiation." Thus, male sweat bees, *Lasioglossum zephyrum*, are attracted to small dark objects when they perceive female sex pheromone (8). (ii) Response to a non-directional cue may initiate a hierarchy of behavioral acts leading toward gathering of more precise information. An insect can generally remain nearly motionless and often hidden while scanning with chemosensory receptors or tactile organs; it will thus be inconspicuous to predators during the initial phase of information gathering. If sufficient stimulation is received, the insect may then expose itself to potential predators by initiating local search.

**DIRECTIONAL SENSORY INFORMATION** Directional information from biotic sources includes trail-laying and trail-following, commonly used in recruitment and as foraging guides by ants and termites (e.g. 96), chemical gradients of pheromone or food odor (5, 28), sound waves (e.g. 75), and direct visual localization (e.g. 39). Insects use topographical features to direct their searching when cues from resources cannot be detected. For example, the predatory mite *Amblyseius potentillae* follows leaf veins or edges while searching for prey (74).

The following principles pertain to the use of directional information: (i) Perception of directional information may cause a switch over from non-directional information to control its orientation: Male grain beetles, *Trogoderma variabile*, switch from sex pheromone-stimulated local search to upwind orientation when a wind current is supplied (85); if the the wind current is terminated, the beetle switches back to local search. (ii) The accuracy of orientation improves with stimulus intensity: females of the cricket *Gryllus campestris* pursue their course direction more precisely as the intensity of the calling song increases (75). (iii) The precision of directional information varies according to modality, so that animals may switch from olfaction (less precise) to vision (more precise) when given the opportunity. (iv) Insects integrate directional cues from more than one modality, as when onion maggot flies, *Delia antiqua*, find and assess onion plants through olfaction, vision, and contact (39). Studies dealing with only one modality inaccurately portray the mechanism used to locate resources and underestimate the real amount of information available.

Directional information from the abiotic environment is also used in searching behavior. There are two categories. First, insects orient at some angle relative to a wind or water current. The current may carry a stimulus, such as

food odor or pheromone, providing a stable directional vector for locating food, mates, and shelters. Second, celestial cues are prominent landmarks by which animals navigate; the long distance of these objects from earth guarantees a constant angle to them (94). The disadvantage of celestial cues is that they change seasonally and daily, and they differ according to geographical latitude. Thus, the information must be integrated with that from biological clocks for an animal to navigate accurately. *Pieris rapae* cannot compensate for the apparent movement of the sun, and it migrates in a series of arcs rather than in a straight line as its heading shifts over the course of each day (4).

**INTERNALLY DERIVED OR STORED INFORMATION** At least some aspects of search orientation operate in the absence of continuous sensory input from the environment, primarily because spatial cues can be stored within the organism. Searching behavior draws upon information from motor commands and proprioceptors. When an ant forages along a route  $30^\circ$  to the left of the sun and is displaced for some reason  $10^\circ$  further to the left, it can, in the absence of the sun to guide it, turn back  $10^\circ$  to the right and onto its previous course. The ant has used information derived from its proprioceptors to "calculate" the error angle, and this information is then "recalled" for turning back to the original course (49). Internal information can also be stored genetically or derived from exogenous sources and stored internally (50). Genetically stored information is exemplified by an isopod (*Armadillidium nasatum*), which turns at a certain angle to reenter a resource patch (80) and by the sequences of moves and turns in local search of other arthropods (reviewed in 9).

How an animal searches is thus partly controlled by information stored internally and partly by information perceived from the internal and external environment. Variation can be embedded in any of these sources of information, and variation can also originate during the execution of the instructions based upon these information sources. Variation built into the locomotory activities of an individual can be adaptive for avoiding attacks by predators and for increasing the perceptual zone during scanning.

### *Scanning*

An important component of search orientation is scanning, the set of mechanisms by which animals move their receptors and sometimes their bodies or appendages so as to capture information from the environment efficiently. Some insects locate resources by casting their bodies or appendages to the left and right of the path, thereby increasing the arc within which prey can be contacted laterally, e.g. larvae of nectivorous flies (Syrphidae) and lacewings (Chrysopidae) (6, 17). The antennae of the American cockroach, *Periplaneta americana*, provide both tactile and olfactory inputs, scanning the environ-

ment in a systematic fashion by tapping the substrate and moving through the air (58).

In scanning the following principles apply. Scanning the environment for resources can be accomplished through physical contact or by visual, chemical, or auditory channels. Most animals scan for resources periodically, a process termed "saltatory search" (67); no scanning is done while moving. This prevents noisy signals and eliminates the problem of discriminating between stationary and moving objects. At one extreme are ambush species that seldom move between long periods of waiting (ant lions, web-building spiders, filter feeding insects in streams, praying mantids). At the other extreme are species that spend most of their time searching (nectivores). In between are species with shorter cycles, alternating frequently between searching and waiting (coccinellid larvae). Both search modes are ways to sample the environment, but the environment "moves past" a waiting insect, whereas the searching insect "moves through" its environment. (iv) The interscan interval may be dependent on whether or not the animal is locating resources, or on environmental factors such as turbidity. How an insect scans is related to the kind of resource it seeks, its own perceptual abilities and movement patterns, and the structure of its appendages.

### *Timing of Search Bouts*

Searching at the right time is as important as searching in the right place, because certain kinds of resources are required periodically rather than continuously. In addition, these resources change both over the short term and the long term. The temporal organization of searching can be based on stimuli emanating from resources, the searching rhythm, or the physiological state. Male insects that begin to search when they detect female sex pheromone exemplify the effect of a resource stimulus. Such responses to external cues are constrained, however, within certain time frames that are determined by circadian rhythms and the physiological state of the animal. Thus, an animal will not (usually) search for food when it is satiated or during its normal inactive period, even if it perceives resource-specific cues. Searching rhythms (circadian, lunar, or circannual) seem to have evolved either in response to competition for similar food sources or to predation. Superimposed upon rhythmic initiation factors are environmental cues that directly affect searching activity. Females of *Pieris rapae* develop eggs, but they refrain from ovipositing during overcast weather (34); an excess egg load builds up, and then on the first fair day they search for host plants and rapidly oviposit. A common proximate mechanism that triggers search behavior is cyclic change in response thresholds that are keyed to circadian rhythms. For example, in male *Trichoplusia ni* there is a circadian change in the threshold for a

behavioral response to sex pheromone (69). Searching behavior may be initiated according to an animal's "physiological state," as in the blowfly *Phormia regina*. Dethier (23, 24) has unraveled the neural and endocrine circuitry that explains why the blowfly begins searching and feeding and why it stops feeding and searching.

### *Resource Assessment*

An animal can assess the quality of a resource unit so as to restrict its search to the best habitats, patches, or resources by comparing "what it knows," its reference, with information perceived at the resource unit. The penalty for inappropriate "decisions" is severe: Eggs fail to hatch when oviposited at unsuitable sites, and offspring may be sterile when males mate with females that are too closely or too distantly related.

A few principles apply across resource types and taxa. A reference may be genetically specified, but experience allows for alterations in quality assessments relative to global changes in resource unit quality, so that an animal's acceptance criterion shifts appropriately. An animal may be able to perceive a resource from some distance and assess it according to specific features or cues, and then approach or pursue the resource (e.g. cricket calling songs). Alternatively, the searcher may detect cues from the resource at some distance from it but may not be able to complete an accurate assessment until it localizes the resource (e.g. host-plant odor). Many types of resources are distinguishable based upon species identification. For example, in the onion maggot fly, *Delia antiqua*, alkyl sulfides mediate host-plant finding and, in combination with specific visual patterns, provide a host plant assessment mechanism (39, 40). Female *Pieris rapae* can recognize the physiological state of plants (untreated or treated with fertilizer); they prefer to lay eggs on fertilized plants. This decision translates into a fitness advantage for the offspring (64). The presence of other users or competitors is an important criterion. In some cases groups of individuals cause interference with resource acquisition or simply sharpen the competition.

## SEARCH MECHANISMS

### *Search Patterns Restricting Insects to Profitable Patches*

Four basic ways exist to restrict search to a profitable patch: The first is a looping or spiraling local search; the animal maintains a turn bias to the left or right, which readjusts over time to straighter locomotion, or it may make zigzag patterns in which the animal alternately moves to the left and right, then readjusts toward straighter locomotion by decreasing the frequency of alternation. Local search is uniquely designed for finding other resources in a patch

once the first one has been utilized. For this reason, local search stimulated by resource utilization is sometimes referred to as "success-motivated search" (89). After resource utilization releases a local search program, the motor pattern then readjusts over time until the motor pattern exhibited prior to resource utilization is reached. Resource-specific cues such as food odors or sex pheromones can also evoke local search. When resource-specific cues stimulate local search, the animal may eventually habituate to these stimuli and leave the patch. Regardless of the proximate mechanism, transition from local search to ranging or some other emigration mechanism ensures not only that an animal will search intensively at the appropriate time and place, but also that it will terminate search and emigrate before too much energy is expended searching a depleting patch. The adaptive significance of this strategy is that an animal searches an area more thoroughly where it has already encountered host or prey; by doing so its chance of finding others is increased. This tactic would fail, however, if resources were sparsely distributed rather than aggregated.

The second way to restrict search is for the animal to decrease movelength (distance walked before stopping to scan) after finding a resource, and to increase movelength when a resource is not encountered.

The third method is leaving a resource in a direction that differs from the arrival direction, as in bumblebees that turn several times around on a rewarding head of clover, which contributes to the randomness in their take-off direction (44).

The fourth way to restrict search is to turn back into a patch when the edge of a patch is detected. For example, a mealworm beetle, *Tenebrio molitor*, remains within a simulated resource patch of high humidity surrounded by an environment of low humidity by turning back in whenever the edge is reached (43).

### *Leaving a Patch Before the Point of Diminishing Returns*

Depletable patches differ in quality before the animal begins to utilize resources, and resource availability within a patch decreases because of a predator's activities. Other things being equal, a profitable patch can usually be defined as one with a relatively high initial resource density, because high density usually translates into a greater resource procurement per unit time than does low density, and most species spend their time in patches with the highest density of resources (41).

**SIMPLE MECHANISMS** If an animal switches to local search after it uses a resource, and if searching in a patch is simply the repetition of this time-dependent change in the motor pattern, this simple mechanism could indirectly determine when, in relation to declining resources, an animal will

leave a patch. For example, each time a *Coccinella septempunctata* larva ingests an aphid, or an adult *Musca domestica* ingests a sucrose drop, locomotory rate decreases and turning rate increases; this is followed by a decay in both measures toward the prefeeding values (16, 62). The proximate mechanism for leaving the patch seems to be that the relatively straight emigration pattern, to which the insect averages after using a resource, decreases the probability of contacting a resource and thus increases the probability of leaving the patch (32). As might be expected, the time spent in a patch is greater when the initial density of resources is high. Another simple mechanism determining when some parasitoids leave a patch is that they become habituated to odors released by hosts within a patch (83, 90,). A wasp within a patch responds to host odor by probing, decreasing locomotion, and by sharp turns back to the patch edge whenever the patch edge is encountered. In the parasitoid *Venturia canescens*, patch time is determined by “the interaction of two incremental processes, the response to the contact chemical stimulus and the response to oviposition, and one decremental process, the waning of the response to the patch edge . . . through habituation” (91). Thus, habituation to host odor in combination with threshold changes in response to resource utilization, constitutes a “timer” for regulating the duration of a patch visit. Habituation is analogous to satiation in flies, and the change in threshold caused by oviposition in the wasp is analogous to the change in locomotory pattern after feeding in the flies.

**SEARCHING BY EXPECTATION** Sometimes insect foragers appear to make decisions about which patches to use based on an “expectation” of a given habitat (e.g. 55), but there are always simpler explanations that satisfy the data. For example, Waage’s (91) results tell us that an animal does not have to “know” at any moment in time the locations and the current profitabilities of patches in a habitat in order to “compute” the optimal set of patches for exploitation. Instead, animals such as parasitoids, houseflies, and lady beetle larvae need only innate responses; they need not depend upon information gained from previous experience.

### *Returning to Previously Visited Patches*

For resources that are renewed or recycled, cropping and traplining are two mechanisms that promote revisiting after a strategic period of time. Traplining insects learn a route and follow it during each search bout, or they learn a certain time interval and search only during that period. For example, individual *Heliconius* butterflies move in a similar sequence between plants from one foraging bout to the next (33). Individual desert ants (*Cataglyphis bicolor*) crop dead arthropods in the vicinity of the nest (37, 95) so as to prevent overlap of areas searched by each individual each day. Another way



to avoid revisits is simply to leave a patch before using all of the resources. This strategy, which would make sense only if resources were plentiful, is exemplified by bees which leave flowers after visiting fewer than the available number of nectaries or after visiting fewer than the available flowers on an inflorescence (53).

### *Learning To Search Efficiently*

If a species has the ability to profit from experience, it can improve its searching efficiency by responding appropriately to changing environments and by capitalizing on information gained through sampling resource patches. Experience may affect subsequent choices among resources or the way an animal searches in a resource unit.

**CONDITIONING** For those species that learn, conditioning is the most common type. Animals commonly learn that one kind of resource (e.g. species, color) of a given resource type (e. g. flower, fruit) is more profitable than another kind, and they subsequently "specialize" on the most profitable resource (e.g. 57). Under conditions of a changing resource environment, when flower constancy is no longer advantageous, nectivores avoid problems of variable resources by "majoring" and "minoring": They concentrate on one species, but they keep sampling one or two other flowers as a type of bet-hedging (46). Another factor competing with constancy is maximizing the ratio of energetic gain to the costs of moving between flowers (92). Where flower species grow intermingled (rather than in clumps), the flower-constancy strategy is not likely to yield the maximum caloric intake for a bee, and under these circumstances, they should fly to the closest flower rather than searching according to color.

**EXPERIENCE** Experience plays a significant role in the arrestment of female parasitoids, such as *Pseudocoila bochei*, on host patches (56). Inexperienced females which showed no arrestment response to a patch containing host odor were exposed to their host, *Heliothis virescens* larvae, in association with the kairomone within one hr after an initial test. After parasitism of several larvae, the formerly inexperienced females were reexposed to a kairomone-contaminated patch, and all of them were arrested. Thus, experience with the cues involved in parasitism led to a change in behavior the next time these cues were perceived. The result is increased efficiency via arrestment in a host patch. In another example, young *Apis mellifera* on their first flight from the hive showed no navigational ability even from distances as short as 20 m, unless by chance an individual arrived sufficiently close to the hive to recognize it by olfaction as the home site (30). At the beginning of the first exploratory bout, bees examine the hive by flying in front of it for a few

seconds before heading off away from the hive. They return a few minutes later and hover in front of the hive before settling. During this flight, by a combination of sun compass and distant landmarks, the bee establishes the position of the hive relative to the surrounding landmarks. Even after the outward phase of its first exploratory bout, a bee can return to the hive from a distance of several hundred meters, and after several bouts it can successfully return to the hive from distances up to 8 km.

**PATCH SAMPLING** An important asset where patches differ in quality is the insect's ability to sample among patches and to use this information to determine if the current patch is still more profitable than some other patch in the habitat. The frequency of sampling between patches is affected by the variance in patch quality, distance between patches, and perceptible sensory cues related to patch quality.

Houseflies can sample among patches and feed primarily in the most profitable patch without learning anything (31). When two patches have sucrose drops of equal concentration, flies spend the same amount of time in each patch. When the patches differ, flies spend more time in a 2.0 M than in a 0.125 M patch. The proximate mechanism for what appears to be "sampling between patches" is simply the consequence of variability in local search duration, caused by the ingestion of 2.0 or 0.125 M sucrose.

## SOURCES OF VARIABILITY

### *External Environmental Factors*

External environmental factors can alter searching behavior directly, by acting upon environment-sensitive physiological processes. An animal can also perceive changes in environmental factors, and based on that information it may alter its behavior. Such alterations in searching behavior may be monotonically related to changes in an environmental factor, or the animal could switch its searching tactic or the resource it seeks.

**ABIOTIC FACTORS** Basic physiological principles account for variability in searching behavior in response to abiotic factors, such as temperature, humidity, and solar radiation, because many ectotherms operate most efficiently at relatively high constant body temperatures. Some depend on environmental sources of heat, often warming up by capturing solar radiation. Individual components of an animal's searching behavior may differ in sensitivity to temperature changes, as in *Pieris rapae* larvae where locomotory rate, but not head-waving, increases as the temperature changes from 14° to 25° C (52). Environmental factors can also influence the resources selected. Energetic

costs of foraging in *Bombus terreicola* increase as the temperature drops, because a bee must maintain a high thoracic temperature in order to continue flying (45). Since different species of flowers produce different amounts of nectar, certain flowers yielding low energy rewards are taken only at relatively high air temperatures.

**BIOTIC FACTORS** Biotic factors affecting search patterns include resource distributions and availability and resource quality, as well as the influence of other individuals.

*Resource density* The number of resources an animal finds is generally proportional to the number available in time and space. For example, a parasitoid will generally oviposit into more hosts when it locates a dense patch (reviewed in 41). For predators, this phenomenon has been referred to as a *functional response*, of which there are four types. The relationships between number of prey available and number of prey captured differ according to influences of handling costs, gut filling, search image formation, emigration, or interference from prey. The pattern of resource finding also reflects the interaction between the resource requirements of an insect and temporal availability of resources in its environment (reviewed in 20).

*Dispersion* Dispersion is the spatial or temporal configuration of resource availability. The pattern of temporal resource dispersion may be to increase or decrease rather steadily, or it may be a pulse or a cycle. For example, tropical fruits often ripen synchronously on any given tree, but different individual trees of the same species frequently produce fruit at different times; on the other hand, midges may emerge in a pulse. Thus, honey bees learn to visit a feeding dish at the time of day when reward was present or was highest the day before (93); this shift is adaptive, since it would be most efficient to visit flowers when the rewards are highest. Analogous to the temporal pulse and cycle are the spatially clumped and uniform distributions. The spatial dispersion pattern of host plants affects the frequency with which lepidopteran larvae locate their host plants. Plant dispersion (uniform or clumped) affects the frequency with which *Pieris rapae* larvae locate collards when the larvae were early instars or unstarved. These young individuals are the poorest searchers, because they are least mobile, and they are able to locate uniformly dispersed collards more readily than clumped collards (15). The highly mobile fifth instar or starved larvae are unaffected by plant dispersion. Perception of the spatial arrangement of sucrose drops in different patterns restricts the area searched by *Drosophila melanogaster* and the geometry of its local search pattern as it works through a patch of sucrose drops (87). The fly has insufficient information concerning the spatial configuration of re-

sources at the beginning of each pattern, but later the foraging behavior of the fly becomes "constrained" by the spatial configuration of drops, and it follows the sequence of resources to the exclusion of another resource in the immediate vicinity.

*Texture* Resource texture refers to the spatial configuration of resources relative to other resources or nonresource objects. Insects can respond in various ways to resource texture, depending on their search strategy and their perceptual mechanisms. For example, a specialist herbivore responding to host-specific cues might be confused or even repelled by nearby nonhost plant species (reviewed in 82), whereas a polyphagous herbivore, orienting to generalized plant characteristics, may perceive diverse plant mixtures merely as dense stands of food.

**RESOURCE QUALITY** Resource quality affects search duration, searching speed, capture rate, and scanning. Resource quality may directly affect the course of time-dependent shifts from local search to ranging, in such a way that an animal remains in a rich patch longer than in a poor patch. For example, search duration is related to the size of the prey consumed in coccinellid beetles (66). The time spent by the blowfly *Phormia regina* searching near a drop of ingested sucrose increases with sucrose concentration (22). Consequently, houseflies remain in a patch of 2.0 M drops longer than in a 0.125 M patch, because the duration of ingestion-dependent local search and handling times is longer after ingestion of each 2.0 M drop than after that of each 0.125 M drop (31).

**EFFECTS OF OTHER INDIVIDUALS** Other individuals can have either negative or positive effects on searching behavior.

*Negative effects* Negative effects suffered through interactions with other individuals include an array of direct and indirect influences, whereby potential prey are frightened or reduced in availability, or where the presence of other individuals necessitates defense or leads to competition. For example, a small bumblebee species, *Bombus ternarius*, avoids a larger species, *B. terricola*, while foraging (61), and female *Rhyssa persuasoria*, an ichneumonid parasitoid of wood wasp larvae, have evolved threat displays and aggressive behavior which they exhibit toward other females (81).

To reduce either predation or intraspecific competition an insect may "adopt" a tactic that minimizes risk. Some species select the most profitable site (e.g. 72), finding and remaining on resources that are concentrated, even though they risk competition (e.g. 63) and predation. Others may "spread the risk" (e.g. 71) by becoming skilled at locating scattered resources. Con-

sequently, they gain access to poorly exploited resources and also are able to escape intraspecific competition and the predators that build up in large numbers in dense resource patches. When survivorship is variable in space, individual females can gain a selective advantage by spreading offspring among many different independent spatial locations. Those species that seek out isolated hosts may not be at such a disadvantage as might be expected from the costs of searching alone. For herbivores, host-plant density may not always be directly proportional to food density, since crowded plants often produce less leaf area and fewer reproductive parts than do plants in less competitive conditions (38). Thus, parsnip webworms, *Depressaria pastinaca*, lay more eggs on isolated host plants than on plants in dense clusters, but the former produce more of the closed umbels upon which larvae feed than do plants growing in dense clusters (84).

*Positive effects* The presence of other individuals can have positive effects on searching success. When groups can capture or carry more resources per individual per unit time than can a lone individual, the influence is positive. For example, thousands of bark beetles are needed to overcome the defenses and kill a healthy tree (reviewed in 13). Single beetles are “flushed out” by sap flow in a healthy tree, whereas a mass attack makes it difficult for a weakened tree to successfully “flush” out all of the invading beetles. Many species of bark beetles carry pathogenic bacteria and fungi that weaken a tree and reduce its ability to counterattack.

### *Internal Environmental Factors*

The internal state of an animal affects its searching behavior, especially in the “choices” it makes as to when to search and for what to search. Papaj & Rausher (68) define “time-dependent responsiveness” as an increase in the probability of an observable response to resource stimuli as time elapsed since performance of a consummatory act such as feeding, ovipositing, or mating.

Deprivation affects search behavior in the following ways: (i) Deprivation increases the probability of responding to resource-related cues: Isolation from males increases the phonotactic response of female field crickets (*Gryllus* spp.) to male calls (14). (ii) Hunger or lack of available food can stimulate animals to move their ambush sites: When ant-lion larvae are starved, they move to another site and construct another pit, rather than increasing the size of their current pit to enhance capture rate of prey (36). (iii) Deprivation increases local search duration following feeding or oviposition. For example, after *Drosophila melanogaster* feeds on a drop of sucrose, the time required for local search to readjust to ranging increases as a result of starvation (12). (iv) Reactive distance in the mantid *Hierodula crassa* increases with hunger in that the insect responds to a housefly at longer distances (47). (v) Starvation

also affects resource finding on a more global pattern. Starvation of fifth instar of *Pieris rapae* leads to increased locomotory rate, decreased head-waving (scanning), and increased directionality (i.e. movement is straighter) (52). Reactive distance also decreases, such that larvae are more responsive to nearby plants. (vi) Some components of searching motor patterns should not be affected by hunger (19). Predators such as mantids and salticid spiders must walk stealthfully regardless of their hunger level, or else their prey would be alerted and escape (26, 66). (vii) Diel rhythmicity in searching interacts with stimulation from hunger, such that in the praying mantid *H. crassa* both gut content and time of day determine capture rate (47). (viii) Deprivation from a given resource could lead to acceptance of a previously unacceptable resource, as with ovipositing checkerspot butterflies, *Euphydryas editha* (77). Deprivation may also decrease latency of acceptance or decrease the number of "errors" during selection.

In all studies of searching behavior in which the variable of deprivation has been assessed, deprived individuals search differently than do undeprived individuals. Thus, unless the experimenter knows or at least can estimate the time since last feeding, oviposition, or other activity, enormous variability can be expected in search behavior and/or choices made by the animal. In the field it is difficult to know if an animal is being efficient because it is designed that way, or because it is starving or has too many young to feed.

### *Genetic Factors*

Several foraging traits in *D. melanogaster* larvae are heritable, including mechanisms of feeding and locomotion, digging, and pupation site preference (reviewed in 79). In *D. melanogaster* and *Musca domestica* various types of adult orientation, components of their local search, olfactory perception, and olfactory preferences are also heritable (references in 9, 65). The capacity for conditioning behavior is genetically determined in blowflies (59), and host plant selection is in part controlled by heritable factors (reviewed in 88).

### *Ontogenetic Factors*

Ontogenetic experiences and maternal influences can affect both search behavior and search success; thus, individual adult animals of a given population may differ in their preferences or abilities because of these experiences.

Maternal influences include the differences in investment that may occur among the eggs or embryos of a single female, and differences between females in conversion of environmental resources into offspring. A phenotypic characteristic often related to maternal effects is body size, which in invertebrates is nearly always directly related to nutritional experiences while immature. Such experiences may be mediated either through vitellogenesis (7) or larval provisioning (2). The more general proximate causes of size

variation in insect populations include temperature gradients, moisture or humidity, larval diet, and temporal fluctuation of resources and population density (29). Body size can have an important impact on searching behavior.

## ALTERNATIVE TACTICS: DISCONTINUOUS VARIABILITY

Differences in the behavior of individuals of the same species may be continuous, as has been illustrated up to this point, or the differences may be discontinuous. To accomplish the same goal, such as locating food or mates, distinctly different tactics may be used by one individual at different times, or by different individuals at the same time. The idea has been formulated into theories of alternative tactics (e.g. 3, 25, 73).

A *searching tactic* is a group of related, often sequential behaviors which, when successful, lead to the locating of a resource that increases an individual's fitness. A *searching strategy* is a "set of rules stipulating which alternative behavioral pattern will be adopted (or with what probability) in any situation through life" (25). A strategy implies a long-term objective, whereas a tactic implies a specific action (27). A strategy then is the overall scheme by which an animal can use the appropriate tactic, depending on its genotype, age, size, or environmental condition. The overwhelming majority of examples of alternative tactics appear to be derived from environmental cues initiating different sets of events in an equipotent individual.

### *Tactics Conditional on External Environment*

Switching between searching tactics may be conditional upon environmental situations, as in male wood butterflies, *Pararge aegeria*, which have two tactics for locating females: perching and patrolling. The tactic played depends on the availability of sunspots in the environment (21). Active patrolling is appropriate in the canopy where females are scarce, while perching is a better tactic in sunspots where females are abundant. To determine if sunspots were important resources, territorial males were removed from their sunspots; as a result other males soon occupied the vacant positions. A male holding a sunspot has a mating advantage over a canopy male, because males in sunspots encounter more females than canopy males. The key element is that any individual male can use both tactics, and which tactic it uses is a function of sunspot availability. When sunspots are totally unavailable, all males patrol, because this tactic is the most effective way to locate females in the absence of sunspots.

### *Tactics Conditional on Internal State*

In naiads of the damselflies *Ischnura verticalis* (18) and *Anomalagrion hastatum* (1), starvation leads to a switch from ambush to search mode. When

deprived of food for more than two days, fifth instars of the mantid *Paratenodera angustipennis* stop ambushing and switch to active searching (48). Insects commonly switch from one complex kind of behavior to another according to internal physiological changes other than hunger. For example, hormonal changes in *Aedes aegypti* correlate with a switch from search for hosts to search for oviposition sites (54).

### *Tactics Conditional on Ontogenetic Effects*

In an anthophorid bee, *Centris pallida*, larger males patrol emergence sites searching for emerging females, while smaller males tend to be hoverers, searching less profitable areas to locate females that escape patrollers (2). The size dimorphism among males is probably the result of differential maternal provisioning of cells.

### *Tactics Conditional on Genotype*

Phenotypic variation in the searching tactic of *D. melanogaster* is genetically determined. The two searching types, *rover* and *sitter*, occur in larvae (78) and in adults (65). Rover larvae have longer foraging trails and traverse a larger area than do sitter larvae (78), and adult sitters have more constricted search paths (longer search duration) than do rovers (65). The different tactics seem adaptive in larvae for locating pupation sites, and in adults for locating patchy versus uniformly distributed resources (79, 87). Genotype-environment interactions affect all of the phenotypic traits related to searching behavior. For example, search duration of adult and larval rovers and sitters is modulated by nutritional quality (sucrose drop concentration in adults, medium quality in larvae), and by level of starvation (11, 35). However, the extent to which these variables affect search duration is still dependent in part on the genotype of the fly.

In the blowfly, *Phormia regina*, high central excitatory state (high-CES), characterized by an increase in proboscis extensions to water after a fly had been stimulated with sucrose, is associated with longer search duration than in the low-CES condition (60). However, this phenotypic correlation disappeared in the F<sub>2</sub> CES hybrid, indicating that the observed variations in CES and search duration were not controlled by the same set of genes. These results indicate that the rover/sitter trait may commonly be found in various species of flies, and perhaps in other animals as well, but that it may be controlled by quite different genetic systems.

## CONCLUSIONS

Searching patterns of insects are good examples of behaviors controlled by mechanisms that are sufficiently flexible to respond to external and internal



environmental factors, but with limits set by the genotype. The flexibility is manifested in either continuous or discontinuous variability, allowing monotonic adjustments to accommodate some factors, and wholesale shifts between tactics in response to others. The degree of plasticity may be so large that genotype often cannot be guessed from phenotype; for example, a starved individual of one genotype may closely resemble the phenotype of a satiated individual of another genotype. One wonders if ability to be plastic is heritable, since that particular attribute strongly affects the magnitude of the response an individual can make in the wake of an environmental change.

Insects use all information channels in their search and resource assessment. The usable information is greatly magnified by mechanisms for cross-channel potentiation, switching between modalities, hierarchical systems, and summation. Scanning is an interesting component of search behavior, because it combines sensory inputs and locomotion, and because it fills dual roles—involved in predator avoidance or vigilance and in locating resources. Scanning mechanisms deserve further investigation, especially with reference to their relation to resource distribution and how these mechanisms are efficient in various kinds of habitats.

Patch orientation can be best seen among insect examples. Mechanisms for locating and remaining in profitable patches can be reduced to relatively simple neural responses. Patch times are regulated by locomotory shifts from restricted to straight walking after resource utilization, satiation, and habituation to patch cues. Through these simple mechanisms insects are able to determine when to leave and when to return to a patch. Although learning may be involved in some animals, as in birds, most (but not all) insect examples can be explained without calling upon learning, counting, or complex decision-making.

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