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Elizabeth A. Bernays; William T. Wcislo

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SENSORY CAPABILITIES, INFORMATION PROCESSING, AND RESOURCE SPECIALIZATION

ELIZABETH A. BERNAYS AND WILLIAM T. WCISLO¹

*Center for Insect Science and Department of Entomology, University of Arizona
Tucson, Arizona 85721 USA*

ABSTRACT

Numerous hypotheses have been proposed to account for the widespread occurrence of specialized behavior, especially with regard to food and host-related resource utilization. None of these hypotheses has been widely accepted, although most are recognized as being important for particular taxa or in certain circumstances. We discuss features of neural function as primary proximate mechanisms involved in resource specialization, which may underlie many of the other hypotheses. Diet and host breadth may be associated with the potential informational complexity of an organism's environment. The processing of complex information ultimately entails costs associated with decision time, relative efficiency of food or oviposition site-selection behavior, and concomitant exposure to potential mortality factors. Sensory focusing, through paying attention, experiential processes, or canalized sensory input decreases these costs. Increased efficiency of host finding, recognition, and discrimination can be expected as a result of a reduced probability of information overload. Such efficiencies should, in addition, decrease exposure to natural enemies.

THE MEANS BY WHICH animals acquire and process environmental information are usually neglected by ecologists and evolutionary biologists (see Lotka, 1925; von Uexkull, 1957; Dusenbury, 1992; Dukas and Real, 1993), despite the influence of such information on the expression of animals' phenotypes (Bates, 1960; Staddon, 1983; Oyama, 1985; Krebs, 1987; Wcislo, 1989). Here we consider relationships among sensory capabilities, information processing, and resource specialization. We often use host ranges in phytophagous insects as examples, but refer to other taxa when appropriate.

An organism's environment contains more sources of information than it can use at any time, while its information-acquiring capacities exceed the processing capacity of its cen-

tral nervous system (CNS) (Dusenbury, 1992). The selection of relevant information is important for regulating behavior, or for shaping the developmental environment of offspring. At times mistakes can be critical. Individuals that develop in abnormal environments often express abnormal behavior (Santibáñez-H. and Lindemann, 1986) or structure (Matsuda, 1987). We hypothesize that economy and precision of information acquisition and processing increases efficiency and precision of search behavior and decision making, accompanied by decreased exposure to certain mortality factors. Considerations of neural processes and learning capabilities are useful in understanding broad ecological patterns relating to resource specificity by herbivores, parasites and predators.

Extreme obligate specialists have inflexible limitations in what is perceived as an acceptable host, irrespective of environmental influ-

¹ Present address: Department of Entomology, Cornell University, Ithaca, New York 14853-0999 USA

ences. Among more generalist lineages, environmental influences on development of choice behavior can occur over different time scales. Experiential effects can occur during brief sensitive periods (e.g., imprinting), and then later the behavior is effectively resistant to changes in experience. The effects also can occur continuously over both short time scales (e.g., attention, habituation) and longer ones (e.g., short-term learning, memory). Increasingly generalized individuals require increasingly flexible means of ensuring shifting attentiveness to those inputs that are biologically relevant at any time.

We give a brief overview showing the widespread occurrence of specialized feeding behaviors or host utilization, and briefly review previous hypotheses proposed to account for these patterns. We outline a neural hypothesis that relates resource specialization to advantages associated with economy of information acquisition and processing, and develop this hypothesis by discussing the concept of attention in both mechanistic and operational terms. Next, we discuss how an organism's potential stimulus environment can overload its information-processing capabilities in the absence of mechanisms to restrict or bias sensory input. We consider possible mechanisms for reducing sensory input, and give examples that show how attention or selective perception, categorization, and various forms of learning lead to more efficient search behavior and decision making. In particular, we argue that significant factors in choice behavior are neural mechanisms that enhance rapid and efficient decision making. Finally, we briefly discuss neuroanatomical correlates of apparent decision-making complexity and the associated memory requirements.

PHYLETIC VARIABILITY IN RESOURCE UTILIZATION

Within an animal taxon there is often striking variability in the degree to which members restrict themselves to hosts or resources of a certain kind (Linsley, 1958; Askew, 1971; Price, 1980; Wcislo, 1987a; Mitter, Farrell, and Wiegmann, 1988; Brooker and Brooker, 1990; Rothstein, 1990). The hen flea (*Ceratophyllus gallinae*), for example, has been recorded from birds of over 65 species in Britain (Roth-

schild and Clay, 1961). We refer to such forms as "generalists." A related species (*C. rossitensis*) is only found on the crow (*Corvus corone*); it is a "specialist." A majority of phytophagous insect species exploit plants of only one or several related host taxa, while other lineages appear to be catholic and utilize many unrelated hosts (Chapman, 1988; Mitter and Farrell, 1991). Even within generalist lineages, individuals may have different host restrictions because of genetic differences, or become restricted as a result of experience (Walsh, 1864; Fox and Morrow, 1981; Via, 1990). The specific recognition cues range from host characteristics to those of the potential host's habitat (Courtney and Chew, 1987; Sheehan, 1991).

Some specialist lineages are derived from generalists, and vice versa, and both specialist and generalist lineages have sometimes radiated to generate large numbers of species, but pertinent phylogenetic information is limited (e.g., J. S. Miller, 1987; Mitter, Farrell, and Wiegmann, 1988; Shaw, 1988; Mitter, Farrell, and Futuyma, 1991; Eickwort, 1992; Mitter, Poole, and Matthews, 1993). Within populations of specialists, some individuals will be unable to obtain sufficient resources, implying there are individual advantages associated with capabilities to increase or maintain resource breadth. Therefore it is the preponderance of specialized forms that presents an evolutionary puzzle (Futuyma, 1991).

HYPOTHESES RELATING TO EVOLUTION OF RESOURCE SPECIALIZATION

Over the past decades, as new findings and methodologies became available, enthusiasm has waxed and waned for various hypotheses advanced to explain the occurrence of ecological specialization (Futuyma and Moreno, 1988; Jaenike, 1990; Feeny, 1992). Each hypothesis has partisans, and not one has been totally satisfactory as a general explanation, although each is probably important under some circumstances, or for particular taxa. The hypotheses generally concern: (1) factors that create ecological opportunities (sensu Dobzhansky, 1950) for restricted host range, and relate to the evolutionary origins of specialization; and (2) factors that are consequences of facultative or obligate restrictions of host ranges, and relate to the evolutionary persistence of specialization.

With respect to (1), the widespread availability of a resource, for example, may lead to specialization on it because use of this resource alone could minimize search time (e.g., sunflowers of many species are widely distributed and abundant throughout central and western North America, and numerous bees from unrelated lineages specialize on its pollen—Hurd et al., 1980). Such ideas are consistent with optimal foraging theory, but a conservative view sees availability as an opportunity for specializing, rather than driving its evolution. Other ecological factors (e.g., body size, relative mobility) likewise may provide opportunities for limiting host range, but do not necessarily select for it.

Competitive struggles for existence among populations of different species frequently have been implicated in determining degrees of resource specialization (e.g., Gause, 1934). Evidence for the influence of interspecific competition on specialization is mixed (e.g., Fontela Rizo, 1989; Van Valkenburgh, 1991; Wine-miller, 1991), and the questions are controversial. At the least, interspecific competition creates opportunities for specialization, but by itself may or may not select for it.

Social (intraspecific) competition for necessary resources such as oviposition sites creates a behavioral environment that might select for condition-sensitive, alternative, specialized phenotypes (see West-Eberhard, 1986). Such flexible restrictions presumably require integration of much information and hence require more elaborate sensory and neural features (Williams, 1966: 75ff.; but see Tierney, 1986). Furthermore, social competition itself potentially increases the amount of information needed to be processed: Competing members of a social group sometimes keep track of factors such as genetic relatedness to other members, or their social status and place of residence (see West-Eberhard, 1983; Fletcher and Michener, 1987; Hölldobler and Wilson, 1990).

Concerning (2), one idea that has received particular emphasis is that a specialist has enhanced performance (e.g., improved digestive abilities), relative to a generalist. In a much-discussed extension of this idea, individuals with different genotypes in popula-

tions of generalist species may have different, but all relatively narrow, ranges of hosts. Negative genetic correlations in fitness on the alternative hosts would provide a basis to select for narrow diets, or to maintain them. The experimental evidence to date is contradictory (e.g., Futuyama, 1991), although it does appear that digestive specialization may exclude an increasingly greater proportion of the potentially available foods (Karowe, 1989; Trowbridge, 1991). Further, if diet breadth has been restricted over evolutionary time, many changes may occur that reduce the likelihood of subsequent generalizing. There is, for example, evidence of increased vulnerability to poisons that are not customarily encountered or consumed (Bernays, 1990), and structural features physically allow exploitation of some hosts but not others (Kennedy, 1986; Bernays, 1991a). Similarly, substrate-specific advantages associated with crypsis or aposematism may make broader host use dangerous, since a novel host might provide a different background pattern (Bernays, 1989). Finally, finding a host may be the easiest way of finding a mate (Colwell, 1986; Diehl and Bush, 1989; Ward, 1991).

The importance of the diverse array of plant secondary compounds (Swain, 1977) in determining insect host ranges also has been frequently discussed. Fraenkel (1969) strongly emphasized their significance as attractants and deterrents, although more recent studies have given preeminence to other roles (e.g., toxins for defense—see, Rosenthal and Janzen, 1979). Toxic compounds provide protection to plants from herbivores that might otherwise feed on them, and specialists are often unusually competent at detoxifying such compounds. Such coevolutionary processes have been hypothesized to explain both the diversity of plant secondary compounds and the evolution of specialized detoxification capabilities (see Ehrlich and Raven, 1964; J. S. Miller, 1987; Farrell and Mitter, 1990).

Fraenkel initially discussed plant chemistry in terms of *regulating* behavior, without reference to postingestive effects. Recent studies provide more support for his ideas. Many plant taxon-specific secondary compounds act as phagostimulants or deterrents for insect her-

bivores. From laboratory studies the correlation between specialized feeding behavior and postingestive suitability of the food is weak: Some deterrent compounds are physiologically harmless to phytophagous insects (Bernays, 1990, 1991b), while some stimulants are not nutritious (Chapman and Bernays, 1977). Consequently, plant chemicals can influence insects' behavior in ways not necessarily related to nutrition.

A NEURAL HYPOTHESIS IN BRIEF

A diversity of suitable hosts provides a searcher with an environment having numerous distinctive and general sensory cues (Brues, 1936; Bernays and Chapman, 1987; Feeny, 1992). Within a sensory-rich environment, we hypothesize that the nature of neural processing itself may bias organisms toward restricted host ranges, owing to advantages with localizing and recognizing resources. We suggest that strong neural and sensory focusing is associated with efficient and effective search and acceptance behaviors, with decreased exposure to enemies. By comparison, the open-ended choices resulting from an individual ability to be generalized imply less efficient behavior when searching on a given resource axis (e.g., the most nutritious or rewarding). Over the life of an individual, sensory focusing may be adjusted either (1) in the form of short-term attention to certain cues, without storing the information in long-term memory; or (2) it may reside in longer-term experiential restrictions of sensory input and transference to the CNS, or retrieval from the CNS. The distinction between (1) and (2) emphasizes the time scale over which experience changes behavior (cf. Gordon, 1991). On a phylogenetic scale, a strongly canalized, nonadjustable ("hard-wired") restriction, in which only a few host criteria are even perceived as acceptable and the automatic outcome is that only a few hosts are recognized as resources, may be an evolutionary consequence of facultatively restricted host range. Its evolution may occur within a lineage, or arise with a new lineage.

Different taxa have different responses to different stimuli. Among some insect herbivores, for example, the use of glucosinolates or their aglycones as points of focus is associ-

ated with restriction on Brassicaceae, while other taxa use the general "green odor" compounds that are common to most plants, or certain visual cues (Feeny, 1977; Prokopy, 1983; Visser, 1986; Lunau, 1992; Harris et al., 1993). Although there are few phylogenetic studies on the evolution of response selectivity [e.g., Proctor (1992) on mate recognition], various authors have hypothesized that this trait is highly labile (e.g., Markl, 1985), presumably owing to evolutionary tinkering with neuronal connections among a set of otherwise conserved neurons (Dumont and Robertson, 1986; Edwards and Palka, 1991).

If focusing on a limited number of sensory inputs is important, restricted host use in individuals of a polyphagous insect species could result from various experiential mechanisms. This facultative restriction may facilitate the evolution of obligate sensory limitations, such that the detection and utilization of alternatives is less likely (see West-Eberhard, 1986; Wcislo, 1989 for discussions).

If plant stimuli are generally important factors in restricted host ranges, one expects more specialists on host lineages with very distinctive cues (Feeny, 1976). Within the Apiaceae, for example, there appear to be more specialists on plants with distinctive chemistry, although this distribution can be interpreted as relating to coevolution rather than to the positive value of distinctive stimuli (Berenbaum, 1983).

Elements of a neural hypothesis have been touched upon by other authors. Levins and MacArthur (1969), for example, created a model that showed how fitness is maximized in the face of uncertainty, assuming that the sensory system provides the CNS with a simple coding of plant quality, and that narrow ranges of foods are easier to make decisions about (also Gould, 1974; Hughes, 1979; Orians, 1981). Neurological sophistication should allow increasingly sophisticated decision rules, and hence allow more polyphagy. Dukas and Ellner (1993) model the relationship between attention by a predator and the probability it detects prey: Their model predicts that if a generalist encounters several cryptic types, it maximizes its net rate of energy intake by paying full attention to, and specializing on, a

single type. If, however, prey are relatively conspicuous, then the predator's attention should be divided equally among the several types (assuming all types are energetically equivalent) (see also Reeve, 1989; Getty and Pulliam, 1991).

Futuyma (1983) showed that a genetically fixed search image could be advantageous, assuming that (1) an ability to process information is limited, and (2) an organism with a fixed search image could locate a specific resource faster than one that learned its search image. Under such conditions, specialization is favored, as is the loss of an ability to recognize rare hosts. Numerous other authors also have suggested that neural limitations may influence host range (Rausher, 1978; Courtney, 1983; Rausher and Papaj, 1983; Stanton, 1984; Lewis, 1986; Papaj, 1986; Papaj and Prokopy, 1989; Dukas and Real, 1991; Menzel et al., 1993).

Jermy et al. (1990), in a somewhat different approach, noted that neural elements can alter by chance in a variety of different ways during embryonic and postembryonic development, or because of mutations. They hypothesized that such changes could sometimes alter neural decision-rules concerning plant acceptability, and alone cause a restricted host range under favorable ecological situations.

In the sections that follow, we discuss mechanisms for reducing sensory input and advantages that accrue from doing so, and describe anatomical correlates associated with mechanisms for reducing sensory input.

WHAT IS ATTENTION?

Only a subset of simultaneously occurring events capture our attention at one time. If we shift our focus of attention, a new set of data from the sensory system is used by the brain (Robinson and Petersen, 1986). The shift in stimulus selection is influenced by neuronal and physiological conditions which, as humans, we might describe as alertness or motivation. We attend more readily to the sight or smell of food if we are hungry than if we just ate. Our perceptual system has limited capacity to simultaneously process a large variety of sensory information (Dusenbury, 1992), and it is known that attempting more than

one mental task at a time makes the attempt at each one less efficient (Broadbent, 1965; Roitblat, 1987). Similarly, our ability to recall information from long-term memory is limited, and we must recode information to increase storage capacities (G. A. Miller, 1956). Strong behavioral evidence indicates that other vertebrates are limited in their ability to simultaneously process information (Maier, 1964; M. Dawkins, 1971; Maki and Leith, 1973; Blough, 1979; Brown, 1991; but see Lamb, 1991).

As used in this paper, attention is a label for largely unknown neural processes (Corbetta et al., 1990) that selectively admit perceptual information into short-term memory for further processing. The concept is central to vertebrate psychology and behavior (James, 1890; Marler, 1963; Posner and Petersen, 1990; Andrew, 1991; Laing and Glemaric, 1992), yet analogous neural processes are traditionally not labeled as such in the context of insect behavior (Hoy et al., 1982; Hoy, 1989; also Griffin, 1984). Processes analogous to our "attention" probably exist in invertebrates too, and may be ecologically significant; several studies at least demonstrate collateral inhibition of neural inputs (e.g., Pollack, 1988). Such collateral effects are known to sharpen an image (i.e., sharpen differences between inputs).

Operational definitions of attentiveness are presented in two types of example:

(1) Specific arousal may be apparent as a preferential response to relevant stimuli determined by physiological state; for example, an animal deprived of food is more readily aroused by food odors than is a well-fed one.

(2) An animal may preferentially respond to one of two equivalent, but different, cues, with either response having equivalent consequences; for example, an animal can utilize either a chemical or a visual food-related cue, yet each is suitable for location of food. The selective use of one cue represents attentiveness to that cue.

For both (1) and (2), in the absence of experimental manipulation, the behavioral response may be the only measure of attentiveness.

WHY AND HOW TO BE ATTENTIVE

How is attention generated? Each sensory receptor is limited in the range of stimuli that influence its activity, with the range determined by physiological conditions and evolutionary history. Attention filters the inputs to certain neurons by regulating the strength of their synaptic connections, and the brain responds selectively to relevant stimuli.

Attention in Relation to State Variables

As the physiological state of an animal changes, various sensory mechanisms decrease input because its information is temporarily irrelevant, or neural mechanisms prevent that input from controlling behavior (e.g., habituation). Processes involved may be peripheral and central (Bernays and Simpson, 1982). For example, following a full meal locusts usually move away from the food item and rest (Bernays, 1980; Chapman and Beerling, 1990), which terminates taste input from the tarsal chemoreceptors; hormone secretion(s) from the corpora cardiaca cause closure of the pores on the tips of the chemoreceptors on the palps (Bernays and Mordue, 1973); and as a result of increased nutrients in the blood, peripheral chemosensory thresholds to the same nutrients rise (Simpson and Simpson, 1992). Collectively, these feedback processes greatly reduce input of food-related stimuli at a time when feeding is not appropriate. Other needs, such as avoidance of danger, can then take precedence and be executed more efficiently. Similar examples can be cited from other invertebrates (Simpson and Simpson, 1990; Barton Browne, 1993).

Phenomena such as habituation and sensitization show that sensory input can also be limited or biased by CNS modifications (Zucker, 1989). For example, the deterrent effect of certain compounds on the feeding responses of some herbivores wanes with repeated exposure to the compounds, in the absence of fatigue or sensory adaptation (Gardner and van Lenteren, 1986). Conversely, if a hungry fly is presented with a feeding stimulant and only a small quantity of food, then after feeding the fly shows increased locomotory activity associated with search behavior (Dethier, 1976; Bell, 1991).

Attention not Dominated by Physiological Variables

Cherry (1966) illustrated selective attention with reference to the cocktail party phenomenon: Most people can focus on one conversation, despite the background din of other nearby conversations, music, and party noise. Abilities to attend to different aspects of the environment enable an organism to deal with multiple sensory inputs about the same or different situations. If inputs occur simultaneously, such as the detection of a predator while feeding, then perceptual filtering is needed to implement decision-making hierarchies. Milinski (1990) provided examples of inefficient behavior that may result from overload of potential information. He pointed out that when a foraging animal has to pay attention to potential predators, it may be unable to pay attention equally well to both foraging effort and escape effort, so one or the other gets priority. Experiments with salmon clearly showed that in the presence of a conspicuous predation risk, significantly more mistakes were made by the fish in attacking edible or inedible pellets, than in the absence of a predator (Metcalfe et al., 1987). In the presence of a predator, sticklebacks preferentially foraged on water fleas that were at low density, but preferentially foraged in high-density areas in its absence (Heller and Milinski, 1979; also Lima and Dill, 1990). These experiments indicate that neural limitations of animals may be ecologically very important, assuming other resources such as time or energy were plentiful.

An ability to focus specifically on one type of input, and neglect others, has been discussed in relation to foraging in birds and other animals, and was first described by Tinbergen (1946). Chicks provided with differently colored grains on various backgrounds fed in long runs on either the cryptic or the conspicuous grains, suggesting that they may be focusing and switching attention (Dawkins, 1971; Guilford and Dawkins, 1987). This response selectivity was one of the bases for the concept of "search image," whereby an animal may selectively perceive food items of a certain type, and thereby acquire efficiency at locating them. The concept is easiest to understand by introspection: When we look at an optical illusion (Boring, 1930), we see one image if we attend to certain features, and see a different image

if we focus our attention on other features. We develop a selective visual model or a search image. Numerous experiments show that the more an animal attends to one feature of a situation the less it attends to others (e.g., Roitblat, 1987). At the physiological level, limits on information-processing capacity (Dusenbury, 1992) imply that there would be an advantage in learning critical features of an object for the development of a search image.

EFFICIENCY AS A CONSEQUENCE OF ATTENTION

It has been shown with humans that when choices are close in a preference order, the latency to decision making is significantly longer than when the differences in preference are strong (Barker, 1942; R. Dawkins, 1969; Newell, 1990). When stimuli vary along a continuum, neural processes divide the input into discrete groups. Such categorical perception, well known in humans (Harnad, 1987) and recently demonstrated in other vertebrates (Nelson and Marler, 1989; Ehret, 1992) and a cricket (Hoy et al., 1982), should reduce latency in decision making by decreasing the bits of information needed to be simultaneously processed. By analogy, we hypothesize that the time needed to discriminate among hosts is on average longer than times needed to discriminate between host and nonhost. We also hypothesize that decision times in the absence of attention or learned preferences would increase with the number of choices available. The number of choices can be reduced by a hierarchical categorization of information for different steps of a decision-making process. Host selection in groups from parasitic insects to trematodes (Waage and Greathead, 1986; Haas et al., 1990) often follows a temporal sequence that reflects a hierarchical decision-making process (e.g., habitat selection → patch selection → host selection). In practice, however, there is usually some overlap between levels (Damman and Feeny, 1988).

When a generalist is in an environment with alternative hosts or foods, each of which is equally suitable and available, there are still potential costs to deciding among the alternatives. First there may be a cost in terms of recognition time. Stephens and Krebs (1986) illustrated this case using a simple model of a predator choosing among prey types. From

their model, it follows that specialization is associated with low recognition times. The second potential cost involves the time spent deciding between two potential foods or hosts. This may involve sampling by biting and tasting in the case of a grasshopper, or flying to and fro between two plants in the case of an ovipositing butterfly. In the laboratory, the tobacco hornworm caterpillar requires 5 to 15 seconds to discriminate between two of its solanaceous host plants (Dethier and Crnjar, 1982). If this duration is representative, then such delays carry risks associated with reduced attention to danger, which is significant since natural enemies are a major source of larval mortality (Feeny et al., 1985; Montllor and Bernays, 1993). Parasitism and predation can be almost instantaneous events, so even brief periods of inattention are significant. Adults and even immatures (e.g., caterpillars) have a variety of antipredator behaviors (e.g., head waving, oral spitting, dropping off plants), indicative of awareness of danger (e.g., Awan, 1985).

Experience can alter how individuals perceive, categorize and respond to information (Wcislo, 1987b, 1992). Blue butterflies (*Glaucopsyche lygdamus*) had runs of oviposition on one of several different potential leguminous host species (Carey, 1992). If a butterfly oviposited on a suitable host plant, subsequent landings on plants of the same species were likely to lead to egg deposition. If, however, landings were on suitable but not recently experienced plants, then oviposition was less likely. A possible explanation resides in the costs of recognition and discrimination, with increasing fitness when paying attention to one item, as demonstrated for other butterflies (e.g., Rausher, 1978; Papaj, 1986; Papaj and Prokopy, 1989). The development of a specific perceptual template means that decision making about subsequent ovipositions can be more efficient. Any choice among other suitable hosts would involve new data for those decisions. This additional processing, in turn, can be expected to reduce the efficiency of decision making.

The fitness values associated with attention to one versus several suitable potential hosts are presumed to be threefold: (1) greater precision in host finding without distraction; (2) rapidity of choice (reduced likelihood of inde-

cision) when foods are in close spatial proximity, or do not differ greatly in quality; and (3) reduction of danger from natural enemies as a result of the reduced exposure times due to (1) and (2).

IS SELECTIVE ATTENTION WIDESPREAD AMONG INSECTS?

Few studies have specifically addressed the question of attention in insects, yet many examples suggest that such a phenomenon is common (Hoy, 1989). One documented case concerns honeybees (*Apis mellifera*) that were trained during two consecutive trials using two stimulus types (two-dimensional information): One dimension (e.g., color) conveyed relevant information while the other dimension (e.g., position) was irrelevant (Klosterhalfen et al., 1978). Bees performed better on the second trial if the dimension with relevant information was the same as in the first trial, suggesting they were paying attention to the rewarding dimension from the first trial. Honeybees can also learn to associate a given stimulus (e.g., odor, color) with a place or with food. If both stimuli are presented together, then the odor "overshadows" the color, and bees preferentially learn the odor association (Frisch, 1967; Couvillon and Bitterman, 1989), indicating preferential attention to odor over color. Other behaviors are indicative of a system of preferential attention: Honeybees also more readily learn floral odors than other odors and learn colors in a rank order that may reflect the abundance of flower colors in the environment (Menzel, 1985).

Individuals of many generalist species that utilize floral resources restrict their visits to flowers of a single species, and show "floral constancy": Efficiency increases as the pollinator becomes experienced with handling a particular flower form (Heinrich, 1976; Laverly, 1980; Waser, 1986; Lewis and Lipani, 1990). Constancy has been extensively studied in bees in the context of learning, and memory limitations have been repeatedly implicated in influencing foraging behavior (Dukas, 1987; Dukas and Real, 1993; Lewis, 1993; Menzel et al., 1993). Yet the occurrence of learning itself is related to the mechanism of paying attention to the most relevant (recently experienced and rewarding) flower. Attention can

reinforce long-term memory by biasing the information admitted into short-term memory, and is probably key to the physiological and behavioral basis for visit constancy, as suggested by Darwin (1876), and more recently by others (Real, 1991). Strickler (1979) showed that a specialist bee has shorter between-flower intervals ("pursuit time") relative to some generalists, but the possibility that bees may learn the search image has not yet been investigated.

Other recent examples that are relevant to the question of attention in insects involve butterfly oviposition patterns where several potential host species are available (e.g., Papaj and Prokopy, 1989; Jones, 1991). A swallowtail butterfly (*Battus philenor*) can switch between sign stimuli associated with broad-leaved and narrow-leaved host plants, depending on their relative abundance. Such results are typically interpreted as a sequential associative learning process, but one of the components of this learning process probably involves attentiveness to the sign stimuli.

In experiments with a polyphagous grasshopper (*Schistocerca americana*), individuals had two high-quality, nutritionally identical, artificial diets from which to choose (Bernays and Bright, 1991, 1993; Bright and Bernays, 1991). Individuals spontaneously switched between these diets significantly more frequently when the two diets had distinctive flavors added than when no flavors were added. Individuals that specialized on one flavor one day, tended to switch to the alternative flavor the next day. If foods have specific signatures, the grasshoppers pay attention to one signature for a period, which is not possible when both foods had identical flavors.

In another polyphagous grasshopper (*Taeniopoda eques*), laboratory experiments demonstrated spontaneous switching behavior influenced by novelty (Bernays, 1992; Bernays et al., 1992). Field observations also showed that individuals frequently switched among food types, but had feeding runs on single plant species, which varied in quality (Fig. 1). Individuals encountered plants of many species in rapid succession, and different species were chosen during different periods.

Laboratory studies using various animals have shown that individuals reared on differ-

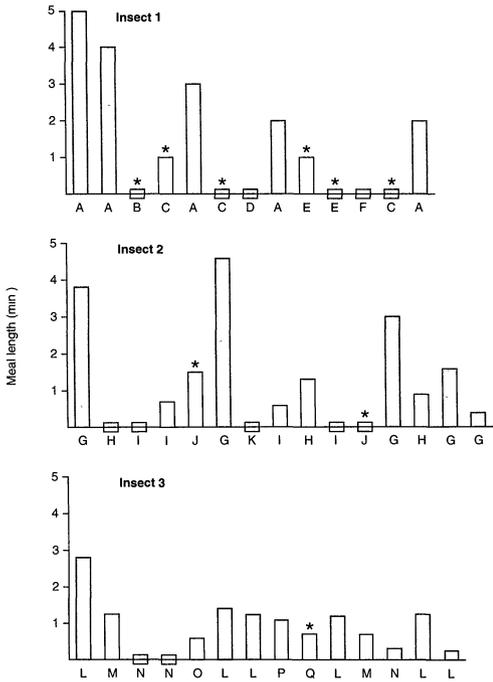


FIG. 1. FORAGING BEHAVIOR OF SEVENTEEN INDIVIDUAL ADULT FEMALES OF THE GRASSHOPPER *TAENIOPODA EQUES* WERE OBSERVED FOR UP TO TEN HOURS EACH UNDER NATURAL CONDITIONS, WHERE PLANT SIZE, GROWTH FORM, DENSITY, AND DISPERSION APPEARED TO INFLUENCE ENCOUNTER RATE

Plants varied in acceptability, and about half of the 74 available species were attractive enough to elicit palpation, biting, or feeding, which lasted from a few seconds to seven minutes. The relative acceptability of the 74 available plant species was used to estimate an acceptability hierarchy.

The figure shows representative foraging sequences from each of three individuals. The letters refer to different plant species, some of which were rejected and some fed upon for different lengths of time. In each case, the insect had major feeding bouts on one plant species (shaded bars), although other plants were encountered and fed upon to a lesser extent during the same period (open bars).

Insect 1 had a series of five feeding bouts on plant A. Between bouts, other plant species were encountered. Of these five other species, the three with asterisks (B, C, E) were higher on the acceptability hierarchy than was A, yet during this period, A was the plant species of choice.

Data for the foraging sequences by insects 2 and 3 are also shown with patterns of majoring for a

ent resources sometimes, but not always, show an increased acceptability for the resource on which they were reared, coupled with a decreased acceptability of any alternatives (Galef, 1981; Jermy, 1987; Caubet et al., 1992). At a proximate level, such processes might be associated with the induction of detoxification mechanisms. Yet induction itself focuses the attention of larval insects on the food they are currently eating, which might increase efficiency of feeding by preventing distraction owing to other sensory input that might cause wandering. Although the neural mechanisms are not understood, there are correlated changes in chemoreceptor thresholds to experienced chemicals, suggesting that the selective attention could, at least partly, involve peripheral changes (Vet et al., 1990; Chapman and Lee, 1991).

Imprinting can also be interpreted as a mechanism to enforce attention to certain environmental features, which later increases efficiency of stimulus recognition (e.g., Rauschecker and Marler, 1987; B. B. Miller, 1988). Imprinting is well known in social insects as a mechanism by which individuals learn cues to efficiently discriminate nestmates from non-nestmates (e.g., Fletcher and Michener, 1987). A fruit fly responds to an oviposition-deterrent pheromone (her own or that of conspecifics) after she herself has oviposited and marked a fruit; she then is suddenly and immediately enabled to respond to it during subsequent encounters (Roitberg and Prokopy, 1987). Similar imprinting phenomena occur in various insect parasitoids after oviposition in a particular host species (Turlings et al., 1993).

ANATOMICAL CORRELATES OF NEURAL LIMITATIONS

Anatole France, with his extraordinary intellect and notably small brain, serves as a caution against simplistic correlations among brain size, neural complexity, and behavioral

period on a single species, even though it is not a preferred host plant.

We interpret such behavior as short-term specialization on ("paying attention to") particular plants. The data overall suggest that these periods of attentiveness last from about 5 to 40 minutes.

complexity (Bonner, 1988). It is not yet practical to quantify the amount of information numerous different individuals process, nor are there obvious comparative measures of neural or behavioral complexity. Despite these difficulties, if neural limitations are ecologically important, one expects to find more sophisticated sensory systems and brains, or relevant regions of brains, in animals that must process a lot of information. Any available correlations are difficult to interpret since many other differences in behavior, ecology and phylogeny are involved. Yet general comparisons suggest that more specific studies are warranted. For example, an adult holometabolous insect such as a predatory wasp has numerous sensory receptors with which it obtains information to locate food, home, or mates, and avoids predators; its larvae, in contrast, live in extremely simple environments (a chamber with a food cache), and have very few sensory receptors (Lomholdt, 1975/76; Ågren, 1989). By comparison, both adults and immatures of hemimetabolous insects such as grasshoppers locate food and avoid predators, and the differences in receptor numbers are less pronounced (Chapman, 1982).

Some mammals and birds have brains larger than expected for a given body size; these forms are apparently associated with life styles involving extensive or complex stimulus environments (Greenough, 1984; Kruska, 1988), including large home ranges (Harvey and Krebs, 1990; Jacobs et al., 1990; Sherry et al., 1993), large social group size (Dunbar, 1992), degree of dependence on previously stored foods (Krebs et al., 1989; Kamil and Balda, 1990), or a social system involving signals such as the complex songs of some birds (DeVoogd et al., in press), and possibly the displays of cephalopods (Moynihan, 1991).

In insects, morphometric studies of the brain have focused on the corpora pedunculata (CP), which receive input from several modalities and seem important as integration centers (Erber et al., 1987; Schürmann, 1987). Social bees, wasps, and ants, whose life styles involve both environmental and social stimuli, often, but not always, have relatively larger CP than do solitary relatives and other insects (Howse, 1974; Cruz-Landim and Zaniboni, 1986/87; Jaffe and Perez, 1989). In a comparative study of ants, behavioral complexity was

related to CP volume (Cole, 1985). Certain long-lived butterfly species with home ranges may have larger CP than other species without home ranges, although sample sizes were small (Sivinski, 1989).

Among individuals, a more direct connection between neuronal and environmental complexity is suggested by intraspecific experimental studies. For example, the CP of fruit flies reared in isolation or in simple environments had fewer fibers relative to flies reared in complex environments (Technau, 1984), while individual *Formica rufa* worker ants that were more efficient at maze learning had broader CP calyxes (Bernstein and Bernstein, 1969).

If decision making and associated memory traits are a significant part of a behavioral repertoire, as it must be for individual generalists, then there are automatic costs in terms of neural investment.

CONCLUSIONS

Many factors discussed in the literature are important for understanding the ecology of resource specialization. In particular taxa, or under particular circumstances, each is realistically important, while hypotheses that combine two or more proposed agents are often even more convincing. Some authors have made the case for including all the hypotheses in an overall picture, and we agree with this pluralism. It is nevertheless important to note that a neural hypothesis is relevant to numerous taxa, and that it therefore has specific merit as an underlying process even though additional factors are important. Other factors must be important, as highlighted by the fact that host specificity is also widespread among fungal, viral, bacterial, and protistan pathogens, all of which lack nervous systems (Chanway et al., 1991; Kohmoto and Otani, 1991; Sutherland and Pegg, 1992).

Most sense organs supply far more information than can be centrally processed at any one time, so that much incoming sensory information is redundant, or temporarily irrelevant. Messages must be selected from the incoming input, and the selection involves such processes as sensory filters, hormonally altered pathways, and differential enhancement of pathways as a result of feedback from current activity (re-afferent information), including learning. Such processes effectively alter the relative signifi-

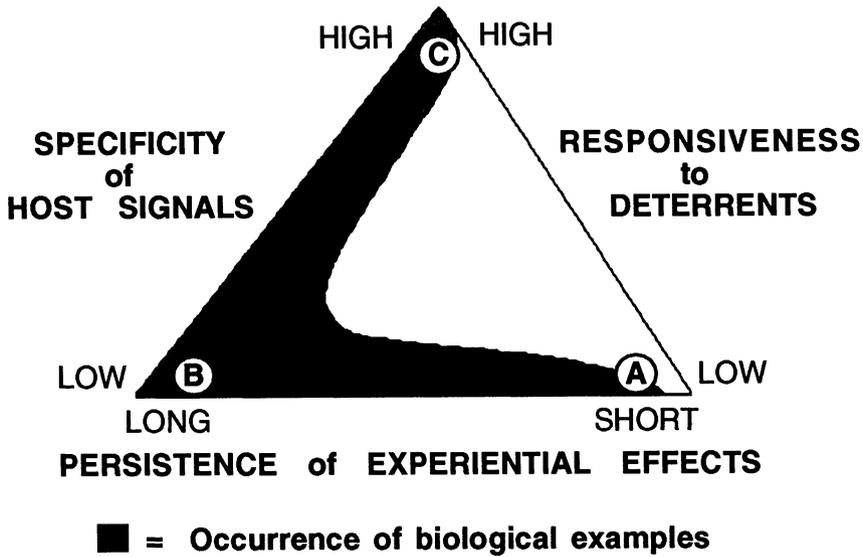


FIG. 2. DIAGRAMMATIC REPRESENTATION OF MAJOR FACTORS THAT LIMIT AVAILABLE INFORMATION
 Insect herbivores provide models for the three extremes (A, B, and C), and for the many intermediates. A point representing a taxon can only be plotted using any two adjacent axes; the side opposite any angle is not orthogonal to the other sides.

A. DEPENDENT PREFERENCE is characteristic of *versatile generalists*. Host preference is dependent on immediate experiential effects associated with short-term focusing (attention), and abilities to selectively filter or channel information. Food-related examples include the generalist grasshopper, *Taeniopoda eques* (a foliage chewer), or various species such as bumblebees that utilize nectar and pollen and tend to “major” on certain flower types. Other examples may include egg-laying site selection by some butterflies and moths. Ecological correlates probably relate to very short-term (within-generation) unpredictability of hosts.

B. AUTOREGULATORY-DEPENDENT PREFERENCE is characteristic of *narrow generalists*. Host preference is dependent on experiential processes only during a limited time period. For example, some insects demonstrate an imprintinglike restriction of host acceptability (seen in larvae of caterpillars like *Manduca sexta*, stick insects, and in adult females of the fly *Rhagoletis pomonella*). In others, aversion learning of foods with an imbalance of nutrients has been shown. Ecological correlates relate to between-generation variability or unpredictability of food resources, but short-term (within-generation) reliability.

C. AUTONOMOUS PREFERENCE is characteristic of *obligate specialists*. Host preference is independent of experience; individuals find many nonhost chemicals deterrent, and often use very particular host cues or combinations of cues as signals of acceptability. Ecological correlates involve reliable and predictable availability and/or quality over both short and long time scales. There are many examples of such specialized behavior in different taxa.

To some extent, chance may have dictated the precise host use along the B ↔ C continuum, in that the use of particular chemical cues will result in a narrower host range if the chemicals are found in few species, and a broader host range if the chemicals are found across a tribe or family of plants.

As bodies and brains get larger it is easier to find examples toward vertex B along the B ↔ A continuum.

Switches along A ↔ C appear to have occurred in some groups. For example, the sibling species, *Heliothis virescens* and *H. subflexa*, show an extreme contrast. In the former, individuals lay eggs on many plant species, and show the A strategy; in the latter, females lay eggs only on one plant genus and demonstrate the C strategy.

cance of different sensory inputs such that an animal attends to a narrow spectrum of them. The narrower the spectrum, the simpler and more effective is the decision making. As a consequence, selection would favor mechanisms that develop attentiveness to one or a few inputs for decisions about host choice. Thus a narrow host range can be advantageous.

Our proposal is a qualitative model for a general process of improved effectiveness in host localization, recognition and discrimination, with reduced risks (see Fig. 2). Variability in the range of host-preference behavior involves a continuum in neural flexibility, which can be described using terms coined by Schmalhausen (1949) for morphogenesis (for applications to behavior, see Wcislo, 1989).

A. DEPENDENT PREFERENCE ("versatile generalists"): Host preference is dependent on very recent experience.

B. AUTOREGULATORY-DEPENDENT PREFERENCE ("narrow generalists"): Host preference is dependent on experience only during a limited time period.

C. AUTONOMOUS PREFERENCE ("obligate specialists"): Host preference is independent of experience.

Limitations in relation to information processing are universal, yet efficient host finding is critical, so we emphasize that neural factors like those discussed in this paper underlie many less general explanations for specialization. The ecological correlates more commonly discussed are indeed important: They vary with taxonomic, environmental, and other factors, and provide extrinsic factors with which neural factors interact. Considerations of sensory ecology should assist in bringing together the different disciplines needed to fully understand the causes and consequences of variation in diet breadths, as well as other ecological specializations.

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