BEHAVIOURAL ASPECTS OF FORAGING IN THE PARASITOID *NEMERITIS CANESCENS* (GRAV.)

BY

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ABSTRACT

An interesting problem in ecology and evolutionary biology is how foraging animals allocate their time in environments of patchily distributed prey. This problem is investigated in the present study with the parasitoid, *Nemeritis canescens* and its host, *Plodia interpunctella*. The primary questioned examined is what determines how long *Nemeritis* spends in a patch of hosts. A patch is defined as an area containing a host secretion produced during feeding which is excitatory to the parasitoid.

The time spent by *Nemeritis* in a patch of particular host density is determined by two distinct responses, (1) a complex orthokinetic response to the host secretion, which includes a probing response by which the concealed hosts are contacted, and (2) a klinotactic response to the disappearance of the host secretion at the edge of the patch, which causes the insect to turn back towards center. The abandonment of a patch results from the waning of responsiveness to this latter patch edge stimulus. Patch time is increased by increasing the concentration of the chemical patch stimulus (i.e., by increasing host density) by oviposition. Oviposition alters the response to the patch stimulus, and the effect of serial ovipositions is determined by their rate rather than their absolute number.

The ecological implications of these results are investigated. A relationship between patch density and patch time is obtained which would clearly lead to aggregation, on the population level, in patches of high density. Short term changes in behaviour due to previous patch experience (habituation) affect subsequent allocation of time between patches. Long term changes (olfactory conditioning) are also shown to affect patch time.

Previous literature on parasitoids is reviewed and related to behavioural and ecological aspects of foraging time allocation.

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CHAPTER 1

INTRODUCTION

The patchiness of natural resources in space and time poses problems of foraging for resource exploiters. These problems are particularly acute for predatory organisms which can, by their own foraging, rapidly alter the patchiness of their prey resources. We might anticipate that through natural selection, predator foraging behaviour has become adapted to the efficient location and exploitation of patchily-distributed prey.

Such anticipations have been formalized in the context of evolutionary strategies for optimal foraging. These consider how efficiently a predator allocates a limited foraging time in an environment of patchily distributed prey (MacArthur and Pianka, 1966; Krebs et al., 1974; Charnov, 1976; Oaten, 1977). The goal of optimal foraging strategies is assumed to be the maximization of the fitness of the predator through the maximization of its rate of prey consumption (expressed, ideally, as nett energy intake). The exact behaviour of the predator, how it apportions its searching time between patches of prey, is considered to be the mechanism by which the optimal strategy is approached. The study of predator foraging behaviour thus affords us a means of testing evolutionary hypotheses derived from the theory of natural selection.

The study of foraging behaviour is also relevant to the ecological problem of predator-prey population dynamics and the stability of such systems. The effect of predators on patchily distributed prey populations has been examined experimentally (Huffaker, 1958; Hassell, 1971b) and theoretically (Hassell and May, 1974; Oaten, 1977b). Mathematical models for such interactions incorporate various elements of foraging behaviour, expressed as either the time of execution of some behavioural response (i.e., handling time, transit time, time wasted in

interference) or the rate of elicitation of a behavioural response (i.e. attack rate, coefficient of interference). Classical models of the functional response of predators to prey populations assumed predator foraging behaviour to involve random search (Holling, 1959). The inclusion of more complex and realistic submodels of foraging behaviour into functional response equations has been shown to confer increased stability upon theoretical predator-prey interactions (Hassell and May, 1973).

The foraging behaviour of polyphagous predators may affect not only the stability of individual prey populations, but that of a prey community in general (Paine, 1974; Comins and Hassell, 1976; Roughgarden and Feldman, 1975). The 'switching' hypothesis developed by Murdoch (1969) proposes that predators may alter their preference and, necessarily, their foraging behaviour, as prey populations vary in relative density. The behavioural implications of such a hypothesis are quite easily as fascinating as its ecological implications.

Having noted the relevance of the study of predator foraging to evolutionary and ecological problems, it remains to stress its obvious importance to the understanding of behavioural processes. Such study reveals the integration of simple stimulus-response units into complex behavioural patterns, and thus links the neurophysiological processes of an organism with the ecological processes which influence their evolution. Relatively few studies have related the input-output processes of a predator's behaviour with their ecological implications (but see Holling, 1965). While prey-finding stimuli have been identified for many predator-prey systems, particularly invertebrate ones, the precise effect of such stimuli, and the dynamics of the responses to them, are poorly understood.

The present study investigates the foraging behaviour of the ichneumonid wasp, *Nemeritis canescens* (Grav.), and its ecological and evolutionary implications. *Nemeritis* is a member of a large and fascinating group of entomophagous foragers known as parasitoids. A number of features of their biology separate parasitoids from true predators on the one hand and true parasites on the other. The following classification of foragers will serve to clarify these differences. True predators must kill and consume many prey individuals during their development from egg to sexually mature adult. In this group we may place virtually all vertebrate carnivores as well as many invertebrates. True parasites only consume a fraction of one prey individual during development, very rarely killing it (although a population of parasites may easily kill one host). Endoparasitic microorganisms and worms, haematophagous insects and leaf-feeding insects are common forms of this sort of forager. Parasitoids tend to fall between these two extremes in that an individual parasitoid requires one prey individual for the completion of development from egg to adult.

Parasitoids are mostly entomophagous insects, the great majority of which belong to the Hymenoptera Parasitica and a number of dipteran families, in particular the Tachinidae and Calliphoridae. While parasitoid life histories are found in only a few animal groups the diversity of species and foraging habits within these is enormous. Thousands of species exist, and the great majority attack a very small range of host species. Evolution appears to be rapid in parasitoids, which presumably both results in, and is a consequence of, their high host specificity.

Parasitoids have also been referred to as protelean parasites (Askew, 1971), as only the immature stages are parasitic. Eggs are usually laid in, on or near the integument of the host by adult females, and larval

development occurs in, or in many situations where the hosts are in protected chambers, on the host. The larvae feed on host tissues and haemolymph.

Parasitoids are ideal subjects for the study of the ecological and evolutionary aspects of foraging behaviour. Firstly, they tend to have very stereotyped host-finding behaviour, which is often resolvable into a series of specific responses to host-associated stimuli. Secondly, the direct association of host-finding with reproductive success facilitates considerations of the adaptedness of foraging behaviour. Natural selection which increases foraging efficiency acts directly to increase fitness by increasing the fecundity of the parasitoid. Finally, the simple algebraic relationship between the number of hosts found and the number of parasitoids entering the next generation facilitates the ecological modeling of the parasitoid-host system. The fact that hosts are not consumed during foraging, and may be re-encountered makes the modeling of foraging somewhat different for parasitoids than for true predators (Rogers, 1972a), and has led to the evolution in parasitoids of variable capacities to recognize already parasitized hosts.

The biology of parasitoids and, in particular, their host-finding behaviour, has been recently the subject of excellent reviews by Viktorov (1976), Vinson (1976) and Weseloh (1976). More classical reviews of parasitoid biology are to be found in Doutt (1959) and Clausen (1940).

Most ecological and evolutionary consideration of the foraging process deals with how a forager allocates its time between discrete patches of prey or between areas in the environment, called patches, which contain different densities of prey. To study the allocation of time between patches we must, of course, define what will constitute a

patch. In particular, it is important to know when a forager has entered and left a patch, and when it is engaged in on-patch and between-patch movement. Many authors have been rather vague about what is considered a patch, and different studies have interpreted the concept differently.

It is fitting, therefore, to begin this investigation of parasitoid foraging with the concept of the patch. A definition of a patch will be advanced which is particularly relevant to parasitoid foraging behaviour (Chapter 2). Following this, in Chapter 3, our knowledge of the foraging behaviour of parasitoids will be reviewed. The purpose of this review is to place the diverse literature into a more structured behavioural framework and relate this behaviour to the way in which parasitoids forage in patchy environments.

In Chapter 4, the various attempts at modeling the foraging process will be analyzed. In particular, I will consider the incorporation of parameters representing behavioural processes and discuss mathematical models for patch-time allocation in terms of their assumptions about the behaviour of foragers. Chapter 5 introduces briefly the biology of *Nemeritis* and discusses the advantages and disadvantages of *Nemeritis* as a subject for studies of foraging-time allocation. Chapter 6 presents the first set of experiments on the response of *Nemeritis* to patches of its host, the Indian Meal Moth (*Plodia interpunctuella* Hubn.). This chapter considers the various stimuli and responses which affect the time spent on a particular patch. In Chapter 7, patch-time allocation is considered in a more ecological context. The overall response to patches of different density are investigated as well as the response to a community of patches offered simultaneously. In Chapter 8, the overall results of the present study are summarized and related to what is known about other parasitoids.

CHAPTER 2

WHAT IS A PATCH?

How are spatially heterogeneous prey populations to be characterized so that spatial allocation of foraging time can be evaluated? A standard way of doing this is to identify a patch as a spatial subunit of foraging area. The interpretations of just what should constitute a patch have been various (Wiens, 1976). In this section, I shall develop a definition of a patch suited to the study of time allocation in foraging parasitoids and predators.

There are essentially two ways to characterize the distribution of a natural population using spatial subunits (Patil and Stiteler, 1974). If the population is distributed over a uniform substrate, arbitrary units may be used, for example, the squares of a grid projected onto the substrate. In this treatment, every grid unit of the substrate is a patch and the patch borders are defined by the imaginary lines of the grid. Artificial patches of this sort have been used in studies of predators foraging in such uniform environments as mud flats (Goss-Custard, 1970) lawns (Smith, 1974) and forest leaf litter (Zach and Falls, 1976). Artificial grids have also been used in tests of predator responses to different prey distributions in laboratory arenas (Murdie and Hassell, 1973).

Alternatively, if the prey population is distributed among discrete, natural units (e.g., leaves, rocks, trees), these units may be treated as patches. In this case, we are saying that there are certain environmental units in which we would expect to find prey (patches), and all other area is to be considered non-patch area. This adds another level to our characterization of prey distribution. Whereas with artificial patches we recognized occupied and unoccupied patches, we now recognize non-patches

and patches, the latter being either occupied or unoccupied. In his study of the foraging of great and blue tits for the larvae of the moth, *Enarmonia conicolana* (Heyl.), Gibb (1958) used artificial patch units (grid squares) to characterize the density of prey in a pine plantation, but natural patch units (pine cones) to characterize prey intensity. Various containers for prey have been used in laboratory experiments to mimic natural patch units (Hassell, 1971b; Smith and Dawkins, 1971; Krebs et al., 1974).

If artificial patches are imposed on a substrate, the dimensions of the patch (the size of the grid square) may be selected for convenience. With natural units, however, we encounter less arbitrary hierarchies of patch dimension. A patch, for instance, may be the leaf of a prey's host plant, an entire plant, or a group of plants isolated in a diverse flora. The appropriate scale of patchiness is, clearly, the scale(s) which the parasitoid or predator itself recognizes while foraging. Accordingly, the term grain has been applied to the way that a forager perceives the distribution of the prey population. Wiens (1976) describes grain as "a behavioural response to an environmental mosaic". Before we can evaluate how a particular parasitoid or predator forages between patches of prey, we must know what the forager recognizes as a patch. Thus, the grain of the forager's response must be determined.

What levels of patchiness do foraging parasitoids perceive? In an environment which is truly uniform (to the forager as well as the observer), the patch must be, as described above, a purely theoretical construct. In such a case, the forager responds only to stimuli perceived when the prey individual is encountered. When, however, the forager, like the observer, recognizes units of prey distribution, its behaviour becomes more complex. We must now consider the responses of

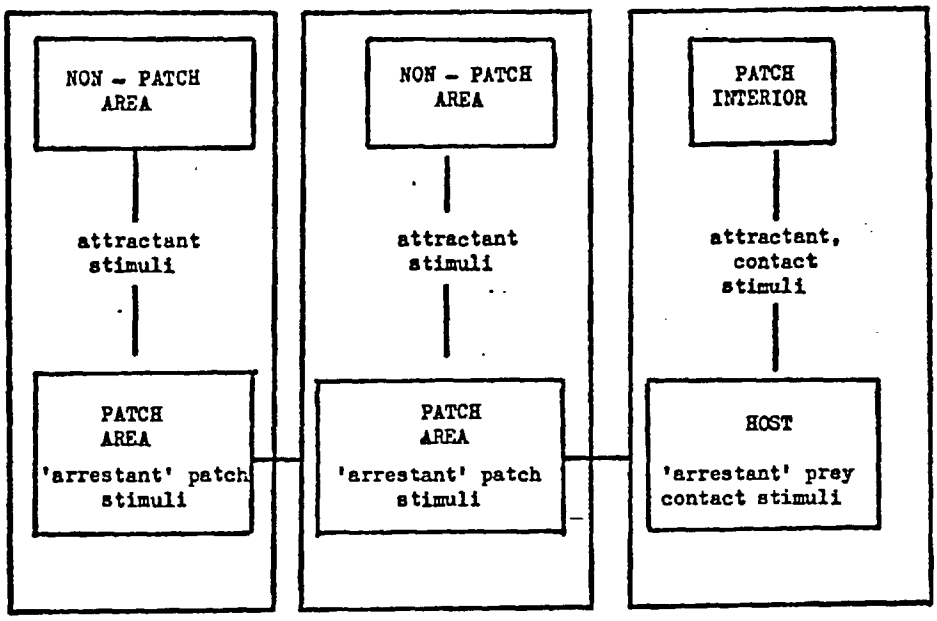
the forager to prey stimuli and to patch stimuli, and their integration. Nor need the forager's response be limited to two levels of stimuli. For instance, the ichneumonid parasitoid, *Diadromus pulchellus* Wesm., which attacks pupae of the leek moth, *Acrolepia assectella* (Zell.), exhibits a behavioural response to three levels of patchiness - the host's food plant, that part of the plant occupied by the host, and the host itself (Noyes, 1974). An identical sequence of discrete, 'telescoping' responses to different scales of host distribution has been demonstrated in the braconid, *Opius fletcheri* Silvestri, which attacks larvae of the melon fly, *Dacus curdubitae* Coguillet (Nishida, 1956).

Responsiveness to several successive levels of patchiness is probably widespread in parasitoids. Indeed, this notion of foraging at different levels is embodied in the classical representation of parasitoid search as host habitat finding - host finding (Doutt, 1964; see also Flanders, 1953; Salt, 1935). The unambiguous identification of these different levels involves the identification of stimuli governing the responses to each level and characterization of these responses. Such rigorous classification is important for the testing of current foraging theories, such as the Marginal Value Theorem (Charnov, 1976), which assume that the forager preceives as discrete units both habitats and the patches which comprise them.

Figure 1 is a schematic diagram of the hierarchical structure of patches and stimuli described above, to which a parasitoid might respond.

Most foraging studies are concerned with only one level of the foraging process. At a particular level of patchiness, how do we characterize what is a patch and what is non-patch area to the parasitoid (or predator) - that is to say, how do we match the natural units of prey

Figure 1. A. Schematic diagram of levels of patchiness in parasitoid foraging. B. Probable foraging levels for Opius fletcheri (interpreted from Nishida, 1956). C. Probable foraging levels for Diadromus pulchellus (interpreted from Noyes, 1974)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attractant stimuli
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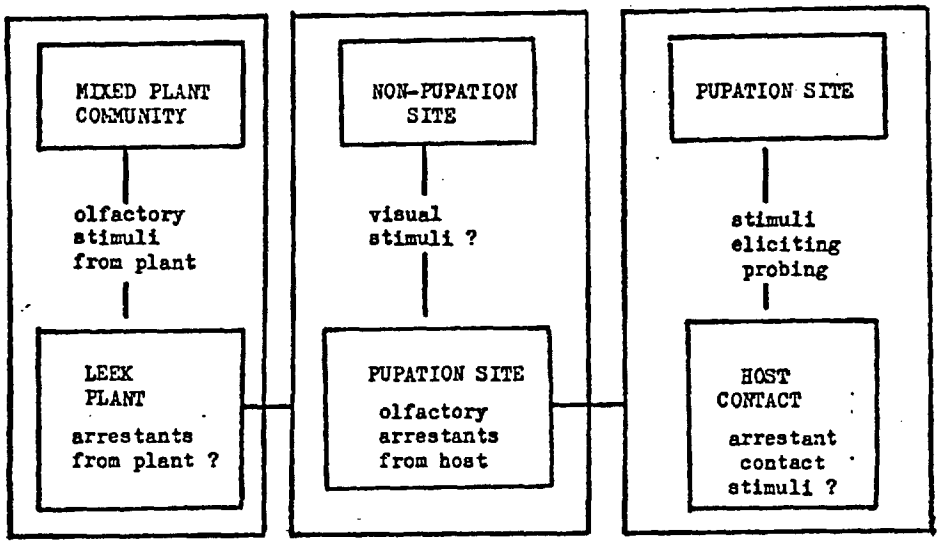
PATCH INTERIOR
attractant, contact stimuli
HOST
'arrestant' prey contact stimuli

A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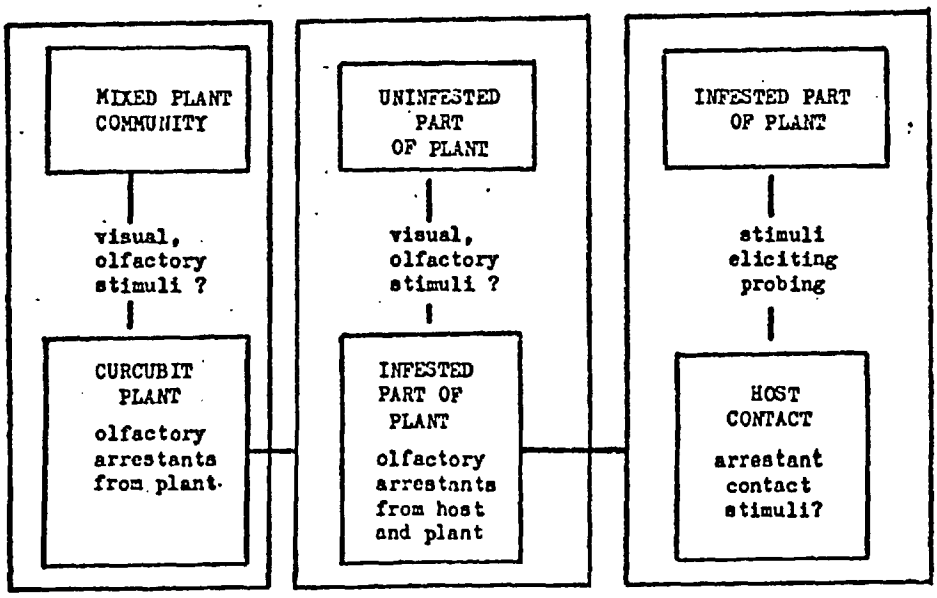
MIXED PLANT COMMUNITY
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stimuli eliciting probing
HOST CONTACT
arrestant contact stimuli?

C

distribution we perceive with those which the parasitoid perceives? Observations on the forager's behaviour provide the key. Specific changes in behaviour as the parasitoid forages may be associated with the recognition of patch and non-patch areas. Many parasitoids, for instance alternate walking in areas where hosts are found with flight between such areas. Areas where walking behaviour is elicited, and associated with the potential contact of hosts, may be considered patches. Patches characterized by such alternation of walking and flying by parasitoids include flower heads - *Eurytoma curta* Walker (Varley, 1941), *Bracon variator* Nees (Picard and Rabaud, 1914; in Clausen, 1940), grass stems - *Collyria calcitrator* Grav. (Walker, 1940), *Centeterus alternecoloratus* Cushman (Chacko and Rau, 1966), and rolled or curled leaves - *Apecthis rufata* Gmel. (Zwolfer and Kraus, 1957), *Ephedrus pulchellus* Stelfox (Stary, 1962).

In these and other foraging situations, we may identify different, mutually exclusive, behavioural activities which, by their alteration, signify the entering and leaving of a patch. This means of patch identification is analogous to the behaviour of the 'hypothetical forager' invented for many foraging models, which invests its foraging time in time spent searching (on-patch behaviour) and time spent in transit (between-patch behaviour) (Charnov, 1976; Oaten, 1977a, b; Cook and Hubbard, 1977).

Although changes in behaviour may be used to define patches, it is the stimulus which elicits the behaviour, and not the response itself, which may be of more value in this regard. This is because the elicitation of a response is dependent both on the intensity of the stimulus and the responsiveness of the predator. If a response defined a patch, there might be less patches in the environment of an unresponsive

parasitoid than a responsive one. Thus, it would be better to define a patch as an area containing a stimulus which, at the proper intensity, would elicit a characteristic foraging activity in a responsive forager.

While many stimuli involved in parasitoid foraging have now been identified, relatively little work has been done on these patch-characterizing stimuli. Many known stimuli are best classified as attractants, which mediate orientation in non-patch areas. Patch-characterizing stimuli would act, by contrast, as arrestants (sensuo Dethier, et al., 1960), eliciting spatial confinement of movement through changes in behaviour such as alighting in flying parasitoids or orthokinesis and klinokinesis in walking parasitoids. In the parasitoid literature, the response to such arrestants has been loosely described as a decrease in the speed and an increase in the intensity of 'search'.

There is some evidence that attractant stimuli, which elicit orientation to the patch, also elicit arrestment, and may be patch-characterizing stimuli. The mandibular gland secretion of the hosts of *Nemeritis canescens* elicits both attraction in a Y-tube olfactometer (Thorpe and Jones, 1937) and intense search and probing when applied to a surface (Corbet, 1971) although different components of this secretion may elicit these responses. Experiments with the pteromalid, *Nasonia vitripennis* (Walker), implicate host odour as eliciting both upwind orientation to the odour source (Edwards, 1954; Wylie, 1958) and careful examination of the surface treated with the odour (Jacobi, 1939).

In many parasitoids, attractants may act as primers for the responsiveness to patch-characterizing stimuli, that is, a parasitoid responding to an attractant stimulus will become responsive to another stimulus that elicits arrestment. Indirect support for this hypothesis comes from the

work of Read, et al. (1970) on *Diaeretiella rapae* (Curtis), a parasitoid of aphids on cruciferous plants. *D. rapae* is attracted to its host by volatile mustard oils produced by the cruciferous host plants. Read and coworkers found that parasitism of aphids on non-cruciferous plants was increased by the presence of mustard oil in the surrounding airspace. One possible interpretation of these results is that the presence of the olfactory stimulus increased the responsiveness to general visual stimuli (the image of a green plant), which elicited landing and search. Other evidence of odour-conditioned responses (orientation and arrestment) to visual stimuli in insects are summarized by Kennedy (1977).

Numerous examples exist of patch-characterizing chemical stimuli which elicit changes in locomotion of parasitoids walking more or less randomly on a surface. Most of these chemicals are products of the host, and their effect will be discussed in more detail in Chapter 3.1.

This chapter has examined the complexity of the patch concept and the relevance of different characterizations to the foraging process of parasitoids and predators. Artificial grid-square patches are useful only in studying the spatial aspects of the response to prey contact (area-restricted search, see Chapter 3.2). In such a case, the forager recognizes no heterogeneity in the environment and may be considered to be searching <u>within</u> a natural patch unit. When natural units are identified as patches, it is important that they be units to which the forager itself responds. The search for prey, their patch, and further levels of patchiness should be unambiguously characterized by stimuli specific to each level and particular responses to them. Within a particular level, patches may be defined by the presence of stimuli which, at a proper intensity will elicit an 'arrestant' searching response in a receptive predator. These patch-characterizing arrestant stimuli may or may not be distinct from attractant stimuli which mediate orientation to patches from non-patch areas.

CHAPTER 3

THE FORAGING BEHAVIOUR OF PARASITOIDS

The characterization of patch and non-patch areas gives us a framework for the ecological and evolutionary analysis of parasitoid foraging. It also, by definition, provides us with a useful classification of complex foraging behaviour into patch-specific behaviour and inter-patch, or transit, behaviour. It should be remembered that this often represents a simplification of an many-tiered foraging process.

Several authors have attempted to relate ecological considerations of foraging time allocation with forager behaviour which may influence this allocation. Krebs et al., (1974) have suggested that foragers must make two sorts of decisions during foraging; which patch to choose and when to leave a patch. Hassell and May (1973) have recognised a similar division in specifying long range attraction to prey and klinokinetic responses to prey capture as behaviours which affect aggregation by determining where you forage and how long you stay there, respectively.

There is a danger in such categorizations of confusing behavioural and ecological processes which should be distinguished. The ecological problem is essentially how a given amount of foraging time is to be allocated among a set of patches of different prey density. This may be resolved into two questions: which patches are entered and how long is spent in each of these patches. For convenience, transit time between patches will be considered constant during the foraging period, but it should be noted that this can be an important variable component of natural foraging time. From an ecological point of view, then, we are interested in the set of patches entered by the forager and the time the forager allocates to the different density patches entered.

From a behavioural point of view, we are interested in the determinants of movement in and between patches. In particular, we wish to identify stimuli and responses which modulate the orientation to patches during off-patch movement and the stimuli and responses which modulate movement on the patch, heretofore characterized as 'arrestment'. Some characteristics of on and off-patch movement will overlap or be shared, but for the most part we may distinguish two sorts of behaviour; distant patch-finding behaviour and patch localized behaviour. These behaviours influence, respectively, which patches are visited and how much time is spent on each patch, and therefore may be identified with the two ecological questions posed above. In the following discussion, parasitoid behaviour will be classified in this manner and related to its ecological implications for foraging.

This chapter presents a review of what is known about parasitoid foraging behaviour. Analogous behaviour in invertebrate predators will be mentioned where relevant, and some comparisons will be made with the foraging behaviour of vertebrates, which has been extensively reviewed elsewhere (Krebs, 1973; Curio, 1976).

3.1 PATCH-FINDING BEHAVIOUR

The behaviour involved in patch-finding can affect foraging time allocation by determining which patches are to be exploited. At one extreme, parasitoids may encounter patches at random. At the other extreme, stimuli from patches may lead to parasitoids selecting patches of the highest host density, thereby leading to non-random selection and aggregation. The potential for non-random attraction to patches is reflected in the ability of the parasitoid to evaluate patches remotely and choose between them. Such evaluation may involve the distant detection of host associated factors or, if the patch has previously been visited, memory

of the patch 'profitability'. This latter effect, which involves learning, will be discussed in section 3.3.

As mentioned in Chapter 2, orientation to patches may be mediated by attractant stimuli perceived at a distance from the patch. Olfactory and visual stimuli are the most frequently encountered attractants among parasitoids. Auditory stimuli, however, have recently been implicated in the orientation of the dipteran parasitoids, *Euphasiopteryx ochraea* (Cade, 1975) and *Colcondamyia auditrix* Soper (Soper, et al., 1975) to their orthopteran hosts.

The responsiveness of parasitoids to patch attractants may be influenced by several endogenous factors. A non-responsive, pre-oviposition period has been identified in the parasitoids *Lariophagus distinguendus* Forst. (Kaschef, 1964), *Pimpla ruficollis* Grav., *Eulemmeria rufifemur* (Thorpe and Caudle, 1938), *Eucarciella rutilla* Vill. (Herrebout and van der Veer, 1969), *Opius fletcheri* (Nishida, 1956), and many others. In at least some species, if not all, it is correlated with the egg maturation process. Once eggs are mature, internal stimuli may elicit appetitive searching behaviour, during which the parasitoid is responsive to patch attractants (Bragg, 1974). Hassell (1976b) has likened this egg pressure in parasitoids to hunger in predators, suggesting that egg depletion acts like satiation in reducing responsiveness to host stimuli. This inhibitory effect of egg depletion on responsiveness has not been examined in parasitoids, but it has been demonstrated in ovipositing lepidoptera (Jones, 1977). The diel periodicity of some parasitoids (Weseloh, 1976a, b) suggests that internal rhythyms may constitute another endogenous factor affecting responsiveness.

The orientation response of parasitoids to attractant stimuli is

poorly understood. The term 'attraction' is used to describe a complex process, the mechanisms of which are still unclear. Orientation to visual stimuli is rather straightforward, as is orientation to auditory stimuli, which probably involves adjusting the path so as to balance the intensity of sound reaching the two tympani (Haskell, 1961). But the majority of stimuli identified as attractants for parasitoids are olfactory, and orientation to odour sources has been a subject of some controversy (Kennedy, 1965, 1977). Orientation up odour gradients (chemotaxis) is a possibility, but this mechanism is challenged by the observation that odour plumes tend to become irregular at distances from the source, and gradients become correspondingly obscured and shallow. Of greater appeal is the mechanism of odour-modulated, optomotor anemotaxis described by Kennedy (1977), in which odour elcits orientation upwind and, consequently, towards the source of the wind-borne chemical. Close to the odour source, where gradients are likely to be steep and undisturbed, chemotaxis may be a feasible mechanism. The ability of a parasitoid to choose between patches may be influenced by the sensory modalities and mechanisms involved in orientation. Mechanisms involving the comparison of stimulus intensities (phonotaxis, chemotaxis), for instance, may be better suited to long-range comparison of stimuli from different patches than mechanisms where the stimulus merely triggers a response to another stimulus bearing no direct patch information (anemotaxis). In the latter case, stimuli of different intensity, above a given threshold intensity, may not be discriminated, and attraction to the patch could be independent of the intensity of the attractant stimulus. Clearly, more detailed studies of orientation mechanisms are required to determine how able parasitoids are to select patches from a distance during foraging.

Turning to the properties of attractants involved in patch selection, studies of host-finding by parasitoid have generally recognized two sorts of attractant stimuli; those produced by the host and those produced by the immediate environment of the host (Finlayson, 1950; Zwolfer, 1962). Attractant stimuli produced by the hosts include chemicals released in frass (Hendry, et al., 1973), during moulting (Marsh, 1937), during feeding (Corbet, 1971), aggregation pheromones (Rice, 1968) and sex pheromones (Sternlicht, 1973; Mitchell and Mau, 1971). The intensity of such olfactory stimuli released from a patch is most likely a linear function of the number of host individuals on that patch, and this probably holds for visual and auditory stimuli as well.

It seems reasonable to conclude that, in general, more host-produced attractants are released from higher density patches. Aggregation by parasitoids could thus result from orientation towards the most intense attractant source in the perceptual field leading to a 'choice' by the parasitoid of higher density patches over lower density ones. Alternatively, if there exists a particular threshold intensity below which a forager will not respond to an attractant, distant or low density patches may simply remain unperceived.

A different situation is presented by stimuli associated with the host's environment, such as stimuli from the food plant of the host. These attractants would, in contrast to host-produced attractants, carry little information about the host density in a patch, and would not contribute to aggregation except by, possibly, attracting parasitoids to areas of high patch density. Important exceptions to this observation are found where the activity of the host itself influences the release of an attractant from the host environment. Feeding by the host undoubtedly releases the plant-produced attractant of *Phaeogenes cynarae* Bragg (Bragg,

1974), and the same is true for *Heydenia unica* Cook and Davis, which is attracted by the pine volatile, a-pinene, released during feeding by its scolytid hosts (Camors and Payne, 1972 and Monteith (1964) has shown that the parasitoid, *Drino bohemica* Mesn.), which attacks sawflies on conifers, is attracted more to the odour of unhealthy conifers than healthy ones. In this case, plant-produced attractants may actually be released from infested plants which are not released from healthy ones. Visual stimuli produced by host plants may also reflect the presence and density of hosts. *Itoplectis conquisitor* (Say) is attracted more to red shoots of *Pinus sylvestris* L. than green shoots (Arthur, 1966). Reddening of the needles is caused by infestations of the ichneumonid's host, *Rhyacionia buoliana* (Schiff).

The attraction of parasitoids by non-host stimuli has another important ecological implication for patch selection. If a patch is located by a response to attractants from the host's environment, say, it's food plant, hosts not associated with that part of the environment or that food plant are likely not to be perceived by the forager. Thus, Zwolfer and Kraus (1957) found that *Apechthis rufata* would parasitize pupae of the fir budworm, *Choristoneura murinana* Hbn. when they were placed in rolled oak leaves, the environment of the parasitoid's usual host. Very large populations of *C. murinana* on adjacent fir trees, however, were never parasitized. A less contrived example of protected host populations is found in *Lygus lineolaris* Beauvois in the North-eastern U.S., which is attacked by the nymphal parasitoid, *Leiophron pallipes* Curtis (Streams, et al., 1968). While the host is a generalist on many species of grasses and herbs, significant parasitization by *Leiophron* occurs only on host plants of the genus *Erigeron*. The smell of *Erigeron* is apparently important in the attraction of *Leiophron* to

host patches and results in this limited exploitation of the host population. More subtle variations in association of hosts with plant-produced attractants may also affect host exploitation. Van Emden (1977), for instance, has found that parasitism of *Brevicoryne brassicae* L. by *Diaeretiella rapae* is less on cabbage varieties low in mustard oils, the attractant for the parasitoid. Host patches which afford protection by the relative absence of attractant stimuli for the parasitoid may be thought of as host refugia in considerations of the parasitoid/host interactions. The effect of such refugia on the dynamics of forager/prey interactions can be considerable, and has been modelled by Hassell and May (1973), Emlen (1973) and Maynard Smith (1974).

Finally, patch-finding behaviour may be influenced by factors which are not related to host-produced or host-associated stimuli. Monteith (1960), for instance, found that the attractiveness of the host's food tree to *Drino bohemica* could be masked by the odour of adjacent trees of different species. The distribution of adult food resources may also influence patch selection by parasitoids. Allen and Smith (1958) attributed the higher parasitism of *Colias philodice* Boisd. by *Apanteles medicaginis* Muesb. in small rather than large fields to the closeness and abundance of bordering food plants in the former localities.

3.2 PATCH-LOCALIZED BEHAVIOUR

A change in behaviour upon entering a patch is elicited by specific patch stimuli, which I have loosely classified as arrestants. This response, in turn, may make the forager more receptive to stimuli perceived when prey are contacted. Stimuli arising from prey contact and their responses may be considered distinct from patch stimuli and their associated responses. Patch-localized behaviour, therefore, is a combination of the response to patch stimuli and prey contact stimuli.

Of course, if the patch is identified with an imaginary unit of space, patch-localized behaviour is influenced by the response to prey contact stimuli alone, as there are no patch stimuli (see Chapter 2).

The arrestant effect of patch stimuli may involve a variety of responses. Responses to visual and tactile stimuli (e.g., landing on a plant, walking onto a leaf from a stem) often involve a change in the speed of movement (orthokinesis). Furthermore the limits of such stimuli (i.e., the patch edge) often influence the path of the moving forager. This has been demonstrated in invertebrate predators foraging on plants. The path of coccinellid larvae (Banks, 1957) and predatory anthocorids (Evans, 1976) on plants is limited by, and often conforms to, leaf edges and veins. Similar factors undoubtedly affect the foraging of parasitoids on plants. In such cases, the shape and morphology of the patch will affect the time that is spent searching it.

At another level of patchiness, chemical patch stimuli may affect the movement of parasitoids on relatively uniform surfaces. Many species, for example, respond to patches of chemicals deposited by their hosts on substrates which they have occupied. These substances are characteristically of low volatility and have been called 'contact chemicals' by Vinson (1976), as parasitoids crossing a surface treated with such compounds usually start tapping or rubbing their antennae on the substrate, thereby making direct antennal contact with the chemical. The response to contact chemicals has usually been described in unfortunately vague terms, such as examination and excitement. According to Vinson, contact chemicals "elicit intense and directed search of the contaminated and surrounding area". While this definition is reasonably descriptive, it raises questions about the nature of this 'directed search' and the capacity of the chemical to elicit responses in areas where it is absent.

A more exact behavioural terminology might be applied to these patch stimuli. From the examples given in Table 1, it will be seen that most contact chemicals elicit either a decrease in speed of movement or stopping, i.e., an orthokinetic response. In addition, many elicit an increase in the rate of turning. From the information at hand it is impossible to determine whether the turning is random in orientation (klinokinesis) or directed (klinotaxis), or, indeed, whether it is elicited by the presentation of the stimulus or by its removal. In most experiments, the border of the chemical patch was not known, and so it cannot be determined whether turning was elicited on the patch area or at its edge. Some parasitoids are, apparently, capable of following chemical trails left by their hosts (Vinson and Lewis, 1965; Doutt, 1964). This suggests that these insects can orient so as to maintain themselves in areas of host odour, perhaps by comparing the sensory input from the two antennae (klinotaxis or tropotaxis).

In general, then, contact chemicals elicit an orthokinetic response and either a klinokinetic or a tactic response, all of which are effectively arrestant and increase the time spent in the chemical patch. Several authors have demonstrated that, as the concentration of contact chemicals are increased, search is intensified and often probing with the ovipositor elicited, this latter behaviour further increasing the orthokinetic effect (Corbet, 1973; Hendry, et al., 1973). Chemical elicitation of probing responses is common in parasitoids searching for concealed prey, which can only be contacted with the ovipositor.

Increasing the concentration of contact chemical, by increasing host density in the patch, may increase the total time spent on the patch by a parasitoid, even in the absence of host contact. Such increased persistence will, of course, also increase the probability of host encounter, as

Table 1. Analysis of parasitoid responses to 'contact chemicals' (patch-characterizing stimuli).

SPECIES AND FAMILY	SOURCE OF CHEMICAL	SUBSTRATE	PRE-CONTACT BEHAVIOUR	POST-CONTACT BEHAVIOUR	INFERRED RESPONSE	AUTHORS
Campoplex haywardi Blanch. (Ichneum.)	host frass	surface of potato	moving, antennal tapping on substrate	stopping, antennal 'investigation'	orthokinesis	Leong and Oatman, 1968
Trissolcus viktorovi Kozlov (Scelionidae)	extract of host ovipositon gland	filter paper	rapid, straight walking	antennal drumming, slow 'zig-zag' walking, stopping, cleaning	orthokinesis klinokinesis/ taxis	Buleza, 1973
Diadromus pulchellus Wesm. (Ichneumonidae)	surface of host pupa	perspex plate	ave. speed 2.45 cm/sec ave. of 1.3 90° turns/cm	ave. speed 0.52 cm/sec ave. of 9.0 90° turns/cm	orthokinesis klinokinesis/ taxis	Noyes, 1974
Microplitis croceipes Cresson (Braconidae)	host frass extract	filter paper	walking	hesitation, stopping, antennal 'examination'	orthokinesis	Lewis and Jones, 1971
Cardiochiles nigriceps Vier. (Braconidae)	host salivary gland extract	filter paper	walking	antennal 'examination', rapid turning, probing	orthokinesis klinokinesis/ taxis	Vinson and Lewis, 1965
Orgilus lepidus Muesb. (Braconidae)	host frass extract	filter paper	walking	intensive 'search' antennal tapping, probing	orthokinesis	Greany and and Oatman, 1972
Phaeogenes cynarae Bragg (Ichneumonidae)	host frass	stem of host food plant	walking, turning	increased turning, 'physical examination'	klinokinesis/ taxis	Bragg, 1974

SPECIES AND FAMILY	SOURCE OF CHEMICAL	SUBSTRATE	PRE-CONTACT BEHAVIOUR	POST-CONTACT BEHAVIOUR	INFERRED RESPONSE	AUTHORS
Lydella grisescens R.-D. (Tachinidae)	host frass extract	cotton	walking	'attraction', oviposition	orthokinesis	Hsiao et al., 1966
Rhyssa persuasoria L. (Ichneumonidae)	host frass extract (with fungus)	filter paper	walking, antennal tapping	'more convoluted path', stopping, probing, rapid antennal tapping	orthokinesis klinokinesis/ taxis	Spradberry, 1970
Megarhyssa nortoni (Cresson) (Ichneum.)	fungus extracts from host frass	filter paper	walking	antennal 'investigation', probing	orthokinesis	Madden, 1968
Nemeritis canescens (Grav.) (Ichneum.)	host mandibular gland extract	glass plate	walking	stopping, antennal 'investigation', probing	orthokinesis	Corbet, 1971
Campoletis sonorensis (Cam.) (Ichneumonidae)	host frass, silk extract	filter paper	walking	'hesitation', stopping, antennal 'investigation', probing	orthokinesis	Wilson et al., 1974
Trichogramma evanescens Westw. (Trichogramm.)	host female scale extr.	cloth surface	rapid movement	intense 'search'	orthokinesis(?)	Lewis et al., 1971

has been demonstrated experimentally by Viktorov, et al. (1975) for the egg parasite *Trissolcus grandis* Thom., and by Lewis, et al. (1972) for the egg parasite, *Trichogramma evanescens* Westw. Thus, chemical patch stimuli may influence both directly and indirectly the time spent on a patch, and may contribute towards aggregation in high density patches.

In the bark beetle parasitoid, *Coeloides brunneri* Vierick, orthokinetic and klinokinetic responses similar to those described above for contact chemicals are elicited by patches of infra-red radiation above host-occupied wood (Richerson and Borden, 1971, 1972).

Responses to parasitoid-produced patch stimuli have been observed in *Pleolophus basizonus* Grav. (Price, 1972) and *Orgilus lepidus* (Greany and Oatman, 1972). Such chemical "trail markers" are apparently deposited by a forager in areas as they are searched, and discourage researching by that, and other, parasitoids. Such behaviour permits systematic search within and between patches, and therefore contributes to the efficiency of the parasitoids foraging process.

The second component of patch behaviour involves the process of prey capture and handling and its effect on subsequent search. Predators, upon perceiving a prey, execute pursuit, capture, ingestion and, perhaps, some digestion before search is resumed. In parasitoids, prey capture and handling have somewhat different components. The host 'capture' is usually followed by host examination (the host-acceptance stage of Doutt, 1964), oviposition, and a refractory period during which the parasite is unresponsive to host stimuli. This process is often very stereotyped and is commonly depicted as a 'chain response' sequence (Edwards, 1954; Schmidt, 1974). Various chemical and tactile stimuli are involved in the process of host acceptance. The Gypsy Moth larval parasitoid, *Apanteles*

melanoscelus (Ratzeburg), for instance, recognizes its host by its "hairiness" and by a chemical associated with its integument (Weseloh, 1974). Other host acceptance stimuli are reviewed by Vinson (1976) and Viktorov (1976). Once a host is penetrated with the ovipositor, chemical stimuli in the host's haemolymph elicit oviposition (Arthur, et al., 1969). Internal chemical stimuli are implicated in the rejection of already parasitised hosts (Rogers, 1972). Recognition of already parasitized hosts may occur before or after probing, and may interrupt the host acceptance process at various stages (van Lenteren, et al., 1976a), leading to a resumption of search. Following oviposition, resting and grooming behaviour is often observed, along with a temporary unresponsiveness to host stimuli.

The time taken for host acceptance, oviposition and the refractory period varies widely between parasitoid species. In *Nemeritis canescens*, which contacts its host while probing, host acceptance occurs in a fraction of a second, while in the mantid egg parasite, *Podagrion meridionale* Masi, the host may be examined for up to an hour before probing (Gerling, 1969). Similar variation exists in the duration of oviposition and the refractory period. The handling times for a number of invertebrate predators and parasitoids have been calculated by Hassell (1976a) and these show a great variability commensurate with the variability of their component parts described here.

A number of studies of vertebrate and invertebrate foragers have demonstrated a distinct change in the searching movements following the capture and handling of a prey item. This behaviour was called area-restricted search by Tinbergen, et al. (1967) in their study of carrion crows foraging on beaches for camouflaged eggs. In this study, the stimuli inducing this behaviour were complex, and the exact response

elicited was not characterized. Subsequent, more controlled, investigations on vertebrates have carefully analysed the change in searching movements of the forager prior to and following prey capture (Thomas, 1974; Smith, 1974). Similar studies have been made on invertebrate foragers, and these, along with more casual observations on area-restricted search, are listed in Table 2. From these examples it can be seen that area-restricted search may involve an orthokinetic component, a klinokinetic component or, as is most often the case, both. Both responses increase the amount of time spent in the vicinity of the last prey capture and, for this reason, area-restricted search has been considered a major mechanism for aggregation by predators (Hassell and Rogers, 1972; Hassell and May, 1974). It is commonly thought that area-restricted search has arisen through natural selection of aggregative responses in foragers attracting clumped prey species. This would suggest that foragers of non-clumped prey should not exhibit area-restricted search. In support of this hypothesis it is interesting to note that whereas aphid parasitoids may show area-restricted search in response to host populations, which are aggregated on leaf undersides (Hafez, 1961), the whitefly parasite, *Encarsia formosa* Gahan, whose hosts are scattered singly on leaf undersides, shows no change in movements after oviposition (van Lenteren, et al., 1976b). Although the aggregative effect and evolutionary implications of area-restricted search in invertebrates are obvious, a close examination of the exact stimuli and responses involved show the phenomenon to be somewhat more complex.

Most considerations of area-restricted search assume the stimulus to be the ingestion of, or oviposition in, a prey item. As can be seen from Table 2, though, host contact alone, with no ingestion or oviposition, is sometimes sufficient to elicit the response. Indeed, the data of Chandler

Table 2. Analysis of responses to prey contact/capture ('area-restricted search') by arthropod predators and parasitoids.

SPECIES/FAMILY	PREY	NATURE OF STIMULUS	CHANGE IN MOVEMENT FOLLOWING STIMULUS		N_{cap}/N_{eno}	AUTHORS
			TURNING RATE (TURNS/DIST)	ORTHOKINESIS		
Stethorus picipes (4°) Casey (Coccinellidae)	mites	prey capture	marked increase in path 'tortuousity'	not recorded	0.34	Fleschner, 1950
Adalia bipunctata (4°) L. (Coccinellidae)	aphids	prey capture	marked increase (measured)	marked decrease in speed (measured)	----	Banks, 1957
Adalia bipunctata (lva) L. (Coccinellidae)	aphids	prey capture	marked increase	not recorded	----	Bansch. 1964a
Coccinella 7-punctata (lva) L. (Coccinellidae)	aphids	prey capture	marked increase	not recorded	----	Bansch, 1964a
Hippodamia 5-signata (1°) (Kirby) (Coccinellidae)	aphids	prey capture	marked increase in patch 'tortuousity'	marked decrease 'moved very slowly'	very low	Kaddou, 1960
Chrysopa californica (4°) Coquillet (Chrysopidae)	mites	prey capture	possible, but not marked	not recorded	1.00	Fleschner, 1950
Conwentzia hageni (4°) (Chrysopidae)	mites	prey capture	marked increase in patch 'tortuousity'	not recorded	0.22	Fleschner, 1950
Chrysopa vulgaris (lva) L. (Chrysopidae)	aphids	prey capture	increase, 'not as much as with coccinellids'	possible increase in speed	----	Bansch, 1964a
Chrysopa perla (lva) (L.) (Chrysopidae)	aphids	prey capture	increase, 'not as much as with coccinellids'	possible increase in speed	----	Bansch, 1964a

SPECIES/FAMILY	PREY	NATURE OF STIMULUS	CHANGE IN MOVEMENT FOLLOWING STIMULUS		N_{cap}/N_{enc}	AUTHORS
			TURNING RATE (TURNS/DIST)	ORTHOKINESIS		
Hemerobius nitidulus (lva) (Hemerobiidae)	aphids	prey capture	marked increase with 180° turns	increase in speed	----	Bansch, 1964b
Lasiopticus pyrasti (lva) L. (Syrphidae)	aphids	prey capture	no change observed	no change observed	----	Bansch, 1964a
Syrphus balteatus (1°) Deg. (Syrphidae)	aphids	prey contact	marked increase (measured)	marked decrease (measured)	----	Chandler, 1969
Anthocoris confusus (ad) Reuter (Anthocoridae)	aphids	prey capture	marked increase (measured)	not recorded	----	Evans, 1976
Asolcus mitsukurii Ashm. (Scelionidae)	eggs of hemiptera	host contact	observed increase	not recorded	----	Hokyo and Kiritani, 1966
Telenomus nakagawai Watan. (Scelionidae)	eggs of hemiptera	host contaot	observed increase	not recorded	----	Hokyo and Kiritani, 1966
Trichogramma evanescens Westw. (Trichogramm.)	eggs of moths	host contact (greater than 2 sec) or oviposition	marked increase	not recorded	----	Laing, 1937, 1938
Diaeretiella rapae (M'Intosh) (Aphidiidae)	aphids	host penetration (not necessarily oviposition)	possible, but not marked	not recorded	0.35	Hafez, 1961
Cyzenis albicans (Fall.) (Tachinidae)	sugar droplets	'prey' capture	marked increase in path 'tortuousity'	not recorded	----	Murdie and Hassell, 1973

SPECIES/FAMILY	PREY	NATURE OF STIMULUS	CHANGE IN MOVEMENT FOLLOWING STIMULUS		N_{cap}/N_{enc}	AUTHORS
			TURNING RATE (TURNS/DIST)	ORTHOKINESIS		
Musca domestica L. (Muscidae)	sugar droplets	'prey' capture	marked increase klinokinesis (measured)	marked decrease (measured)	----	Murdie and Hassell, 1973
Phormia regina (Meig.) (Calliphoridae)	sugar droplets	'prey' contact (application to tarsal chemoreceptors)	marked increase -turning in the direction of the tarsus stimulated	not recorded	----	Dethier, 1976

(1969) indicates that stimuli from ingestion of the prey actually inhibit the area-restricted search response. Such inhibition is also implicit in the data of Evans (1976). This suggests that, perhaps, area-restricted search is actually elicited by prey contact, and inhibited by satiation resulting from subsequent ingestion of the prey item. Table 2 presents, where data was available, the frequency of successful prey encounters, N_{cap}/N_{enc}, that is, the fraction of encounters that lead immediately to feeding or oviposition on that item. As can be seen, the success of individual encounters is strikingly low in species exhibiting area-restricted search, and many prey apparently escape, at least from the first encounter. This suggests that area-restricted search might be an adaptation which enhances the capture rate by increasing the probability of capturing a prey which has just escaped an encounter. A similar function has been ascribed to the turning behaviour of muscid flies in response to contact of sugar solutions (Dethier, 1976). Actual prey consumption opposes this response, through the inhibitory effect of satiation. If satiation (egg depletion) does not result from prey handling, area-restricted search will occur after prey handling, leading to the observation that it is adaptive to foraging for clumped prey.

Clearly, area-restricted search will contribute to the foraging efficiency of parasitoids searching for clumped prey. It is worth noting, though that clumping does not necessarily render the prey more vulnerable to parasitism. Defensive or escape reactions of prey may be optimized when they are clumped. For instance, alarm pheromones in aphids, released by parasitoid attack, spread more successfully through clumped populations, permitting unattacked individuals to escape (Ruth et al., 1975). In Canada, the introduced sawfly parasite, *Exenterus amictorius* Panzer, prefers solitary to aggregated hosts, possibly because of the defensive

behaviour of host colonies, which regurgitate resin collected from the food plant (McLeod, 1972). A native species, *E. diprionis* Rohwer, on the other hand, prefers colonies, in which it adopts very slow and careful movements, thereby not eliciting the defensive response of its hosts. In the absence of defensive reactions, aggregation may be advantageous for prey simply because it protects individuals inside the aggregate from attack. This sort of protection may account for the observations of George (1957), on *Diaretiella rapae* attacking *Brevicoryne brassicae* on cabbage. He found that per cent parasitism was higher on upper leaves, where prey colonies were small and diffuse, than on lower leaves, where colonies were large and densely aggregated, and attributed this to the greater number of aphids exposed to attack on the perimeter of colonies on the upper leaves.

The phenomenon of area-restricted search has been shown to be but one of a number of factors contributing to the patch-localized behaviour of a parasitoid and the time it spends on a patch. The response to patch stimuli, which may be influenced by host density, and the responses to stimuli involved in prey capture and handling, also contribute to patch-time. Aggregation by foragers on patches of high host density may be attributable to one or more of these patch-localized behavioural responses.

3.3 LEARNED RESPONSES AND PARASITOID FORAGING

So far, I have treated the components of patch-finding behaviour and patch localized behaviour as innate responses to stimuli associated with the prey or prey environment. Most theoretical models of foraging time allocation, built for and tested with vertebrate foragers, assume that the forager makes decisions based on memory of previous patch experience (see Chapter 4). This learning component of foraging behaviour can greatly influence the patch selection and patch-time processes, part-

icularly in situations where patches can become depleted and time can, thus, be wasted revisiting already exploited areas. The importance of learned responses in the foraging of parasitoids is not clear, as their learning abilities have been little studied. It is commonly thought that invertebrate nervous systems are simpler than vertebrate ones, and consequently less capable of learning, and there is some neurophysiological evidence for the first premise (Horridge, 1968; p. 414). That invertebrates are incapable of vertebrate-type learning is less certain. This assumption is implicit in the classic ecological characterization of Type II (invertebrate) and Type III (vertebrate) functional responses by Holling (1959), who argues that the sigmoid, Type III response arises from the addition of a learning component absent in invertebrate behaviour (Holling, 1965). But does the relative simplicity of invertebrate nervous systems mean that invertebrate foragers are incapable of solving vertebrate-type learning problems, or that they simply solve them in a different manner?

An interesting comparison of learning in vertebrates and invertebrates has been made by Schneirla (1962). He studied the maze learning ability of ants (*Formica* spp.) and rats in identical mazes, scaled to the size of the animals. The rate at which maze problems were learned was, as anticipated, much slower for the insects. Beyond this, Schneirla concluded that the structure of the learning process itself differed between invertebrates and vertebrates. Ants learned maze problems in a step-wise manner, involving and initial period of conditioning of each correct response at successive turns in the maze, followed by an integration of these steps into a smooth overall pattern of movement. By contrast, rats mastered mazes with very few experiences, rapidly integrating the information gathered throughout the maze into a solution.

Furthermore, the final solution attained was more easily modified by rats in response to minor changes in maze structure or the context of the test situation. Ants reacted to altered mazes or test situations (e.g., runs from food to nest rather than from nest to food) as entirely new problems which had to be completely relearned.

Schneirla's experiments suggest that insect foragers solve learning problems in a different manner than vertebrates, and may be less efficient at learning over short training periods and less able to generalize learned situations. That some insect foragers can generalize learned cues has been demonstrated by van Beusekom (1948) in his experiments with the wasp, *Philanthus triangulum* Fabr.

To begin this discussion of learning in parasitoids, I shall define learning according to Kimble (in Alloway, 1972) as "any relatively permanent change in behaviour which occurs as a result of practice", and emphasize that care must be taken in distinguishing learned from innate responses. A case in point is Taylor's (1974) experiments with *Nemeritis canescens* which, he claimed, demonstrated that *Nemeritis* learned areas where it had found hosts, as indicated by its tendency to remain in and return to those areas. The work of Corbet (1971) and data to be presented later in this dissertation, demonstrates that for *Nemeritis*, attraction to and arrestment in the host area is elcited by a specific chemical produced by the host. The wasp was not necessarily learning anything, and the innate response to this host chemical is fully sufficient to explain Taylor's observations.

Alloway (1973), following Thorpe (1956), classified invertebrate learning into a number of types. Of particular relevance to the present discussion are habituation, classical conditioning, instrumental learning and latent learning.

Habituation is a very simple form of learning involving a decrease in responsiveness to a stimulus which is presented repeatedly. This change is at the level of the central nervous system, and not merely the result of the adaptation of the animals peripheral sense organs. In as much as habituation may terminate responses to patch or prey stimuli, it is probably very important in determining when a forager leaves a patch. Habituation to patch and prey stimuli in parasitoids has been shown or suggested in *Diaeretiella rapae* (Hafez, 1961), *Cardiochiles nigriceps* (Vinson and Lewis, 1965), *Microplitis croecipes* (Lewis and Jones, 1971) and *Nemeritis canescens* (Corbet, 1973). This form of learning will be taken up in more detail in Chapter 5. At this point, however, it is interesting to note that habituation may provide a simple mechanism for aggregation by foragers. Habituation to patch stimuli of a given intensity might lower the subsequent responsiveness of the forager to patch stimuli equal to or below that intensity, thus favouring the selection of patches with high stimulus intensity (high prey density). The influence of such a mechanism on aggregation would depend, of course, on the specificity and duration of the habituation effect.

Classical conditioning may be described in the following manner: a conditional stimulus (CS) is presented with (usually shortly before) an unconditional stimulus (UCS), which normally elicits an unconditional response by the subject (UCR). After one, or a series of such presentations, a conditional response (CR), similar, if not identical, to the UCR, is elicited by the CS. The existence of reinforcement is usually implicit in most treatments of classical conditioning, and in predator conditioning, such reinforcement is equated with the capture of prey, a more or less direct consequence of the UCR (and CR). For invertebrate foragers, such learned associations between patch stimuli or attractants

and normally indifferent stimuli could alter the patch selection process. For instance, if high densities of polyphagous hosts were associated with a particular plant species, associative conditioning of the parasitoid to the odour of that plant species (CS) by its pairing with host attractants (UCS) could lead to preferential attraction to hosts on that plant, aggregation by the parasite, and consequent disproportionate exploitation of host populations.

If the CS is itself a product of the host, classical conditioning converges with the 'learning to see' phenomenon of searching image formation, which has been so widely applied in vertebrate foraging. Conditioning, as in the example above, to stimuli associated with the host environment, does not, however, constitute searching-image formation in the strict sense (Krebs, 1973).

Classical conditioning has been demonstrated in several parasitoids. Monteith (1965) showed that *Drino bohemica* would learn to orient (CR) towards a tray moved in its cage (CS) if that tray had previously been presented with host larvae, the UCS being the odour of the larvae and their movement. This learned response lasted several days. Arthur (1966) demonstrated that *Itoplectis conquisitor* would learn to probe paper tubes (CR) of a particular colour (CS) which had, on previous occasions, been filled with hosts. The nature of the UCS here is not certain, and this example might be better interpreted as instrumental conditioning, which differs from classical conditioning not so much in its underlying mechanism, but in its emphasis on the conditioning of a reinforced response, rather than the conditioning of a paired stimulus (the UCS) (Mackintosh, 1974). Retention lasted for about eight days.

Conditioning to olfactory stimuli has been demonstrated in *Nemeritis*

canescens (Arthur, 1971). Following the presentation of the chemical, geraniol (CS) with a dish of hosts (host odour, here, probably being the UCS), wasps would learn to spend more time (CR - arrestment?) on dishes with only geraniol present than in empty dishes. This learning effect lasted two days. Recently, Vinson and Henson (1976) has demonstrated remarkable, classical conditioning in the parasitoid, *Bracon mellitor* Say, which can rapidly learn to search and probe in response to a number of different chemicals which have been presented with the host odour and hosts.

Latent learning is a form of learning proposed by Thorpe (1956) to explain the attraction of *Nemeritis canescens* to the smell of a non-host species, *Achroia grisella* (Fabr.), on which it had been reared, or to the odour of which it had been exposed shortly after emergence. The unusual aspect of this form of learning was that no UCS or reinforcement could be identified for the conditioning process. In fact the necessity of a reinforcement (indeed, of a UCR) in classical conditioning is currently under question (Mackintosh, 1974), and it is possible that an association could be made between the UCS and the CS by their simultaneous presentation alone (sensory preconditioning). As probing behaviour in *Nemeritis* is elicited by a specific host chemical (Mudd and Corbet, 1973), and probing occurs in unconditioned wasps presented with *Achroia*, the UCS may be a compound present in secretions of both *Achroia* and the normal hosts. The CS, therefore, could be another chemical present only in the *Achroia* secretion, and a conditioned response to this latter chemical may effectively amplify the response to the attractant compound, here in very low concentration. Thus, in this case, latent learning may be more simple classical conditioning to chemical stimuli. The capacity to learn without the reinforcement of oviposition is suggested, as well, in some of the results of Vinson and Henson (1976) with their braconid parasitoid. It

would be interesting to see if Arthur's (1971) experiments would give similar results using only host odour (and not host odour plus hosts) during the training period.

A more complex form of association, place learning, is particularly well developed in the higher Hymenoptera. The digger wasp, *Philanthus triangulum*, learns to locate its nest by using objects and patterns in the surrounding landscape (van Beusekom, 1948). Place learning in nesting sphecids apparently involves an orientation flight around a newly built nest to frame it in a visual landscape which is learnt by the forager (Evans, 1966). There is no firm evidence for place learning in parasitoids, but more thorough investigations may reveal that it does occur in at least some species. The capacity to learn patch positions may greatly facilitate the rejection of exploited patchs or the finding of rich, renewable patches.

Various aspects of host capture and handling are subject to modification by learning. The aphid parasite, *Lysiphlebus testaceipes* (Cresson), improves its ability to parasitize hosts with experience (Eikenbary and Rogers, 1974). The recognition of parasitized hosts by *Pseudocoila bochei* Weld. has been shown by van Lenteren and Bakker (1975) to have a major learned component.

It is interesting to note that learned response may take very different forms. Conditioning of an animal to stimuli from a particular patch may subsequently facilitate either attraction to or avoidance of that patch. Learning to avoid a patch may occur in a very similar manner to learning to prefer a patch. For a particular forager, the use of learned responses reflects the ecology of its specific foraging situation and, in particular, the relative rates of patch depletion and renewal

(Zach and Falls, 1976). A parasitoid limited to several eggs a day, or a sphecid wasp provisioning a nest, may cause relatively little depletion in the course of a patch visit, and may therefore learn to return to patches of high profitability. A proovigenic parasitoid, on the other hand, may completely deplete a particular patch in one visit. In such a case, learned cues may be used to avoid patches already visited.

CHAPTER 4

THE MODELLING OF FORAGING BEHAVIOUR

The previous chapter has reviewed what is known about the foraging behaviour of parasitoids. In this chapter will be discussed how observed behaviour has been incorporated into models of foraging time allocation.

To a great extent, the development of foraging models has involved the sequential addition of more realistic elements to the equations, and, in particular, the addition of behavioural elements. Behaviour finds its way into foraging models as abstract mathematical parameters fitted into a population equation. Such parameters are usually expressed as either the time of execution of a response or sequence of responses (e.g., handling times, transit times), or the rate at which a response is elicited (e.g., attack rates, parasite encounter rates).

The parasitoid-host model of Nicholson and Bailey (1935) will serve as a starting point for this discussion of modelling. This model merely postulated, that the number of hosts encountered by a parasitoid in a generation, N_a, was the product of the number of hosts present, N, and the area of discovery of the parasitoid, a. This latter constant represented the area traversed by an average forager in its lifetime, and Nicholson (1933) envisioned it as a path, as wide as the forager's perceptive field, twisting through the host area. As the forager's path was not influenced by its own previous path or the distribution of prey, searching movements were random and, thus, involved no responses to patch stimuli.

The value of a was influenced by the parasitoid's overall longevity, speed of movement, perceptive field and capture success, but these components were constant for a particular host species and not influenced by host density. Thus, no behavioural responses to host stimuli were

incorporated into the model. Royama (1971b) has observed that some response to host stimuli must, however, be involved if Nicholson's hypothetical parasitoid is to capture hosts in its path which it has not physically contacted. Such short range orientation to hosts would involve a departure from random searching movements. It is interesting to note that this assumption of random search by individual parasitoids is not essential to the predictions of the model, as long as the movements are random on the population level (Nicholson, 1954).

The Nicholson-Bailey model incorporated no responses to either prey or patch stimuli. In 1959, Holling modified this simple model to include the effect of prey stimuli on foraging behaviour. In his "disc equation", a randomly searching forager took a fixed amount of time, T_h, to "handle" each prey item captured. The rate of prey capture was represented as

$$N_a/T = a'N/1+a'T_hN$$

Here, T represents the total foraging; time, a', the instantaneous rate of discovery, and T_h, the time taken to handle one prey item. Holling distinguished three behavioural components of handling time - the time taken to identify prey (the host-acceptance stage of Doutt (1964)), the time taken to utilize the prey (feeding or oviposition), and the time per prey captured spent resting due to satiation or egg depletion.

In the disc equation, total foraging time, T, is thus composed of handling time, N_aT_h, and searching time, T_s. As in the Nicholson-Bailey model, the rate at which areas are covered (a') is independent of host density, and is expressed here as the area covered per unit of searching time. The Nicholsonian area of discovery of the forager is equal to $a'T_s$.

Because the disc equation does not allow for the effect of prey

depletion on future search, it is valid only for capture rates over very short periods or where captured prey are immediately replaced, unless the assumption of random search is abandoned in favour of systematic search, where already covered areas are avoided. Rogers (1972a) has modified Holling's model to incorporate exploitation effects, and to distinguish between foraging by predators and foraging by parasitoids. Rogers' Random Parasite Equation applies to parasitoids searching randomly and not discriminating between parasitized and unparasitized hosts,

$$N_a = N(1-\exp(-a'TP/(1+a'T_hN)))$$

For predators, which consume their prey, or parasitoids which take no time in recognizing and rejecting already parasitized hosts, Rogers' Random Predator Equation applies,

$$N_a = N(1-\exp(-a'(PT-N_aT_h)))$$

In fact, these two equations represent the hypothetical extremes of what is to be observed in parasitoid foraging behaviour. As pointed out in Chapter 2, many parasitoids avoid superparasitism to a certain extent, but execute a certain fraction of the handling sequence before rejection. Thus, there is an element of handling time associated with encountering already parasitized hosts (cf., the Random Parasite Equation), but parasitized hosts are, to some extent, only 'consumed' once (cf., the Random Predator Equation).

Further studies of arthropod functional responses have considered the behavioural components of $\underline{a}'$ and how changes in host density may affect the forager's speed, perceptive field, and capture success (Hassell, et al., 1976). Responses to prey stimuli such as area-restricted search may modify the speed or path of the forager. Conditioning to prey stimuli may lead to modification of the perceptive field (e.g., searching image formation) or increased capture success.

The sigmoid nature of some arthropod functional responses may be attributable to such variation in foraging behaviour with density (Hassell, et al., 1977).

Theoretically, a randomly searching predator or parasitoid will exhibit a functional response which is independent of prey distribution in the foraging 'universe' (Rogers, 1972a). The assumption that a' varies with prey density forces us to abandon the notion of random search and predict that prey distribution will affect the functional response. This prediction has been borne out in experiments on parasitoids foraging for prey in clumped vs. regular distributions (Burnett, 1958; Matsumoto and Huffaker, 1974). Hassell and May (1974) have constructed in mathematical model demonstrating how area-restricted search, a component of a', results in non-random foraging and concentration of foraging time in areas of high prey density.

So far, all foraging models discussed have considered only responses to prey stimuli. In this sense, they represent intra-patch situations, where the forager is not responding to patch stimuli and, thereby, recognizing discrete units of prey distribution in its environment. To incorporate responses to patchily-distributed prey into the functional response, one need simply describe a prey population as a set of patch populations, each characterized by a functional response. Modifying Rogers' Random Parasite Equation in this manner for one parasitoid, we get,

$$N_a = \sum_{i=1}^{n} N_i(1-\exp(-a'T_i/1+a'T_hN_i)), \text{ where } T = \sum_{i=1}^{n} T_i$$

But here we face the real problem: how long does a forager spend in a particular patch - what determines T_i? As mentioned in Chapter 3, this problem of the allocation of foraging time is really two problems, one of

patch selection and one of patch time. As most modelling has been concerned only with patch time mechanisms, it should be stressed that patch selection can be just as important. For instance, aggregation of foragers on high density patches may result as easily from density-biased patch selection with constant patch time as from random patch selection with density-biased patch time.

A number of patch time models have been proposed, which I classify here into three mechanistic categories:

1. fixed number mechanisms - leave the patch after a fixed number of prey are captured.

2. fixed time mechanisms - leave the patch after a fixed amount of time has been spent there.

3. fixed rate mechanisms - leave the patch when the rate of prey capture falls below a fixed threshold rate.

These three models and their effect on patch time are graphically represented in Figure 2, where Rogers' Random Parasite Equation has been used to generate an 'exploitation surface' for different patch densities over time.

Mechanisms 1 and 2 are equivalent, respectively, to the 'hunting by expectation' hypothesis of Gibb (1962) and the hunting by time expectation hypothesis, proposed by Krebs (1973) as an alternative to Gibb's theory. Krebs envisioned the fixed time to be the total time on the patch, including handling time. An alternative fixed time model might involve a constant searching time (T_s) per patch (see Figure 2).

Essentially identical fixed rate models have been formulated by

Figure 2. A. Hypothetical 'exploitation surface' generated by iterating the Random Parasite Equation (Rogers, 1972a) over successive time units from an initial prey density. Axes:

x - time since entering patch

y - initial prey density on patch

z - instantaneous rate of prey capture on patch

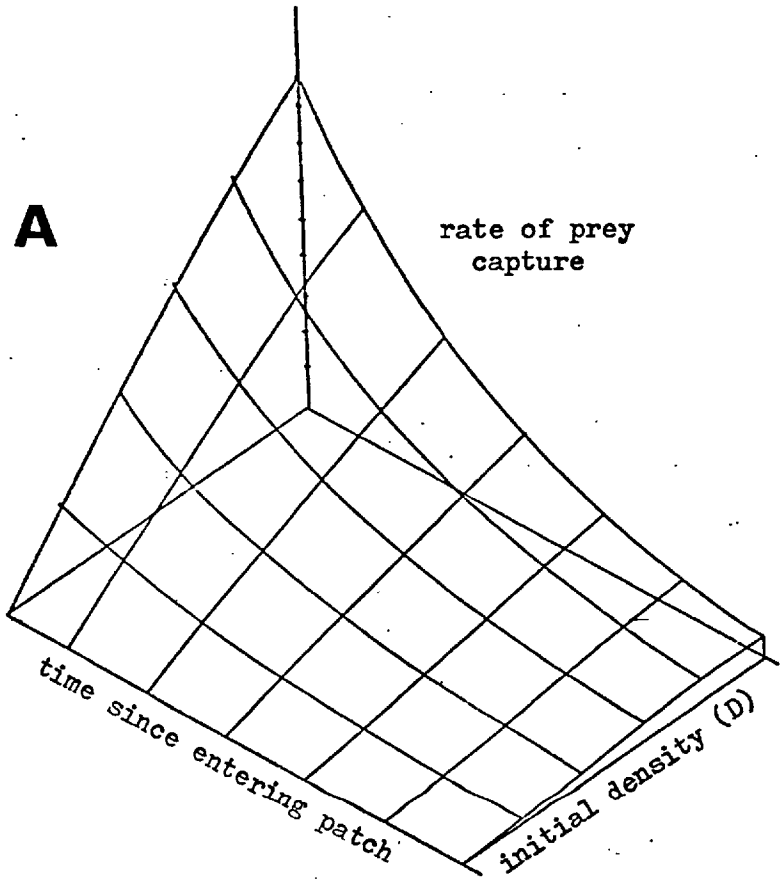
B. Different forms of patch-time model. D = prey density per patch, T_i = patch time.

1 - fixed time mechanism (total time) produced, for instance, by cutting surface in 2A parallel to y-z plane

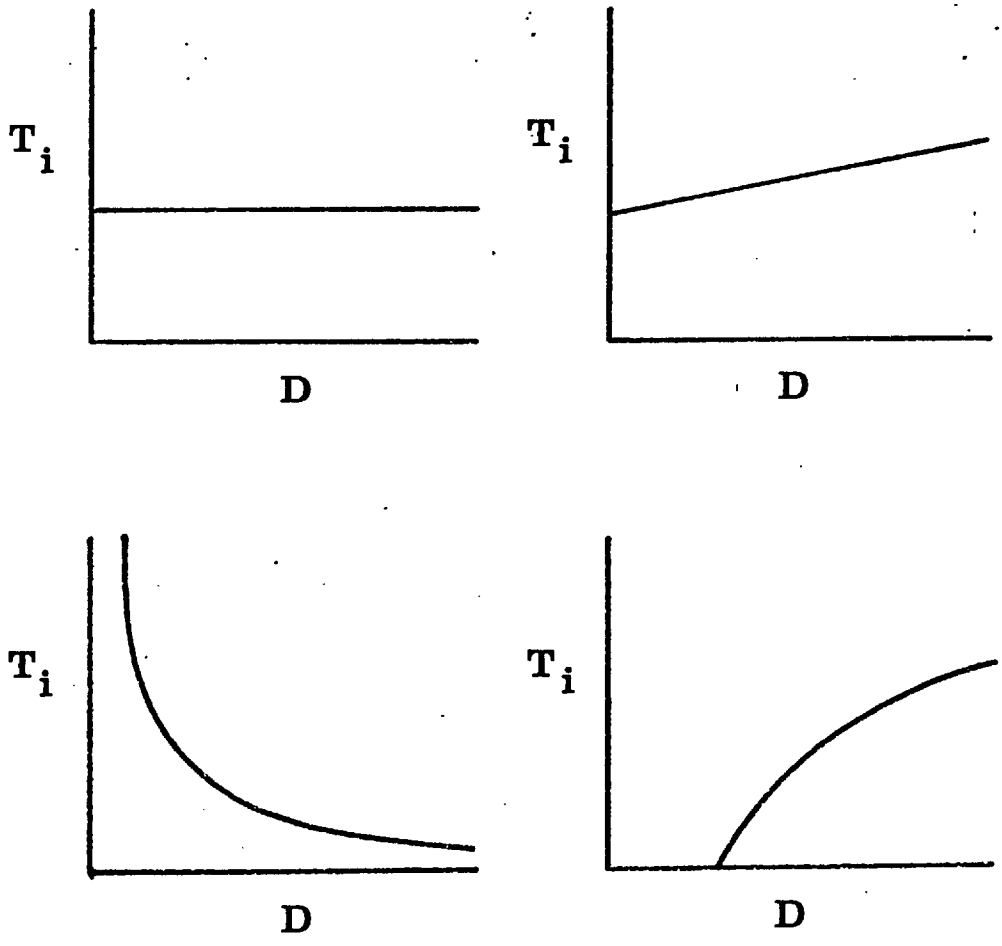
2 - fixed searching time mechanism, produced by holding T_s constant in Random Parasite Equation. Positive slope due to increasing total T_h with D.

3 - fixed number mechanism, produced by holding N_a constant in R. P. Equation.

4 - Fixed rate mechanism, produced by cutting surface in 2A parallel to the x-y plane


A
rate of prey capture
time since entering patch
initial density (D)

B


T_i
D
T_i
D
T_i
D
T_i
D

Murdoch and Oaten (1975) and Hassell and May (1974). The exact mechanism of these models is as follows: a forager entering a patch will spend a fixed time, S, searching it before leaving, presumably in response to patch stimuli. Capture and handling of a prey item 'resets' the forager's 'clock' to zero, whereupon it continues foraging for S time units, and then leaves. Thus, a forager will remain on a patch as long as it encounters prey, while searching, at a rate greater than 1/S, and it will leave a patch S time units after the termination of the $\bar{T}_h$ for the last prey captured. A fixed rate hypothesis yields a time per patch curve which is either monotonically decelerating or sigmoid, depending on the threshold rate, 1/S.

All three patch time models assume that patch finding is random. Density-biased patch selection could significantly change the patch time curves for all of these models.

It seems rather obvious that patch time mechanisms determined by capture rate would be more efficient, and more adaptive, than fixed number or time mechanisms. This conclusion, however, is only appropriate to situations where the variance of prey distribution per patch is high. If the density of prey per patch was fixed, a fixed number or fixed time mechanism could be more efficient than a fixed rate mechanism, because it would not involve time wasted searching a patch (S) after the last prey was taken.

The question of the efficiency of patch time allocation has prompted the formulation of optimal foraging models. These models take as their strategy the maximization of fitness by the maximization of prey capture rate. As optimal foraging equations are meant to compute the theoretically ideal allocation of foraging time, the foraging mechanisms they

imply are not intended to be realistic. However, it is interesting to see just how foragers would have to behave to be foraging optimally, and so I shall now consider the foraging behaviour implicit in these models.

In 1970, Royama proposed a theory of optimal patch foraging as an alternative to the searching image hypothesis of Tinbergen (1960). He suggested that foraging titmice learned to respond selectively to patch stimuli rather than prey stimuli, preferring certain type of patches (those with high prey density) rather than certain types of prey. Royama identified the 'profitability' of a patch with the rate of prey capture therein, and suggested that optimizing foragers monitored the profitability of different patches and foraged on those of maximum profitability. In this model, patches were not depletable, which was probably an acceptable simplification for the nest-provisioning system he was working with.

In a subsequent modification of his model, Royama (1971a) incorporated a functional response which allowed for patch depletion, and generated a graphical model by which the optimal foraging solution could be calculated for a set of patches of different densities. The model resembles graph 3 in Figure 2, where a plane cutting the z axis was set at the optimal capture rate, to which all patch densities intersected should be lowered. This optimal rate was influenced by the amount of time available for foraging and the number of foragers present. Thus, given a fixed amount of time and a set of patches of different densities, Royama's forager apportions various fractions of its time to a subset of patches - the optimal set - so as to optimize its overall rate of prey capture.

Royama's model does not state how the patches in the optimal set are

to be utilized, that is, whether the most or least dense patch is to be visited first, or when a particular patch should be left for another. But a foraging mechanism does emerge if we consider what happens as we slowly increase the allocated foraging time. With a very short foraging period, only the most profitable patch is included in the optimal set. As foraging time is increased, the terminal capture rate on that patch is lowered. When this rate reaches the initial rate of the next most profitable patch, this second patch is brought into the optimal set, and both patches are exploited simultaneously at an equal rate (there is no transit time). As foraging time increases, more patches are brought in in this manner.

Thus, we need not postulate that the forager is aware of how much time it has to forage. If it behaves in the manner just described, starting with the most profitable patch, it will behave optimally for any length of foraging period.

Table 3 presents the various behavioural assumptions of foraging models. As can be seen, Royama's forager (4) must be aware, prior to foraging, of the number and density of the patches in the set it can exploit. With this information it can compute the optimal procedure. While foraging it need only measure the capture rate of the patch it is on, and be aware of the location of the next most profitable patch. Royama (1971a) suggested that knowledge of the various patch profitabilities could come from sampling, which must, necessarily, decrease the efficiency of search. Although sampling could involve patch depletion, this would not affect the formation of the optimal procedure, as the forager would set patch profitability as the rate of capture when it left.

A mathematical model for optimal foraging in parasitoids has been

Table 3. Comparison of mechanisms suggested by various foraging models. See text for full discussion

Relevant Models	What forager must know before bout	Computations	Sequence of patch visits	What forager must measure on patch	Patch-time
1. Hunting by Expectation (Gibb, 1962)	nothing	none	random	total number captured	leave after fixed number
2. Hunting by Time Expectation (Krebs, 1973)	nothing	none	random	total time on patch	leave after fixed time
3. Threshold Rate Model (Hassell and May, 1974) (Murdoch and Oaten, 1975)	nothing	none	random	instantaneous capture rate= time since last prey capture	leave at threshold rate = S time units after last capture
4. Profitability Model (Royama, 1971a) (Cook and Hubbard, 1977)	number of patches location of patches profitability of patches	none	non-random: selects highest density patch in all transits	instantaneous capture rate	leave when rate fall below rate on another patch
5. Marginal Value Theorem (Charnov, 1976) and Profitability Model (Royama, 1971a) (Cook and Hubbard, 1977)	number of patches location of patches profitability of patches total time for foraging	compute ave. rate for habitat	random	instantaneous capture rate	leave when rate falls below average rate for habitat

recently proposed by Cook and Hubbard (1977) which uses the Random Parasite Equation to compute patch profitability. This model is very similar to Royama's graphical model, except that it incorporates a fixed transit time for the foraging bout, which represents the sum of all transit time for the period. Like Royama's model, the Cook and Hubbard model predicts an optimal set and threshold rate dependent on foraging time and number of foragers. The foraging mechanisms implied is the same as Royama's.

These two foraging models predict the total time a forager should spend on a patch of a given density, but they do not indicate when a patch should be left. According to the mechanism proposed above, a forager should leave a patch when its profitability falls below that of another patch. When several patches have been brought to the same profitability, the duration of each patch visit must be short and the visits to a particular patch frequent. The other possibility, as mentioned above, is that the forager knows precisely how long it will be foraging, and computes the terminal foraging rate for all patches in the optimal set. Then, it should leave a patch when this threshold rate is achieved.

This latter mechanism, which requires more computation by the forager, and the knowledge of a fixed foraging time, is implicit in the optimal foraging model developed by Charnov (1976). This Marginal Rate Theorem states that, given a set of patches which the forager will visit in a fixed foraging bout (the habitat), the overall rate of capture (energy intake) will be maximized if the forager leaves each patch when the rate of capture there falls below the average capture rate for the habitat. In this model, the set of patches to be included in foraging is not selected by the forager but given. Furthermore, unlike previous optimal foraging models, a transit time is associated with each patch

visit, and each patch is only visited once.

Prior to foraging, Charnov's hypothetical forager must know the number and density of patches in the habitat and the total time it will search, so that it can compute the average rate for the habitat which will determine patch time. Charnov, et al., (1976) have argued that the forager can determine this average rate while it is foraging in the habitat, i.e., without prior sampling of all the patches and without prior computation. This would, presumably, involve averaging the capture rates from patches already visited and, therefore, computing the rate for each patch visit. The rate for a patch depends, however, on how long the forager stays there, which, in turn, is determined by the average rate for the habitat. The circularity of this argument reveals that the average rate of capture for the habitat must be known before foraging commences.

It appears that, for all optimal foraging models, some prior knowledge of the area to be foraged is necessary. This may involve a 'sampling bout' which precedes the foraging bout. This hypothesis compels us to recognize two very different responses to patch and prey stimuli, sampling behaviour and foraging behaviour. Alternatively, knowledge of the foraging area could be obtained from previous foraging bouts. This assumes, of course, that the patches are renewed between bouts to their original density. Such renewal might be realistic in some foraging situations, such as nectar collection by sunbirds (Gill and Wolf, 1975). Training to renewed resources is, of course, possible in laboratory situations, and Krebs, et al. (1974) have shown that such training can lead to the adoption of optimal foraging behaviour in chicadees. Alternatively, of course if all habitats are identical in patch number and densities, prior knowledge of the foraging area may be

inferred from previous exploitative experience in other areas.

One drawback to optimal foraging mechanisms is their postulation of a fixed habitat of patches which is to be exploited. More realistic mechanisms would, presumably, treat foraging as a more continuous process, and recognize only those levels of patchiness to which the forager itself responded. Another problem is the determination of capture rates while foraging. Optimal foraging and fixed rate models treat prey capture as a deterministic process, while, in reality, the stochasticity of capture rate must complicate its measurement. Oaten (1977b) has considered the effect of such stochasticity in optimal foraging models.

Clearly, there is a gulf between the relatively simple fixed number, time and rate mechanisms of foraging time allocation and the complex mechanisms implied by optimal foraging models. Incorporation of sampling behaviour and patch selectivity into the former might bridge this gulf. Modification of the fixed rate mechanism by incorporating some rate adjustability based on experience (Krebs, et al., 1974) is another possibility. Such mechanisms will be considered in later chapters. Theoretical considerations notwithstanding, the realistic modelling of foraging behaviour must have, as its ultimate foundation, experimental studies on how animals forage. It is to such a study that I now turn.

CHAPTER 5

THE BIOLOGY OF *NEMERITIS CANESCENS* GRAV.

Nemeritis canescens is in many ways an ideal subject for the study of parasitoid foraging behaviour since there exists already an extensive literature on its host-finding and on the ecology of its interactions with its phycitid hosts. The wasp is a thelytokous parasitoid of the larvae of a variety of meal moths, in particular *Plodia interpunctella* Hubn., *Ephestia kuehniella* Zeller and *Cadra cautella* Wlk. Although it attacks primarily the Phycitinae, it has also been recorded in the field from a few other Pyralidae, as well as Tineidae, Yponomeutidae and Tortricidae (Salt, 1976). Adult *Nemeritis* emerge with nearly a full complement of eggs and are able to oviposit immediately after eclosion. In the culture used, the average egg complement was about 100. When fed on soaked raisins, adults lived over two weeks at 30°C and 75% RH, while unfed wasps survived for only two days under those conditions. In Northern Europe, *Nemeritis* inhabits granaries where its hosts are found in patches on the surface of grain piles. Wasps apparently leave these granaries frequently to feed on flowers in nearby fields (Beling, 1934), and Ahmad (1936) has shown that phototactic and scototactic responses are involved in the alternation of food-seeking and host-seeking behaviour, respectively. Hungry wasps are attracted towards light and, therefore, out of the granaries, while satiated wasps are attracted to darkened areas which, together with possible attraction to the odour of host medium (Thrope and Jones, 1937), may lead them back to granaries.

Casual observations in the laboratory suggest that flying *Nemeritis* orient towards the source of a host-produced odour and land on the substrate in the vicinity of this source. Excitatory compounds in the mandibular gland secretion of the host are probably responsible for this attraction. A chemical which elicits probing by *Nemeritis* has been

identified from this secretion (Mudd and Corbet, 1973), but its large size (MW 392) suggests it is not sufficiently volatile to act as a long-range attractant. Smaller compounds in the mandibular secretion, possessing structural units similar to this MW 392 compound, may serve as attractants (Mudd, pers. comm.). It seems likely, therefore, that attraction to the patch and probing and other activities on the patch may be elicited by different chemical compounds, as was originally suggested by Williams (1951).

When a walking *Nemeritis* encounters traces of mandibular secretion on the substrate, it begins to tap the surface rapidly with the tips of its antennae. At high enough concentrations, the host secretion elicits a probing response (Corbet, 1973). During this, the wasp stabs the substrate with the tip of its ovipositor. If a host larva is pierced during probing, oviposition may or may not occur, depending presumably on chemical factors in the host haemolymph. These factors are detected by chemoreceptors on the tip of the ovipositor (Simmonds, 1943; Dethier, 1947a). Rejection of already parasitized hosts occurs at this stage, probably in response to chemical changes in the host haemolymph following a previous oviposition (Rogers, 1972).

Following oviposition, the wasp usually rests and may clean its antennae and/or ovipositor. A characteristic "cocking" movement follows, signifying the delivery of a new egg into the ovipositor tip (Rogers, 1972b). The cycle of probing, ovipositing, resting and cocking has been fully described and illustrated by Rogers (1972b).

Aspects of superparasitism in *Nemeritis* (the deposition of more than one egg in a single host) have been studied by Simmonds (1943), and Fisher (1961) has examined multiparasitism (the parasitism of a host by

more than one species) by *Nemeritis* and *Horogenes chrysostictos* Gmelin. Wasps tend to avoid laying eggs in already parasitised hosts, but only after a certain "oviposition factor" has spread through the host from a previous oviposition, which takes about 15 minutes (Rogers, 1972). Fisher and Ganesalingam (1970) have demonstrated a chemical change in host (*Ephestia kuhniella*) haemolymph after parasitism by *Nemeritis* which may be involved in detecting parasitised hosts. The morphology and development of the egg, larval and pupal stages has been examined by Diamond (1929), Corbet and Totheram (1965), and Salt (e.g., 1975, 1977). The energetics of the developmental process has been recently investigated by Howell and Fisher (1977).

The role of learning in the host finding process of *Nemeritis* has been studied by Thorpe and Jones (1937), Thorpe (1938), Arthur (1971) and Taylor (1974). As mentioned in Chapter 3, both classical conditioning and latent learning have been demonstrated in the species.

The potential of the *Nemeritis*-phycitid system for ecological studies of parasite-host relationships was first recognized by Flanders (1958). Since then, ecological studies on this interaction have dealt with the functional response to host density (Matsumoto and Huffaker, 1973a, b, and references below), interference between parasitoids (Stinner, 1970; Hassell, 1971b) and responses to patchily distributed prey (Takahashi, 1968; Hassell, 1971a). Recently, Cook and Hubbard (1977) have applied these latter studies to a model of optimal foraging.

While the ease of rearing *Nemeritis* and the extensive literature on the species make it desirable for foraging studies, there exist as well some disadvantages. Any consideration of the evolutionary adaptedness of *Nemeritis* behaviour suffers from the absence of information on the

actual biology and behaviour of the species in the field. Granary populations in Northern Europe cannot survive in the wild, and probably were established from wild Mediterranean populations. The Mediterranean region is probably the centre of radiation of the species, as it is from this area that its primary hosts have spread (Richards and Thomson, 1932). In the field, *Nemeritis* has been occasionally recorded emerging from Lepidoptera infesting citrus and dates around the Mediterranean and citrus in California, where both host and parasitoid are presumably introduced (Salt, 1976). As fallen fruits, nuts and seedpods are the natural food of its phycitid hosts (Richards and Thomson, 1932; Ebeling, 1959; Cox, 1974), we may conclude that field populations of *Nemeritis* forage for hosts scattered in small patches on fallen fruit beneath trees. This is a rather different foraging situation from granaries, and the question remains, to what sort of foraging situation has the behaviour of *Nemeritis* studied here and in other experiments been adapted?

A further complication is the long period over which *Nemeritis* has been in laboratory culture. The culture used in the experiments to follow, for instance, is at least several years old, and a small part of it may actually be descended from that used by Thorpe and Jones (1937). Quite possibly, prolonged culture has resulted in the change or loss of some components of foraging behaviour. Evidence of such behavioural changes in lab cultures has recently been provided by Prokopy, et al. (1976), who found that lab culture of the fruit fly, *Rhagoletis pomonella* (Walsh), resulted in a substantial decrease in the production of an oviposition site marker pheromone and changes in its application behaviour, all of which could significantly affect the way oviposition sites were utilized.

It is interesting in this regard to note that Beling (1932) reported that her granary-caught *Nemeritis* produced a strong odour, while the wasps used in the present study possess no detectable odour. Such aromas are apparently common in many wild ichneumonids (Townes, 1939) and may be involved in defense and, possibly, trail marking. Somewhat reassuringly, the foraging behaviour observed in *Nemeritis* from a recently collected granary population appears to be very similar to the behaviour of wasps used in the present study (Cook and Hubbard, pers. comm.).

CHAPTER 6

STUDIES ON THE PATCH-SPECIFIC BEHAVIOUR OF *NEMERITIS*

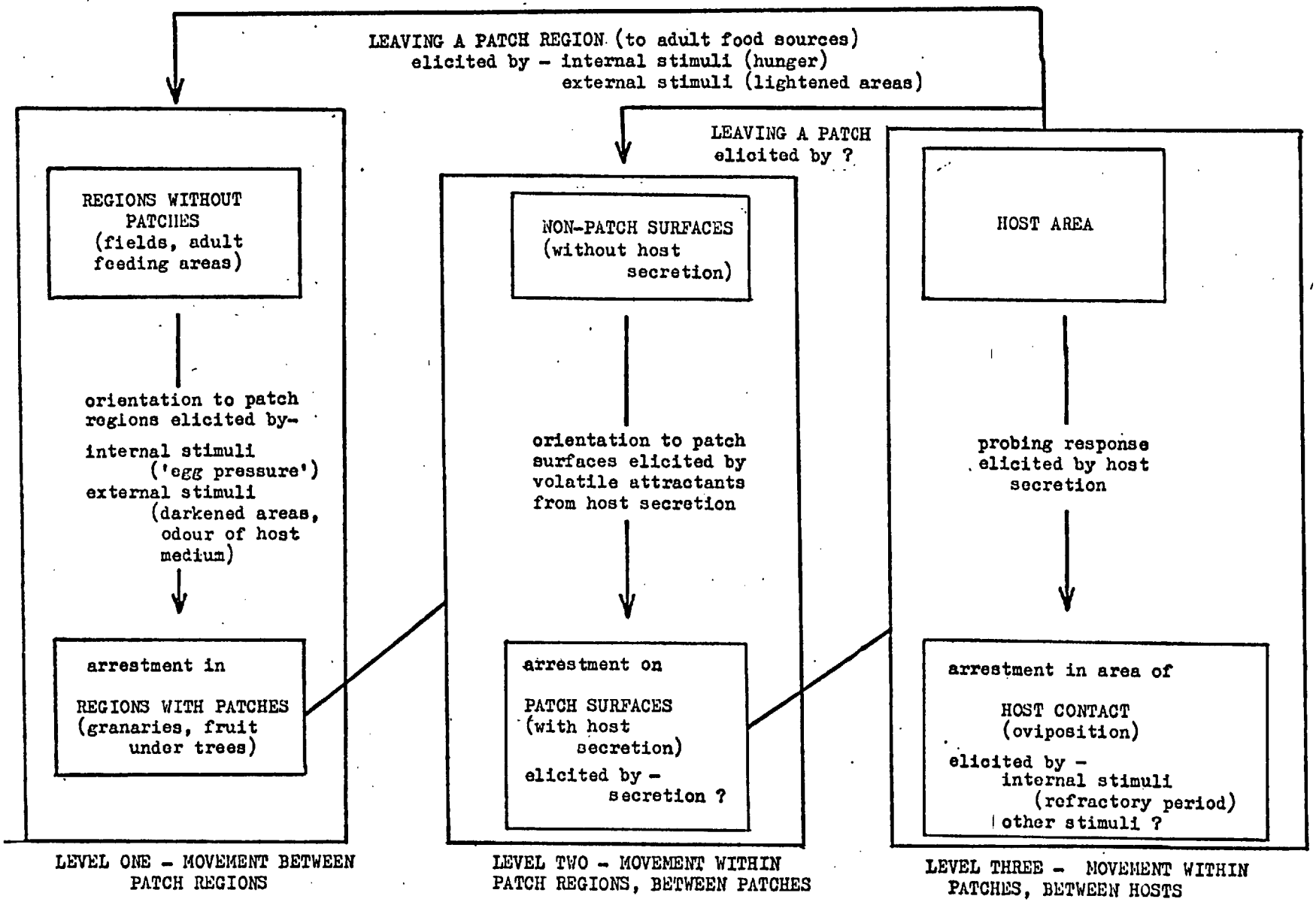
6.1 INTRODUCTION

From the preceding chapter, we may tentatively identify several levels of response leading to host-finding by *Nemeritis*. At one level of patchiness wasps, at least those from granary populations, distinguish between darker and lighter areas of their environment. Attraction to darker regions in pursuit of hosts is presumably mediated by internal stimuli such as hunger and "egg pressure". These factors affect the responsiveness to external visual stimuli, which elicit the scototactic response. Attraction to chemical stimuli from the host medium may also be involved at this level.

Once in a "patch" of darkened area, *Nemeritis* searches at another level of patchiness, recognizing as patches areas containing the host mandibular secretion. This secretion is deposited by hosts in the process of feeding, silk production and contacting other hosts, which leads to the formation of a chemical "patch", the borders of which mark the range of a given population of host larvae. That these areas of chemical may be considered patches in the sense defined in Chapter 2 is confirmed by the arrestant response elicited in *Nemeritis* by the chemical stimulus. In particular, the probing response elicited by host secretion constitutes a distinct arrestment which is essential to the contact of hosts and the consummation of the foraging process. Attraction to these chemical patches from non-patch areas by flying or walking may be mediated by more volatile components of this secretion.

In Figure 3, known responses of *Nemeritis* to various stimuli have been combined to suggest a foraging process composed of several hypothetical levels.

Figure 3. Hypothetical steps in the foraging process of *Nemeritis canescens*.


LEAVING A PATCH REGION (to adult food sources)
elicited by - internal stimuli (hunger)
external stimuli (lightened areas)
LEAVING A PATCH
elicited by ?
REGIONS WITHOUT PATCHES (fields, adult feeding areas)
orientation to patch regions elicited by-
internal stimuli ('egg pressure')
external stimuli (darkened areas, odour of host medium)
arrestment in
REGIONS WITH PATCHES (granaries, fruit under trees)
NON-PATCH SURFACES (without host secretion)
orientation to patch surfaces elicited by volatile attractants from host secretion
arrestment on
PATCH SURFACES (with host secretion)
elicited by - secretion ?
HOST AREA
probing response elicited by host secretion
arrestment in area of
HOST CONTACT (oviposition)
elicited by -
internal stimuli (refractory period)
other stimuli ?
LEVEL ONE - MOVEMENT BETWEEN PATCH REGIONS
LEVEL TWO - MOVEMENT WITHIN PATCH REGIONS, BETWEEN PATCHES
LEVEL THREE - MOVEMENT WITHIN PATCHES, BETWEEN HOSTS

This study will be concerned with only a part of the host-finding process, namely, the determinants of time spent on chemical patches. The patch-finding process will not be considered except insofar as experience on a patch may influence its subsequent selection relative to other patches. The precise question to be addressed is "What determines when *Nemeritis* leaves a patch of host chemical?". Two major components of patch time will be investigated, the effect of the chemical patch stimulus and the effect of stimuli arising from host contact and oviposition. Another factor of possible importance in determining patch time is the contact or perception of other searching parasitoids. This factor has been investigated by Hassell (1971a) and, since all experiments in this study will be conducted with individual wasps, it will not be considered here.

Several other responses of *Nemeritis* to host and patch stimuli make very minor contributions to patch time, but these are worth mentioning before the major factors are investigated in detail. These include responses to tactile stimuli described by Williams (1951) and confirmed by observation in the present study. Specifically, the probing response of *Nemeritis* is prolonged and intensified by (1) a decrease in the resistance of the substrate being probed, as would occur when a crack was located with the ovipositor, and (2) movement of the host larvae sensed when it is "pricked" with the ovipositor. This latter stimulus often elicits a series of rapid 180° turns by the wasp along with intense probing activity, which presumably increases chances of the wasp contacting the larvae just missed (cf. Chapter 3.2 and Table 2). Finally, discontinuities in the substrate such as cracks, which are detected by the antennal tips, often elicit stopping and investigation and add to the arrestant effect caused by the chemical patch stimulus.

6.2 THE EFFECT OF CHEMICAL PATCH STIMULI

GENERAL METHODS AND OBSERVATIONS

What happens when *Nemeritis* enters a patch of host chemical? To answer this question, artificial patches of exact dimension were made and wasps were exposed to them in such a way that any observed response would be attributable only to the slightly volatile chemical patch stimulus.

Patches were made by confining a certain number of *Plodia* larvae for 15 hours at 25°C between two sheets of terylene net (Figure 4a). The lower sheet, now containing a circular patch of host silk and mandibular secretion, was stretched over a petri dish, which was raised on a microscope jack (Figure 4c) to 1 mm or so below another terylene screen. This latter screen served as the bottom of a plastic experimental chamber into which was placed a standardized wasp. Standardized wasps had emerged the day before and been kept at 25°C or 30°C (depending upon the experiment) for 24 hours in a standardization chamber (Figure 8a) with food (soaked raisins).

When a wasp, walking across the bottom of the experimental chamber, crossed over the edge of the chemical patch, several changes in behaviour were observed. The wasp usually stopped at the patch edge and then proceeded walking at a slower speed, occasionally stopping and beginning to probe. During probing, the insect moved forward at a much slower speed than during walking, and occasionally made sharp turns, recrossing areas already covered.

Of particular interest was the response of the insect to the patch edge as it walks out of the patch. When the wasp crossed the edge it usually turned sharply so as to bring itself back into the patch. This

Figure 4. Apparatuses for testing responses to chemical patch stimuli. A. Construction and dimensions of a 'patch'. See text for explanation. B. Chamber used to s tudy patch edge response. See text for explanation. C. Chamber used for general observations on patch localized behaviour. See text for explanation.

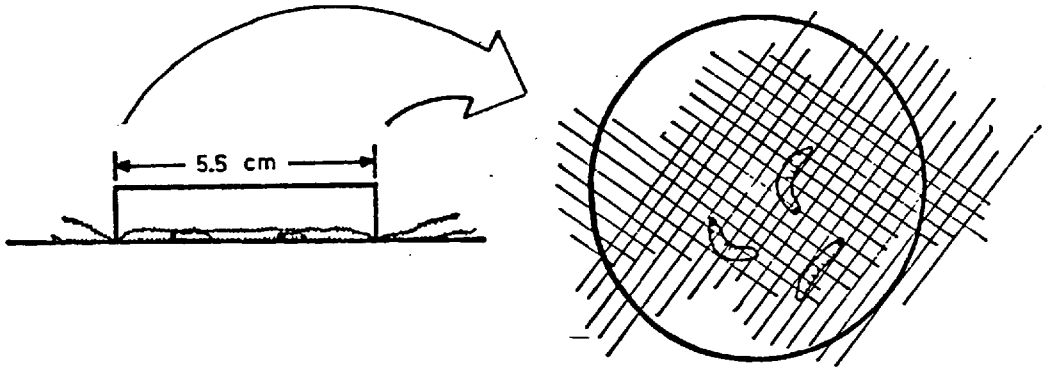
Symbols - W - plastic box forming walls and top of experimental chamber

X - glass plate on which patch was drawn

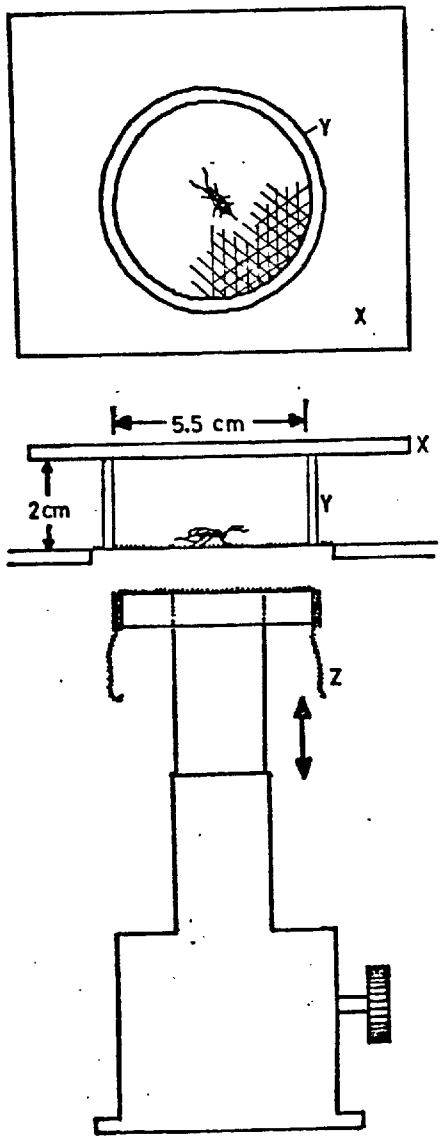
Y - patch-sized glass ring forming walls of experimental chamber

Z - terylene screen with patch of host chemical (= lower screen under dish in 4A above)

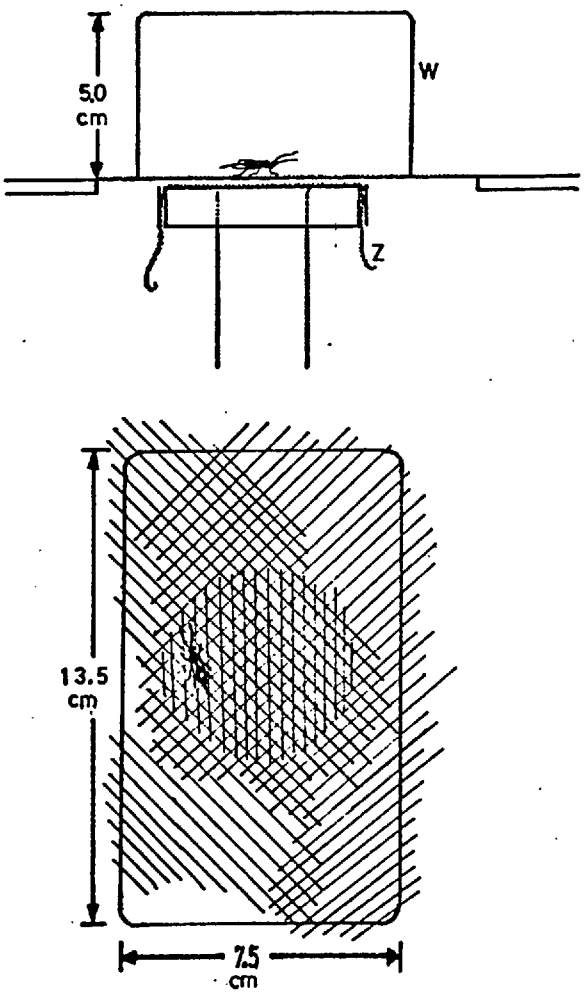
A



B



C



behaviour greatly prolonged the time spent on the patch by the wasp, as is clearly shown from Figure 5b, where the occurence of a number of behaviours over 6 minutes after entering a patch are presented. In the top trace, where the concentration of the patch stimulus is too low to elicit probing, the patch edge is encountered many times before the insect finally crosses it and leaves the patch. Often, the wasp follows the patch edge for a few seconds before turning back into the interior of the patch. In the lower trace, which represents a higher stimulus concentration, the rate of encounter with the patch edge is reduced by the orthokinetic effect of the probing response.

An example of the path of a *Nemeritis* in a patch is presented in Figure 5a. For this trace, the patch was created by spreading a 1 ml ether extract of 10 pairs of host mandibular glands from fifth instar larvae on a glass plate. The movements of the wasp were traced with a felt tip pen on a glass plate suspended above the treated plate. The concentration of the chemical was too low to elicit probing, and the wasp soon left the patch, but not before it made a number of clear turns at the patch edge (arrows). These turns varied in their angle and sharpness of curvature. Virtually identical responses were observed at the edges of chemical host patches made in the host food medium or other substrates which hosts had occupied.

The response to the patch edge is clearly of major importance in determining patch time and, therefore, an experiment was designed to analyze its exact mechanism.

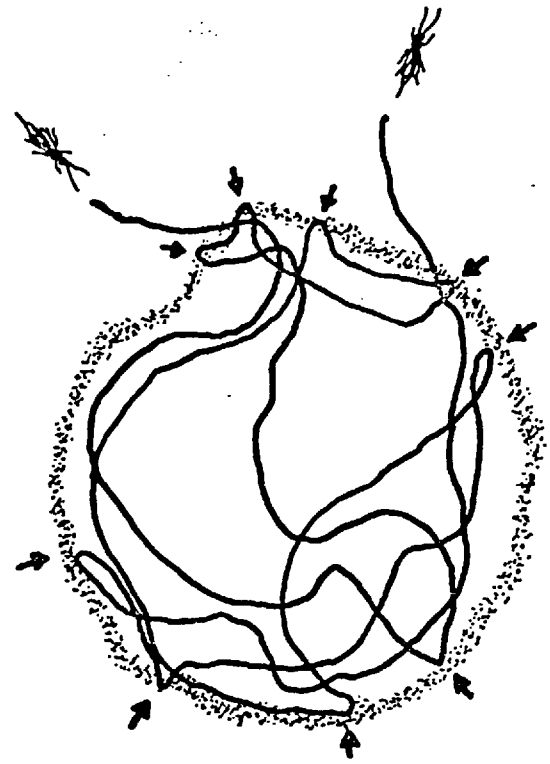
EXPERIMENT 1: THE RESPONSE TO THE PATCH EDGE

MATERIALS AND METHODS

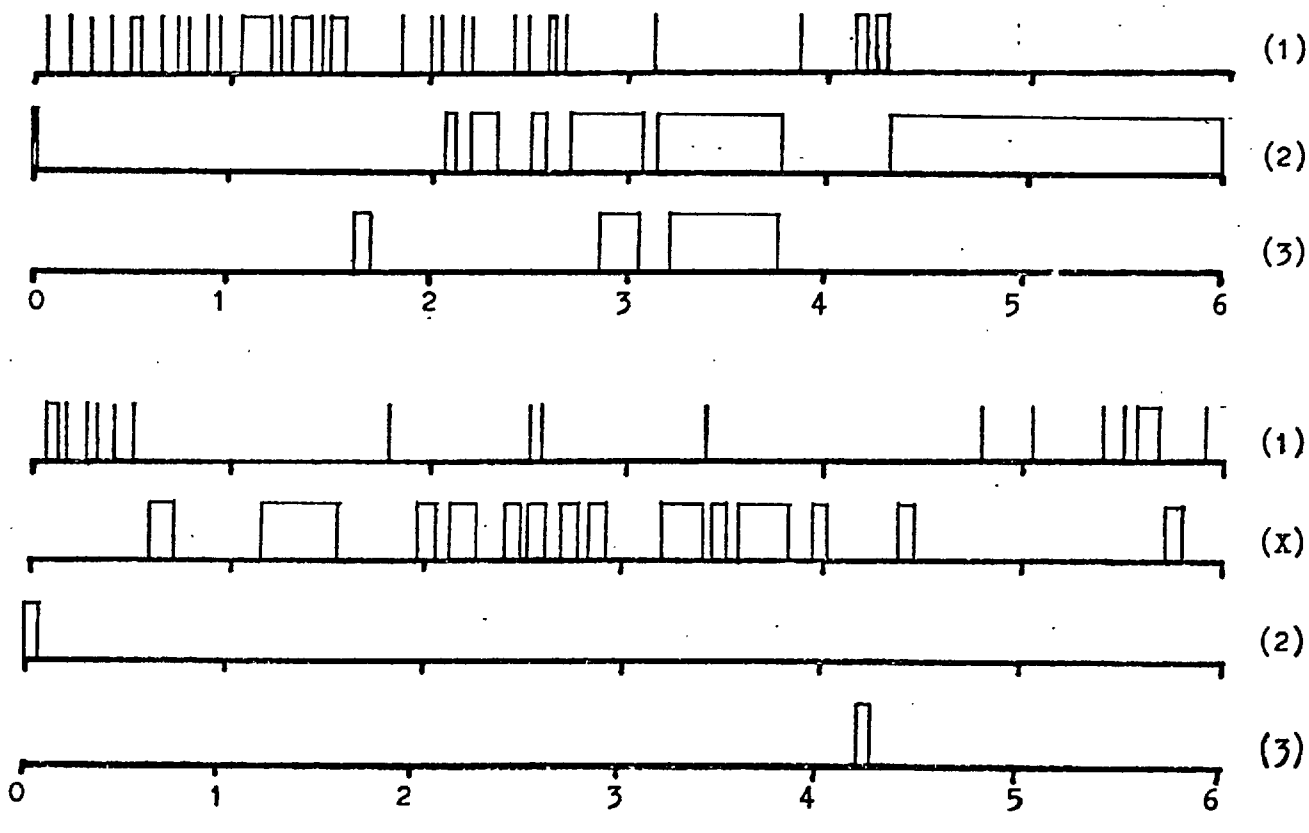
The apparatus illustrated in Figure 4b was used for this experiment.

Figure 5. A. Path of a wasp on a patch of ether-extracted mandibular gland secretion of Plodia interpunctella. Stippling indicates the approximate edge of the patch, arrows indicate turns made at the patch edge by the parasitoid.
B. Recordings of Nemeritis activity on and off patches of host chemical over a six min period. Top trace: (1) contact with the patch edge (coming from within the patch) (2) time spent off the patch, (3) time spent resting. Lower trace: at a higher stimulus intensity, (X) time spent probing, others as above. In this trace the wasp left the patch after 35 min.

A



B



It resembled the one described above (Figure 4c) except that the experimental chamber conformed exactly to the area of the patch below it. Standardized wasps placed in the chamber were exposed to the patch stimulus by jacking up the contaminated screen until it was about 1 mm below the chamber floor (also made of terylene net). By raising and lowering the contaminated screen, the experimenter could control when the wasp was 'on' and 'off' the patch and, thereby, examine the exact responses to the chemical stimulus.

The odour concentration on the contaminated screen was always sufficient to elicit probing when raised. The movements of a probing wasp over 20 seconds were traced on the glass plate above the chamber with a felt-tip pen. Then the contaminated screen was quickly lowered and the wasp's path immediately traced for another 20 seconds. This lowering of the screen (about 12 cm) was interpreted as the removal of the patch stimulus, as would occur at the patch edge. In fact, as the mandibular secretion is slightly volatile, the lowering of the screen must be accurately interpreted as the removal of most of the stimulus. Such a sharp decrease in stimulus intensity, rather than a stimulus on-stimulus off switch, is probably characteristic, as well, of the crossing of natural patch edges.

The experiment was carried out under indirect lighting at 25°C in a well ventilated room. Ten wasps, standardized at 25°C, were tested, each four times in succession with 30 seconds to 1 minute between recordings. The paths drawn were enlarged, copied and measured with a map measurer. Path tortuosity was evaluated by measuring the angles between tangents drawn at 1 cm intervals along the path (see Figure 7). The rapid movement of the insect did not permit the recording of unit time intervals on the path, and so changes in the speed of the parasitoid

could not be measured except as averages over the 20 seconds.

RESULTS

The path of a *Nemeritis* over the chamber floor before the presentation of any odour was more or less straight, with turns occuring only when chamber sides were contacted. This path was not recorded as above because it never continued for 20 seconds without contact being made with the chamber sides.

The response to the presentation and subsequent removal of the patch stimulus is described in Table 4. Data from 40 replicates (10 wasps, four replicates each) is summarized. Removal of the patch stimulus results in a marked increase in the speed and rate of turning of the insect. The change in speed is attributable to the transition from the strong inverse orthokinesis of the probing response to a rapid walking behaviour. The change in the angle turned per second can be attributed largely, if not entirely, to the change in speed of the insect, as the average angle turned per unit cm (column 3) did not change. Thus, the angle turned per unit distance remained relatively constant but, because of the rise in the velocity of the insect, the angle turned per unit time increased sharply.

Although the angle turned per cm averaged over 20 seconds did not change following the removal of the stimulus, a marked change did occur in the angle turned over successive cms within the 20 seconds, as shown in Figure 6. Over the first cm following the removal of the stimulus, wasps turned an average angle of 157^{o}, which was significantly greater than angles turned over subsequent cm intervals. The orientation of this turn is more clearly represented in Table 5 where the change in direction over each successive cm is given relative to (1) the initial

Figure 6. Average angles turned (with 95% conficence intervals) per cm over the first 7 cm after removal of the patch stimulus.

Figure 7. An example of how a Nemeritis patch was measured over 4 successive cm. Hatched areas represent (A) the angle turned relative to the orientation of the preceding cm, and (B) the angle turned relative to the initial orientation.

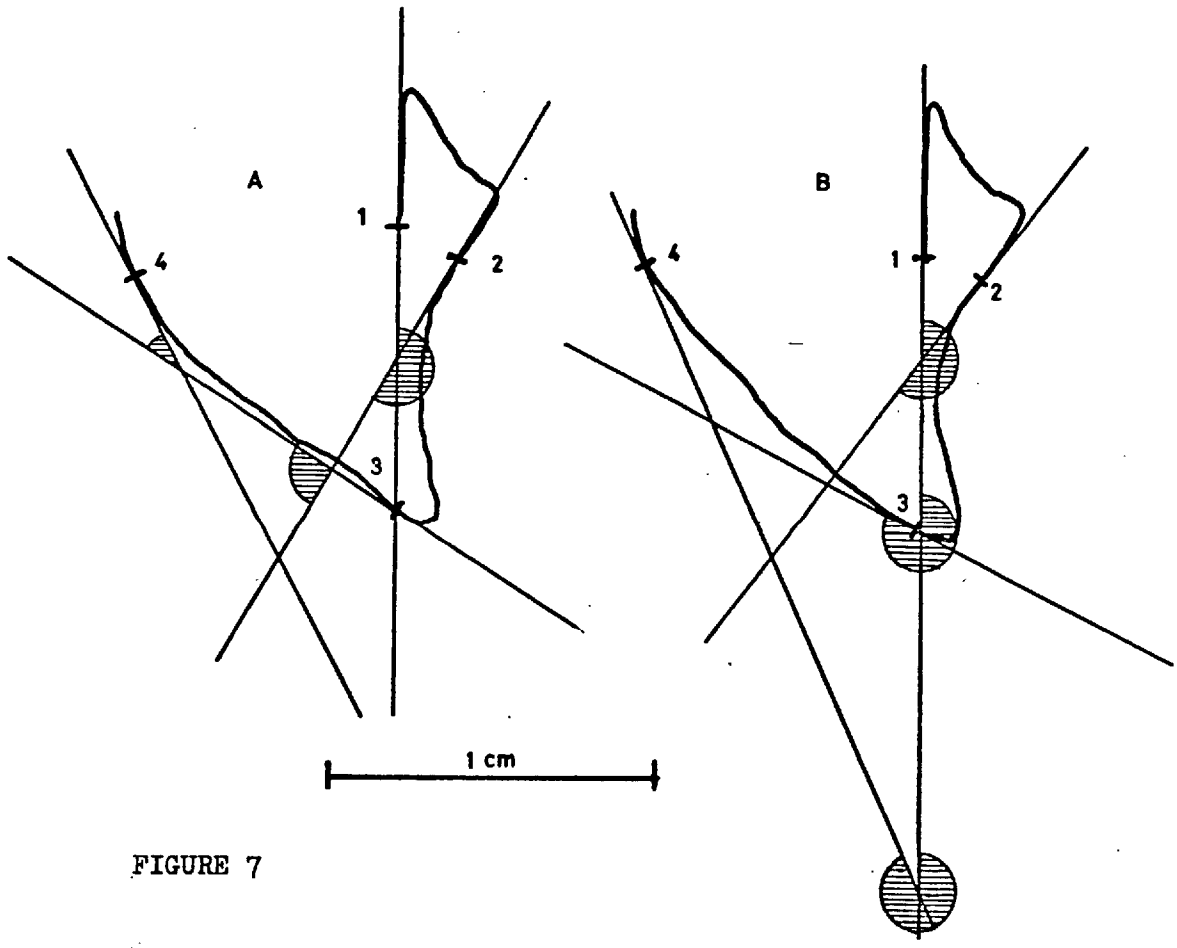


FIGURE 7

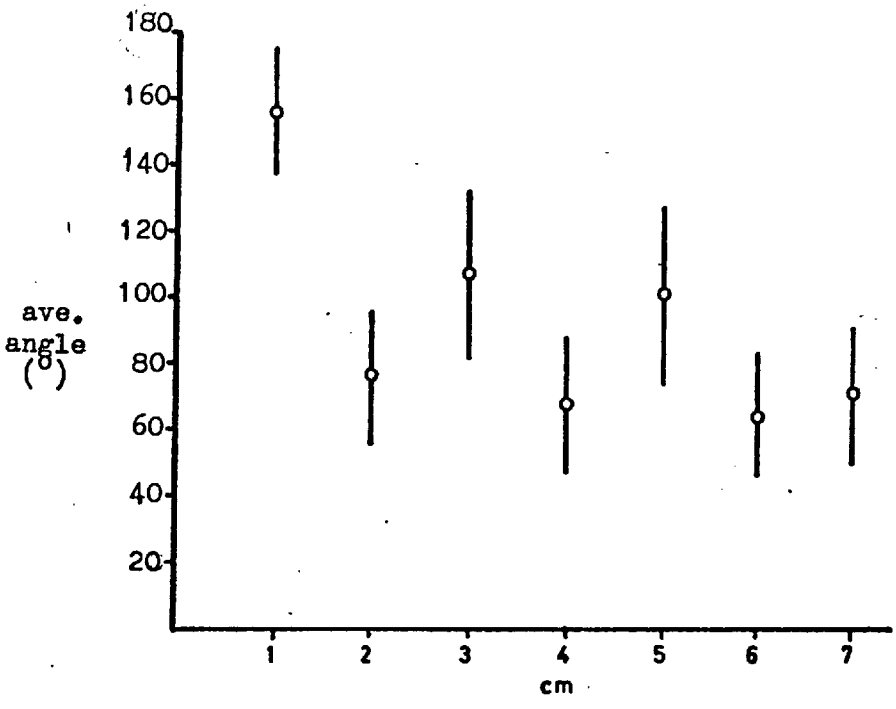


FIGURE 6

TABLE 4. Changes in locomotory behaviour of *Nemeritis* with the removal of the patch stimulus. Average for 40 replicates (with 95% confidence limits) recorded over 20 sec periods prior to and following lowering of odour source.

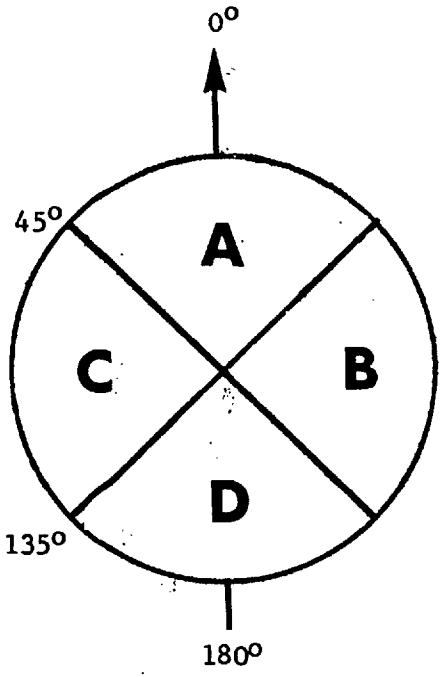
	Average speed cm/sec	Average angle turned degrees/sec	Average angle turned degrees/cm
Prior to removal	0.189 ± 0.023	14.79 ± 2.31	89.64 ± 11.89
After removal	0.641 ± 0.075	50.89 ± 5.21	82.39 ± 4.58

orientation of the wasp when the odour was removed and (2) the orientation of the wasp in the preceding cm. Significant Chi-Squares indicate a deviation from random orientation of turns (klinokinesis). The response over the first cm is clearly klinotactic, in the broad sense that the majority of turns are through a large angle relative to the previous patch and, as a result lead the wasp back towards the point where the stimulus was removed (the "edge" of the patch). Over subsequent cms the behaviour appears klinokinetic, with the angle turned being more or less random relative to the initial or immediately preceding orientation, with the exception of cm 4. This oriented turn may reflect some hidden complexity in the orientation response or may simply indicate a decay of the turning response and the "straightening out" of the path. In any case, it should be observed that the orientation of the turns over cm 4, although non random, is not nearly as clustered as in cm 1.

DISCUSSION

We can conclude from this experiment and earlier observations that the effect of the chemical patch stimulus on the duration of a patch visit is determined by an orthokinetic response to the presentation of the patch stimulus and a klinotactic response to its removal. The observed turning on the patch, away from the edge, may also contribute to patch time. This behaviour might be a response to odour presentation, but it seems more likely that it is a turning response elicited by local decrease in stimulus concentration. Such local variation is to be expected, as the host secretion is deposited in the form of discrete, oily droplets which will not be distributed regularly across the patch. Alternatively, turning on the patch may be a response to tactile sensations through the ovipositor, as described by Williams (1951, see p. 70).

TABLE 5. Analysis of direction of turn per cm in successive cms relative to (1) 0° orientation at start of track, and (2) orientation at previous cm.



		EXPECTED DISTRIBUTION OF TURNS	OBSERVED DISTRIBUTION OF TURNS PER SECTOR AT EACH CM INTERVAL					
			1	2	3	4	5	6
(1)	A	10	2	5	13	14	7	9
	B	10	6	11	9	6	13	8
	C	10	7	8	11	17	14	13
	D	10	25	16	7	3	6	10
	CHI-SQUARE	-	31.40**	4.60	2.00	13.00**	5.00	1.40
(2)	A	10	2	15	8	20	12	16
	B	10	6	6	11	5	5	5
	C	10	7	12	5	9	11	12
	D	10	25	7	16	6	12	7
	CHI-SQUARE	-	31.40**	5.40	4.60	14.20**	3.40	7.40

** $p < 0.01$

If a wasp were to keep turning back at the edge of a patch it would, of course, never leave. As illustrated in Figure 5b, upper trace, the response to the patch edge gradually disappears, leading to short walks off the patch and, finally, abandonment of the patch altogether. The underlying behaviour mechanism involved in the disappearance of this response will be discussed in Section C, but for the time being it is sufficient simply to acknowledge that factors affecting the decay of this response will influence patch time. One likely factor in this regard is the concentration of the patch stimulus.

The amount of mandibular secretion deposited over a given period in a given area increases with increasing numbers of host larvae. In small, confined areas, concentrations of chemicals appear to increase exponentially with host density (Corbet, 1971). This is presumably because production of secretion under such conditions results primarily from encounters between larvae and such encounters, assuming the hosts move at random, will increase exponentially with larval density. In less confined areas with host food available, a more linear relationship of chemical concentration and host numbers is expected, because most secretion is produced during feeding and silk deposition. To examine the effect of patch stimulus concentration on the duration of patch visits, the following experiment was conducted.

EXPERIMENT 2: THE EFFECT OF PATCH STIMULUS INTENSITY ON PATCH TIME

MATERIALS AND METHODS

For this experiment, patches were prepared as previously described, except that larvae were placed with one gram of food medium (5 parts middlings/1 part glycerol). Different stimulus intensities were produced by placing 1, 5, and 10 larvae for 15 hours between the screens. The contaminated patch was stretched over the floor of the experimental

chamber as shown in Figure 8b, and a 5.5 cm diameter dish raised below it for reasons which will become clear in the next section. The floor of the chamber was filled with untreated host medium until it was flush and continuous with the patch. This created a natural granary situation with a uniform surface of meal containing a patch which differed from its surroundings only in the presence of host silk and mandibular gland secretion. A standardized wasp was exposed to the surface by carefully transferring the top part of a standardization chamber (Figure 8a) onto the experimental surface (Figure 8b). In this way, the wasp suffered minimum disturbance.

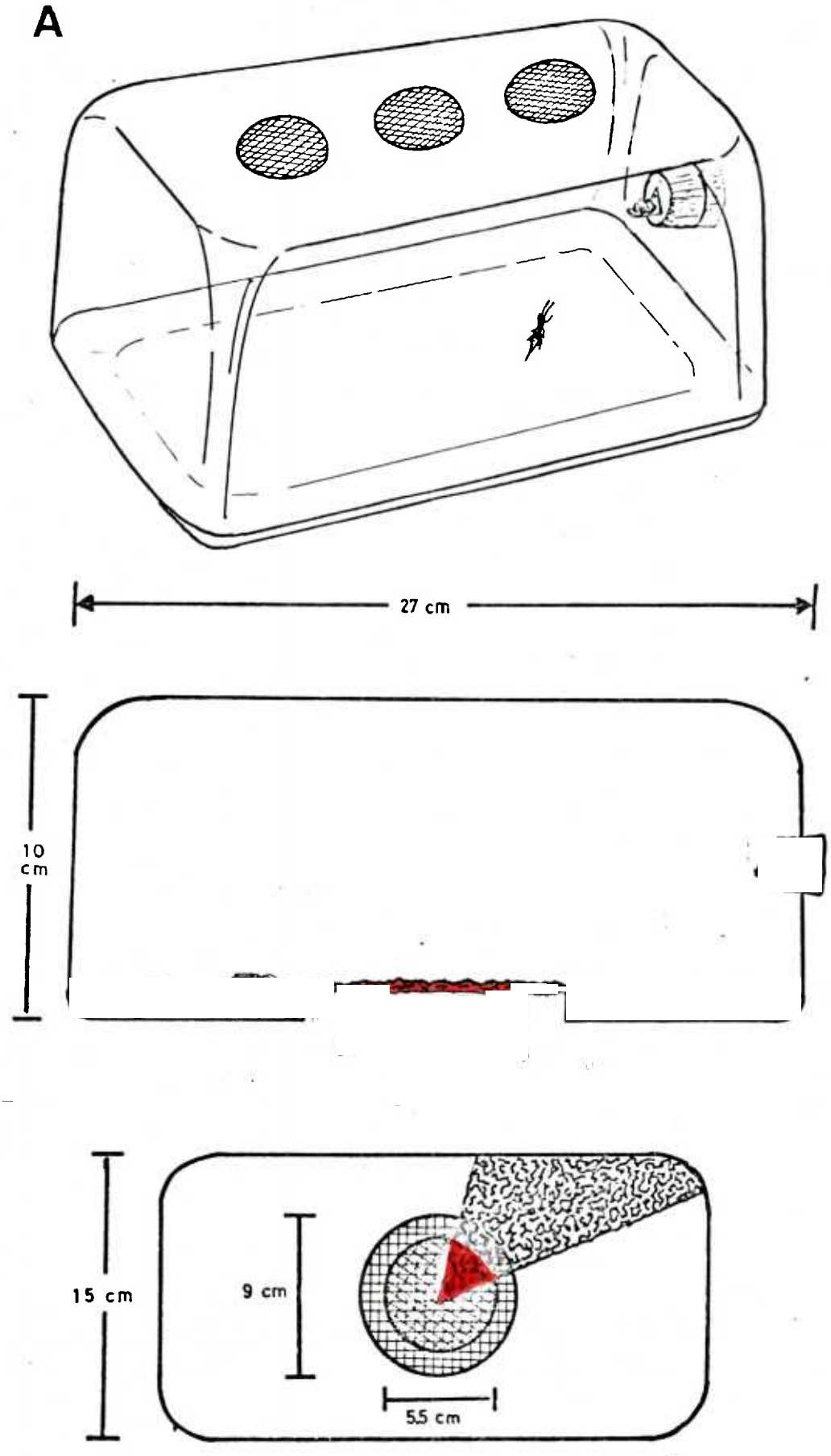
Occasionally, wasps remained inactive on the sides of the chamber for long periods after transfer. Because of this, a criterion was established whereby *Nemeritis* which were selected for testing had to have found the patch by walking over the experimental surface within 12 minutes after exposure to the middlings. A wasp which did not find the patch in this period was removed and a new standardized wasp was placed in the chamber.

The behaviour of a wasp was observed for one hour after it had entered the patch, and the duration of the following activities was recorded on a Rustrak 8-channel event recorder: presence on the patch, presence off the patch, presence on the side of the chamber, probing, resting, flying and walking. The observer sat behind a transparent red plastic screen (cine film red) through which the insect could not see. This was necessary because the insects were very sensitive to movements outside the experimental chamber. Recordings at each stimulus intensity were replicated twelve times.

Figure 8.

A. Standardization chamber. Cork on side has platform with soaked raisin. Dimensions as with (B)

B. Experimental chamber. Side view (above) and view of chamber floor (below). Darkened areas represent middlings, red areas are contaminated middlings (the 'patch'). This chamber used for Expt.s 2, 3 and 4.


A
27 cm
10 cm
15 cm
9 cm
5.5 cm

RESULTS AND DISCUSSION

The evaluation of patch time is complicated by the determination of when a forager has actually left a patch. For example, a *Nemeritis* engaged in probing will occasionally cross a few mm over the patch edge, carried out by its own momentum, before turning and continuing probing within the patch. In other instances, wasps have been observed to step a few mm outside the patch, stop and clean their antennae and ovipositors for up to 15 seconds before turning and starting to probe again within the patch. Clearly, it is not desirable to treat such events as patch leaving and thereby equate them with situations where the insect walks directly off the patch, across the medium and onto the walls of the chamber.

To solve this problem, an arbitrary time period was chosen for determining whether a patch had been left. Table 6 and Figure 9 present two such evaluations of patch time for the different stimulus intensities. By one criterion, a wasp had to be walking and/or flying off a patch for 14 seconds (3 mm on the recorder tape) to have left the patch. By the other criterion, a wasp had to be off the patch, engaged in any activity (including resting), for one minute. Application of these criteria gives similar results, namely, that patch time increases markedly as stimulus intensity increases.

Another arbitrary index of patch time was obtained by calculating the total time spent on a patch by the wasp over the hours' observation. The total time spent probing was also recorded, and these values are presented in Table 6, row 4. A trend with increasing stimulus intensity similar to that observed with initial patch visits is apparent, but the causes for this trend are more complex. The total time spent on a patch over an hour is a function of (1) the tendency of a wasp to remain on the

TABLE 6. The effect of increasing patch stimulus intensity on the time *Nemeritis* spends on a patch.

Time in minutes	PATCH STIMULUS INTENSITIES 1	5	10
Time until walking (or flying) off patch for 14 sec	7.86 ± 2.86	12.81 ± 3.84	32.14 ± 9.98
Time until off patch for one minute	9.02 ± 3.89	13.75 ± 3.57	39.82 ± 11.76
Total time spent on patch over one hour	15.34 ± 5.40	26.83 ± 5.83	47.59 ± 4.88
Total time spent probing	2.85 ± 1.50	10.90 ± 3.71	26.37 ± 5.36
Average duration of patch visits (not including first visit)*	1.76 ± 0.50	3.29 ± 1.02	7.70 ± 2.51
Average duration of inter-patch intervals*	5.24 ± 1.21	3.84 ± 0.61	3.57 ± 1.40

* see text for explanation

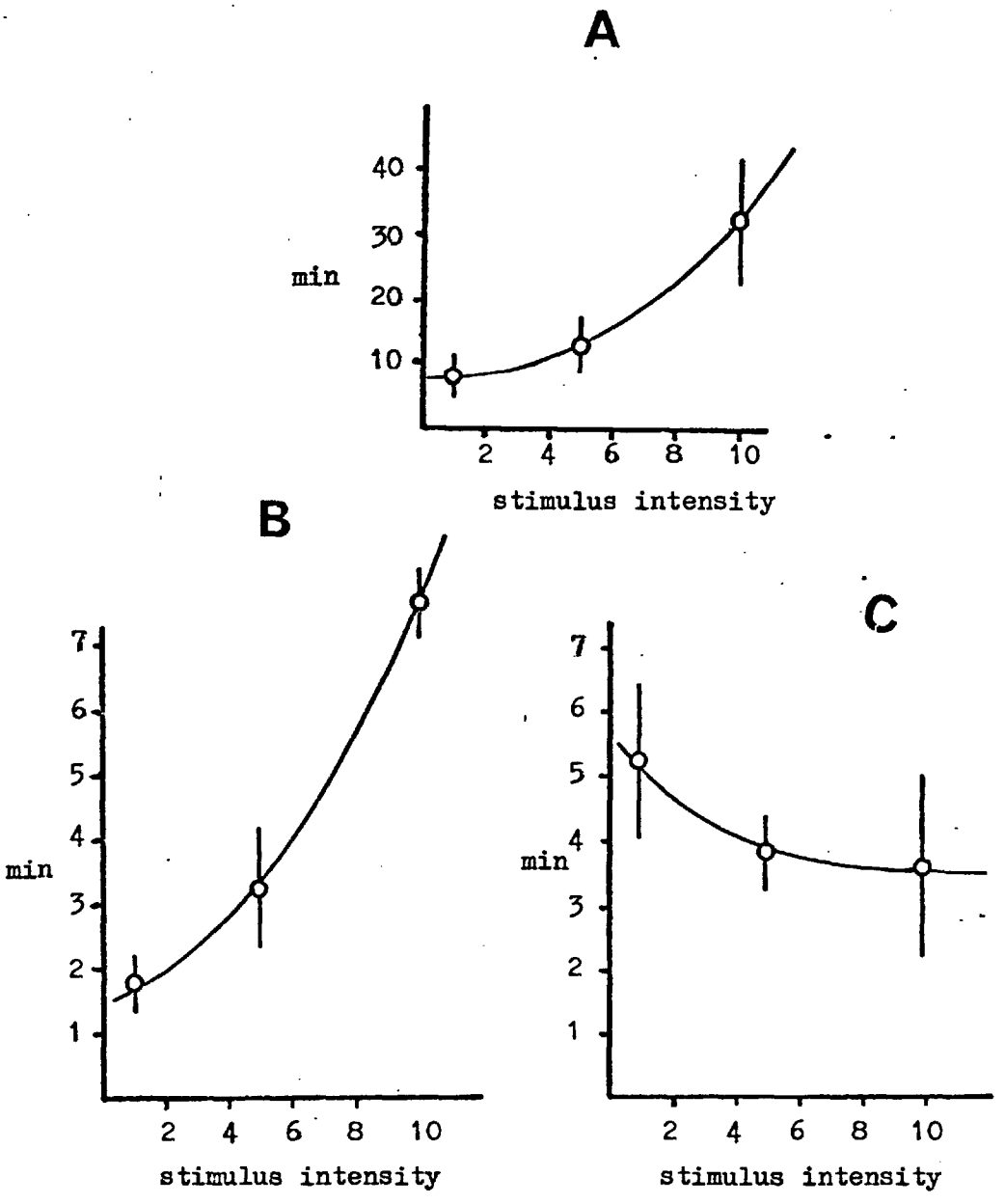


Figure 9. Changes with increasing patch stimulus intensity of (A) patch-time (till off 14 sec), (B) average duration of patch visits (excluding first), and (C) average duration of interpatch intervals. Curves fitted by eye. See Table 6, rows 1, 5 and 6 and text for explanation.

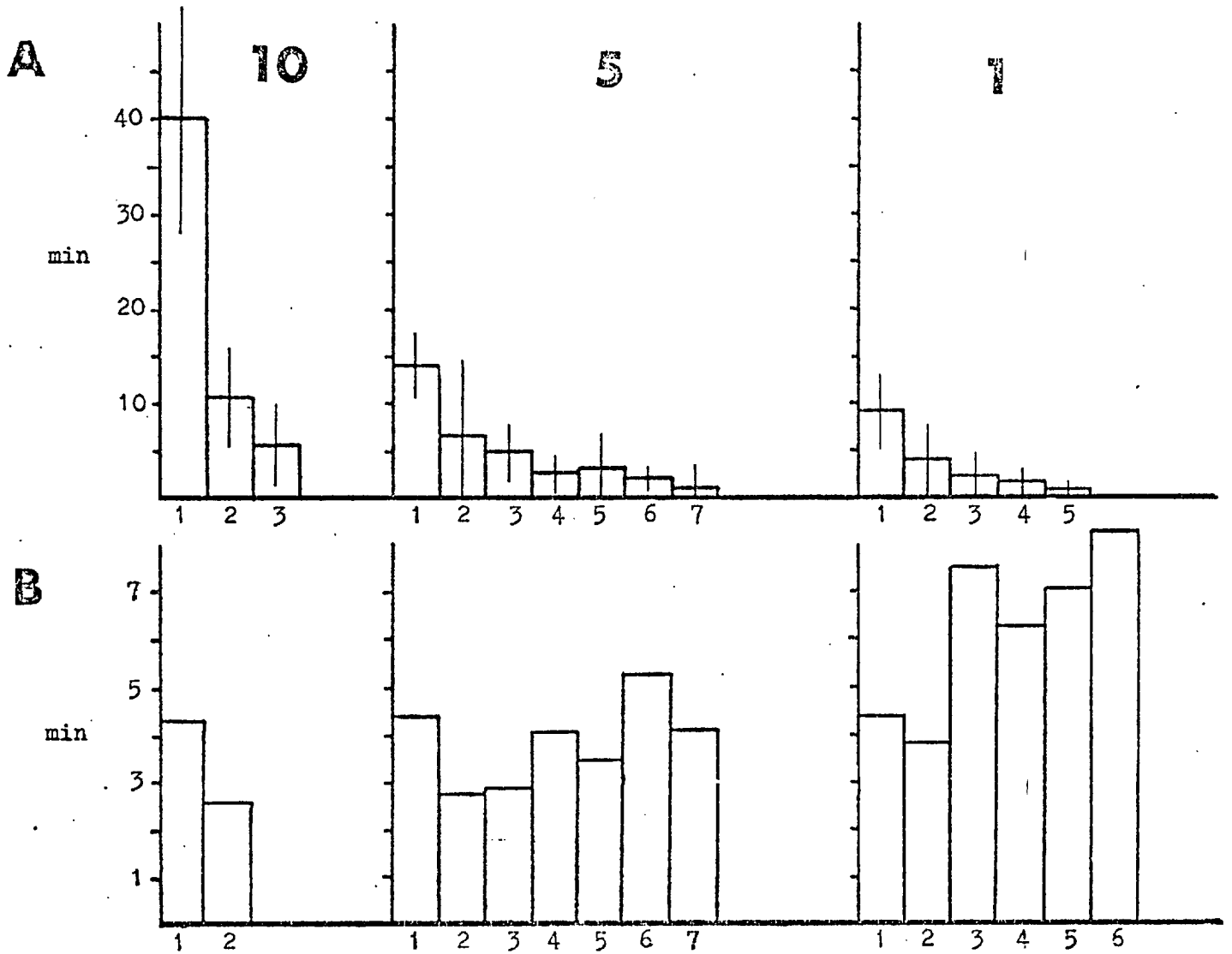
patch at each visit and (2) the tendency of the wasp to return to the patch each time that it leaves. Both of these tendencies may be affected by the intensity of the patch stimulus and by the duration of previous periods on and off the patch.

In order to look at this complex response in more detail, the average duration of successive patch visits and successive periods between patch visits (interpatch intervals) were calculated for each stimulus intensity. A patch visit was defined as the time between entering a patch and leaving it for more than 1 minute. This means that interpatch intervals had a minimum duration of 1 minute. The results obtained are presented in Figures 9 and 10, and Table 6. The number of values for each intensity reflects the number of replicates obtained from the original data. Only values with 5 or more replicates were included.

At all stimulus intensities, successive patch visits decrease in duration. The duration of these return visits is higher, at each visit, for higher patch stimulus intensities. The interpatch interval, which may be interpreted as the tendency to return to the patch, shows a marked decrease in duration between stimulus intensities of 1 and 5. Too few replicates are available to evaluate this effect for a stimulus intensity of 10. It is interesting to note that the first interpatch interval is, on average, similar for all stimulus intensities, and that marked differences in the tendency to return to the patch appear only after several visits have been made.

Changes in patch stimulus intensity affect not only the duration of first visits to a patch, but the duration of later visits and the time between these visits as well. Raising stimulus intensity increases both the tendency to return to a patch and the tendency to remain on the patch returned to.

Figure 10. A. Average duration of successive patch visits (with 95% confidence intervals) for patches of stimulus intensity 1, 5 and 10. B. Average duration of successive interpatch intervals for patches of stimulus intensity 1, 5 and 10.


A
10
5
1
40
30
20
10
min
1 2 3
1 2 3 4 5 6 7
1 2 3 4 5
B
7
5
3
1
min
1 2
1 2 3 4 5 6 7
1 2 3 4 5 6
NO. OF PATCH VISIT / INTERPATCH INTERVAL

All of the above analyses of patch visits and patch time are based on arbitrary assumptions of when a patch is left. A more realistic form of analysis might be to evaluate the instantaneous probability that a wasp will be on a patch at a given time, t, after entering the patch. An approximation of this probability function is given in Figures 11, 12 and 13, where the fraction of each of the 60 minutes spent on the patch and spent probing on the patch by an average wasp is plotted against time. The general form of the patch time functions is an initial period at a probability of 1.00 followed by a gradual decay. As patch stimulus intensity is increased, this initial period is lengthened and the subsequent decay appears less steep. To illustrate this better, these patch time probability functions are presented in Figure 14, and curves of different y intercepts but identical slope are fitted to the data, leaving out points at 0.99 to 1.00 which represent the initial "plateau" of the function. These curves were fitted using a selective regression procedure (Draper and Smith, 1966; Chapter 6) which provided the best fit for 3 lines with identical slopes and different intercepts. This choice of fit was arbitrary, as the data could be described as well by 3 lines of common intercept and three slopes, but it serves satisfactorily to indicate the change in the probability of being on a patch at different times with changes in stimulus intensity.

In natural situations where the movement of a wasp is not restricted within a box, we might expect such probability functions to decay more rapidly with the inter-position of much longer intervals between patch visits.

6.3 THE EFFECT OF HOST CONTACT STIMULI ON PATCH TIME

GENERAL METHODS AND OBSERVATIONS

In the previous section, it was established that patch time is

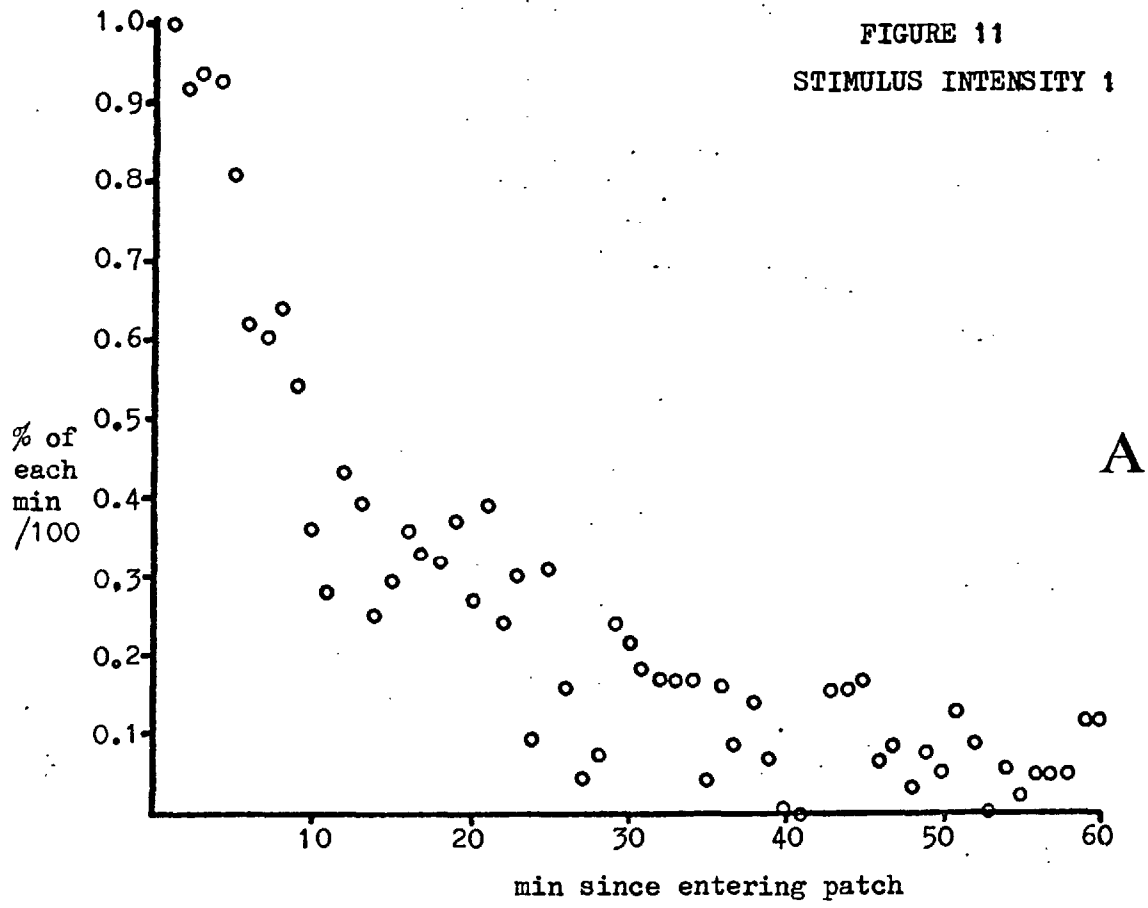
Figure 11. A. Fraction of each minute spent by an average wasp on a patch of stimulus intensity 1. B. Fraction of each minute spent probing on the patch.

Figure 12. A. Fraction of each minute spent by an average wasp on a patch of stimulus intensity 5. B. Fraction of each minute spent probing on the patch.

Figure 13. A. Fraction of each minute spent by an average wasp on a patch of stimulus intensity 10. B. Fraction of each minute spent probing on the patch.

FIGURE 11

STIMULUS INTENSITY 1



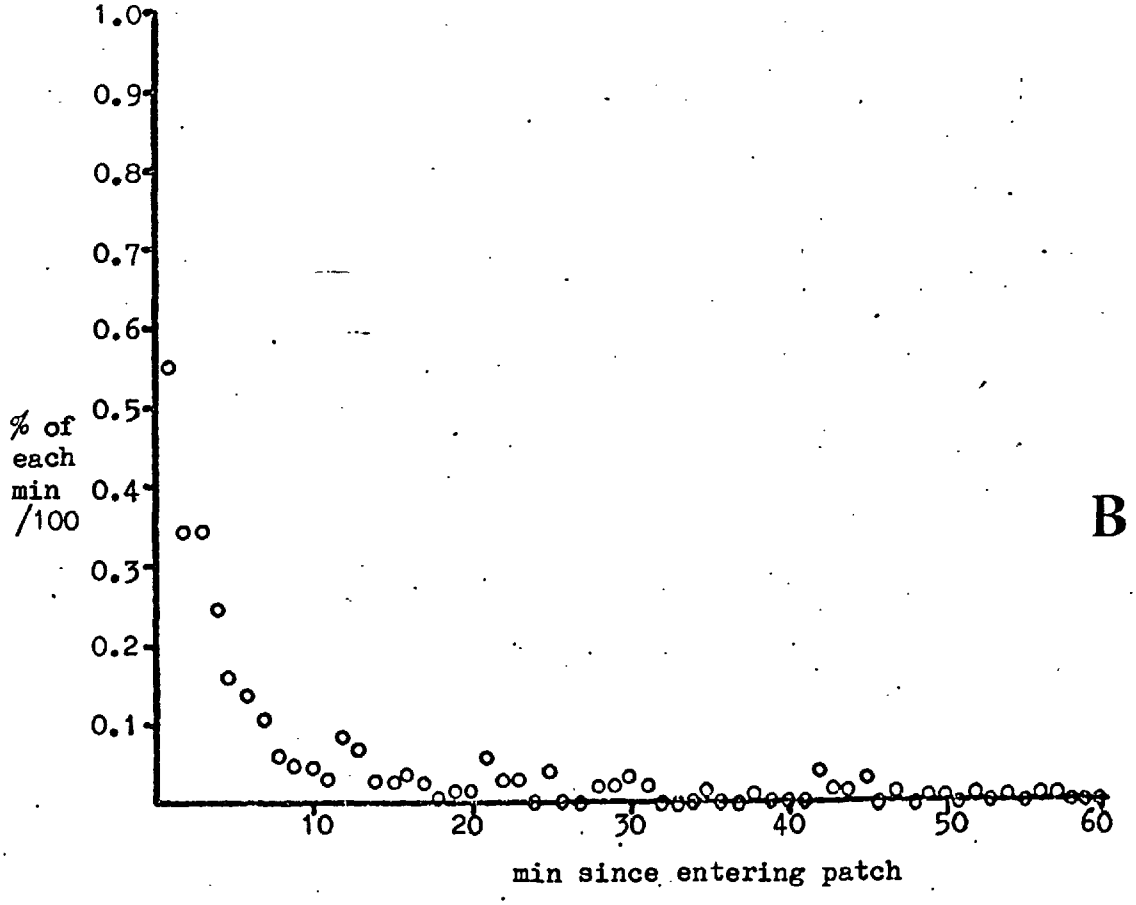
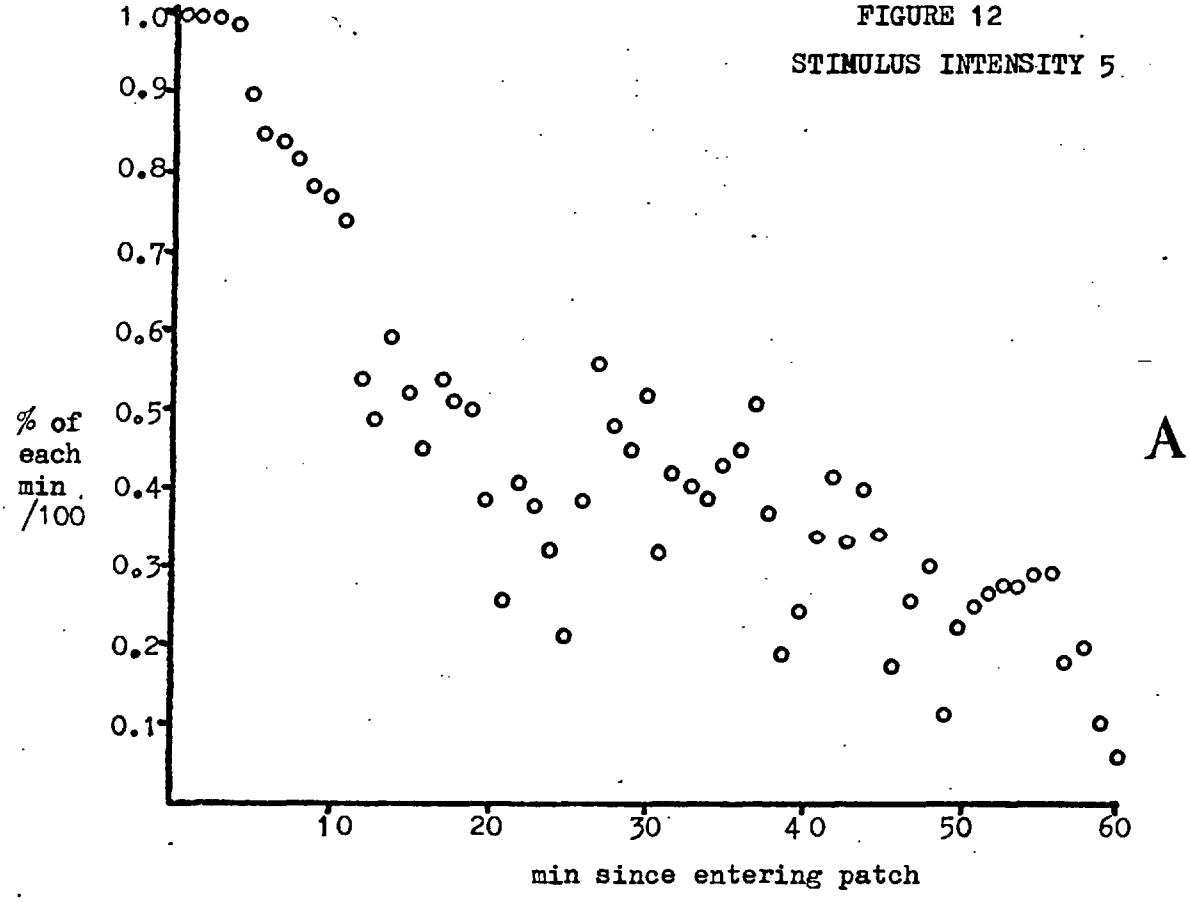
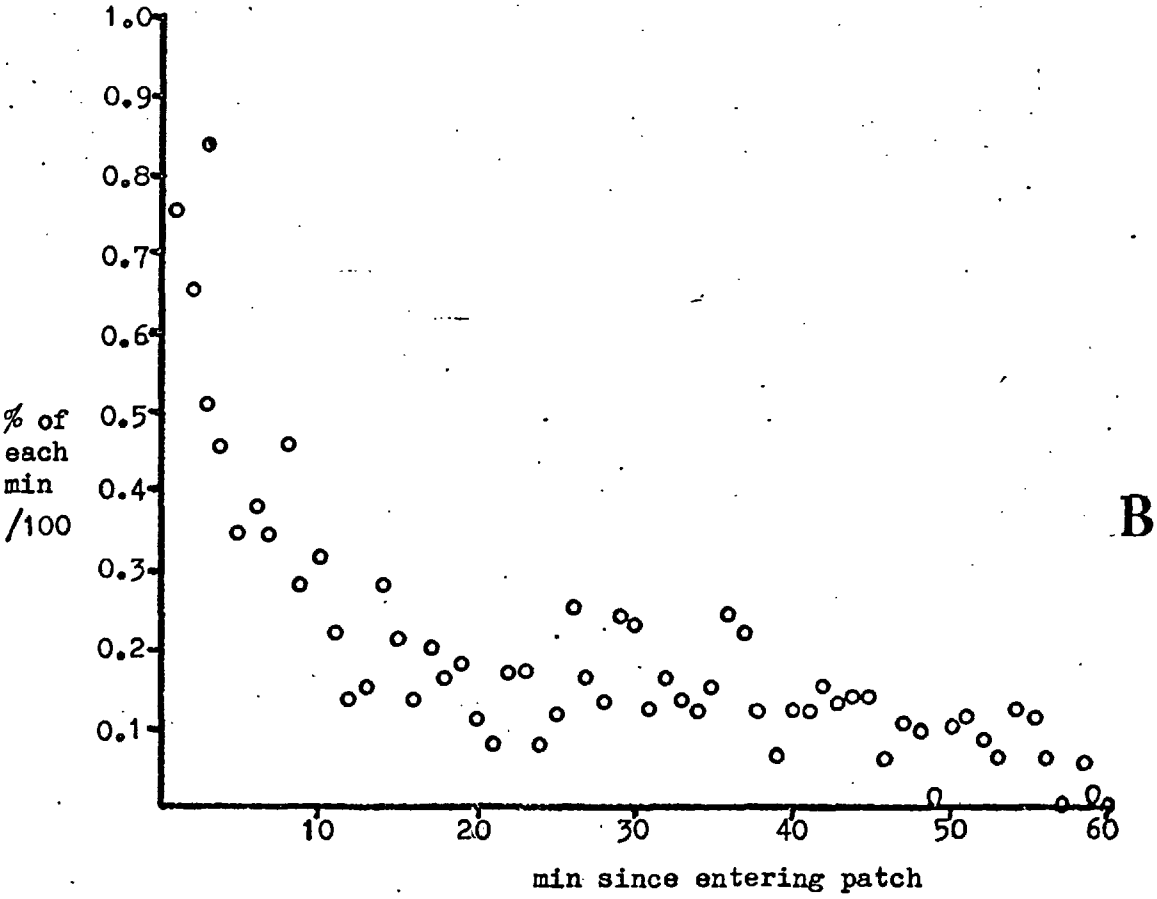


FIGURE 12

STIMULUS INTENSITY 5



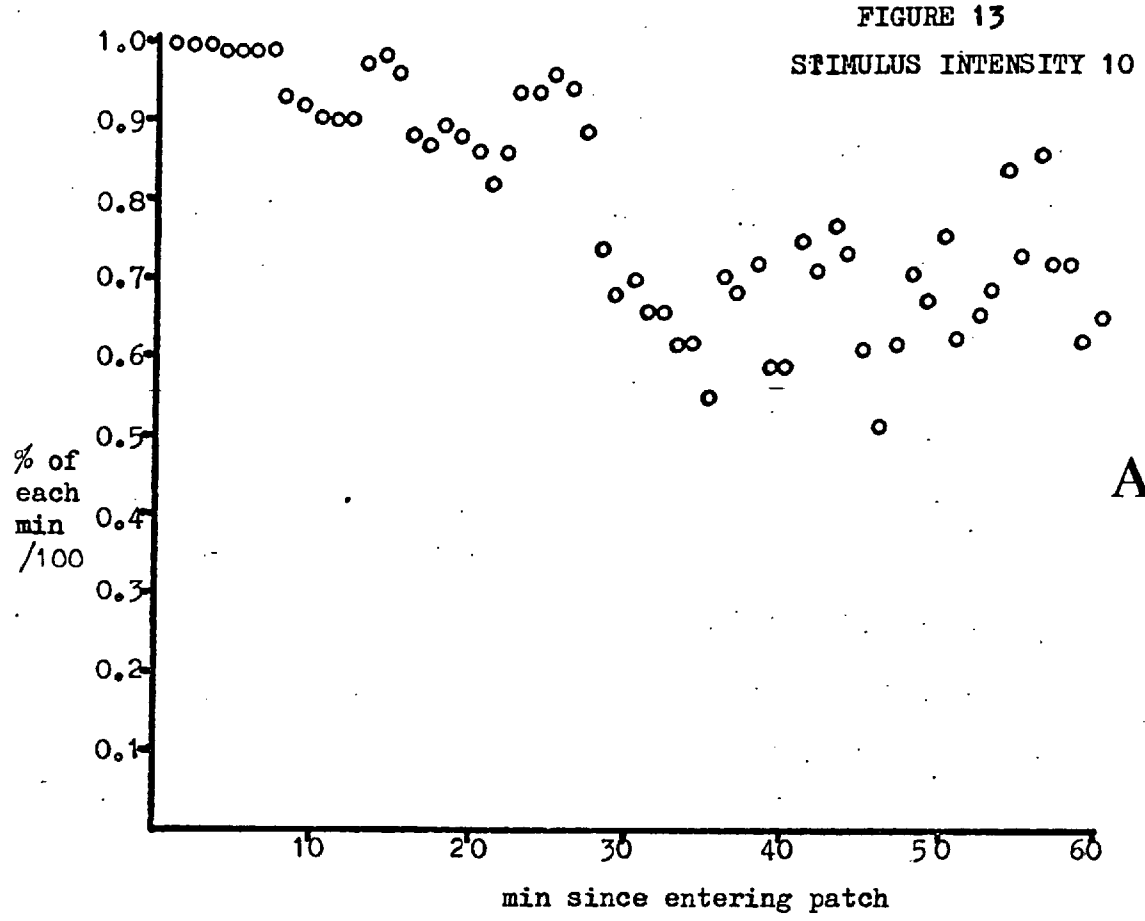
A



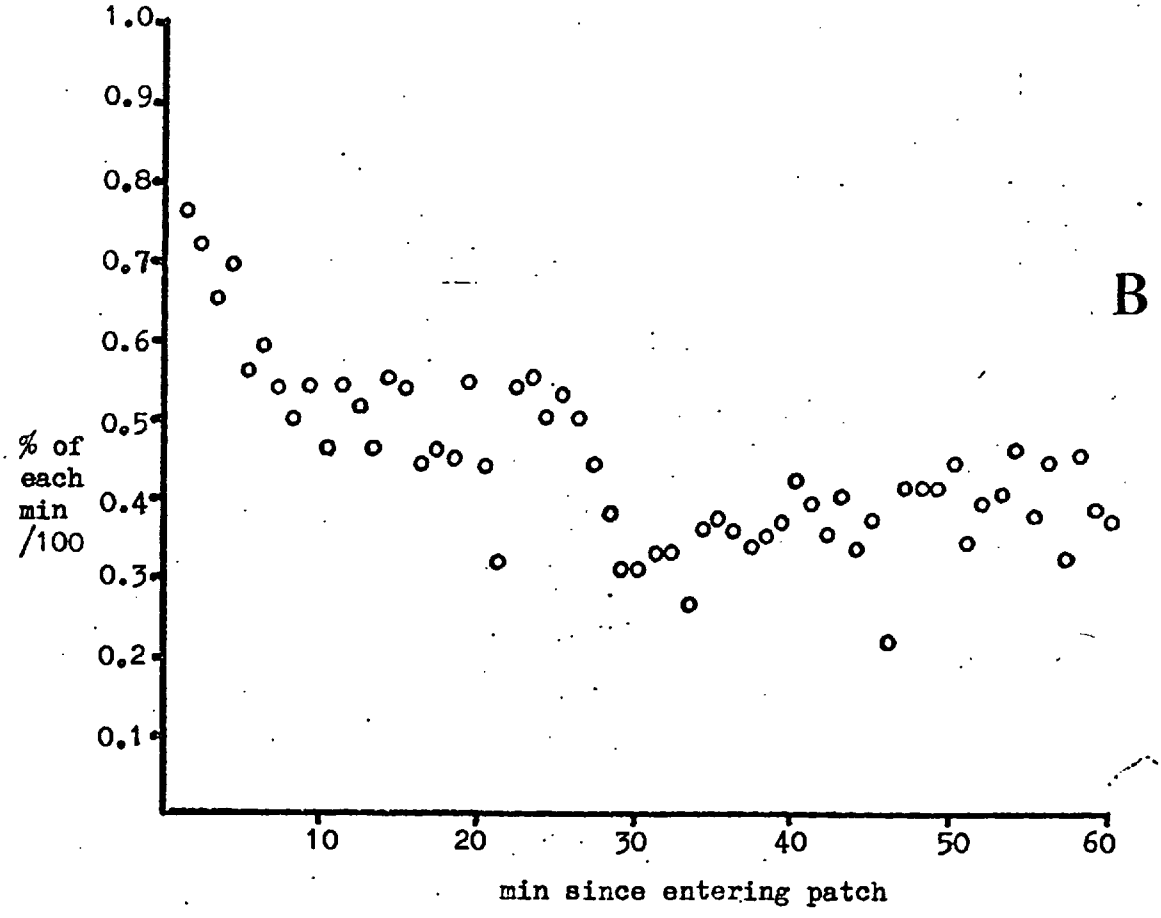
B

FIGURE 13

STIMULUS INTENSITY 10

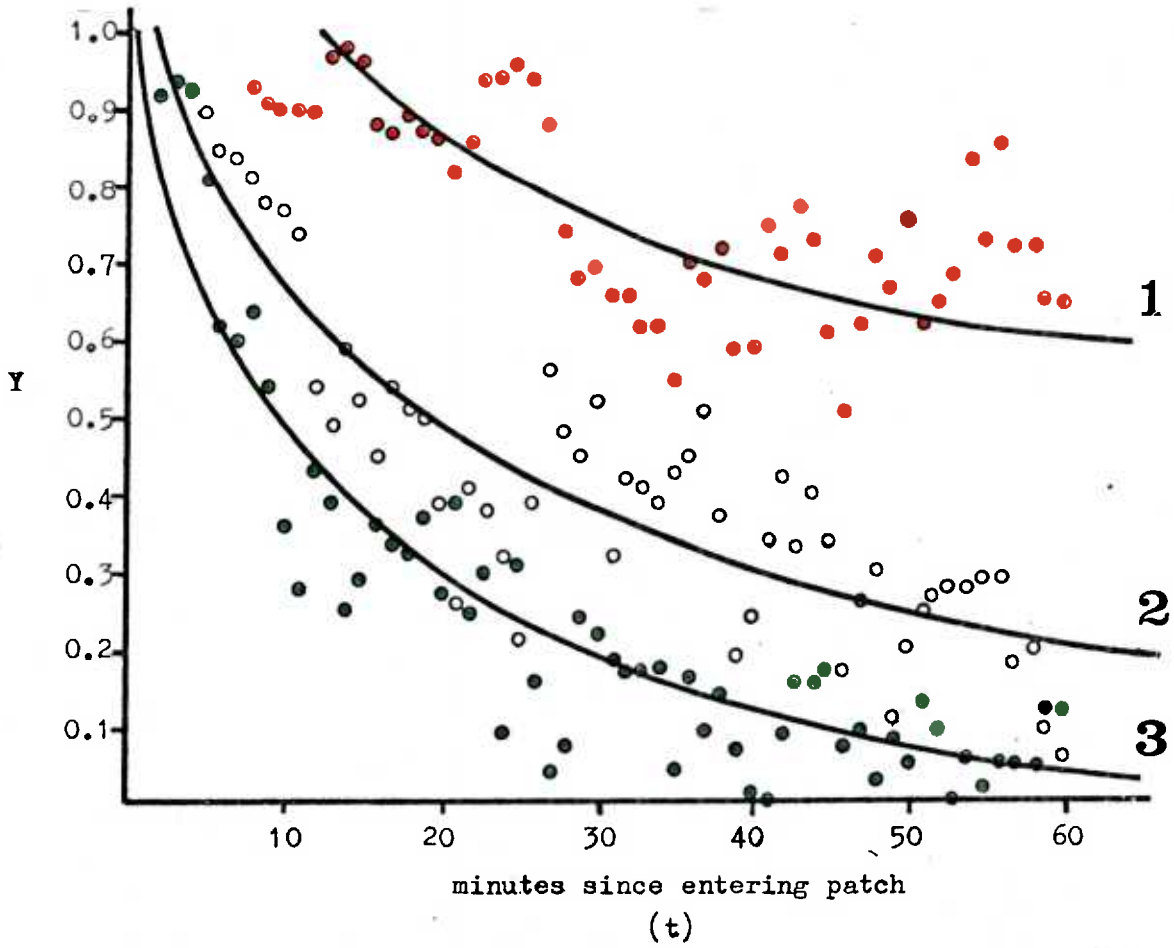


A



B

Figure 14. Comparison of the probability of being on patches of different density over an hour. Ordinate, Y = fraction of that minute spent on the patch by the average wasp. Curves are fitted to data for each intensity, ignoring points of value 0.99 and 1.00 (the upper plateau region of each curve). Curve 1 - stimulus intensity 10 (red points), Curve 2 - intensity five (white points), Curve 3 - intensity one (green points).



●	Curve 1	Y = 1.63 - 25.3 ln(t)
o	Curve 2	Y = 1.25 - 25.3 ln(t)
●	Curve 3	Y = 1.06 - 25.3 ln(t)

influenced by the intensity of the chemical patch stimulus and, therefore, by the density of hosts in the patch. This section investigates the effect of host contact stimuli on patch time. The assumption that this is the second primary determinant of patch time for *Nemeritis* is inferred from what is known about parasitoid foraging in general (Chapter 3) and from the evolutionary argument (Chapter 4) that a patch time mechanism based on the rate of prey capture is likely to be most efficient. Obviously, it is important first to demonstrate that a response does occur to host contact which increases the time a wasp spends on a patch.

Because it is difficult to observe the actual contact of hosts in their medium by the ovipositor of a probing *Nemeritis*, oviposition and its associated stimuli, was chosen as the host contact stimulus. It is therefore the after-effect of oviposition which is investigated here. The cocking action, together with the commonly observed post-oviposition grooming and resting behaviour, was used to establish that an oviposition had actually occurred. While Rogers (1972b) had shown that cocking of the ovipositor was the inevitable consequence of oviposition, for the purpose of the present experiments the converse had to be shown, that is, that oviposition was the inevitable antecedent of cocking. To establish this, each of 15 standardized *Nemeritis* were allowed to stab their ovipositors into 10 fifth instar *Plodia* larvae presented sequentially to them in 3X1 glass tubes. If, following stabbing, the wasp cocked its ovipositor, the larvae were transferred to food medium for five days and then dissected. Due to mortality in the larvae, only 142 transferred larvae were ultimately dissected. Of these, 132 (93%) contained eggs or larvae of *Nemeritis*. As *Nemeritis* eggs are easy to overlook in larval dissections, this 93% rate of recovery is close enough to 100% to conclude that cocking is, indeed an indication of oviposition.

EXPERIMENT 3: THE EFFECT OF A SINGLE OVIPOSITION ON PATCH TIME

MATERIALS AND METHODS

In this first experiment on the response to oviposition, wasps were given one oviposition immediately upon entering a patch and observed for one hour following. The experimental set up was identical to that in Experiment 2 with a patch stimulus intensity of five. The dish beneath the patch (Figure 8b), however, contained approximately 30 fifth instar *Plodia* larvae under the terylene screen. This density ensured that oviposition occurred soon after probing on the patch commenced. During the wasp's subsequent resting period, before cocking, the dish was lowered and replaced with an empty dish like that used in Experiment 2. The same activities were recorded over the hour after entering the patch as during Experiment 2.

RESULTS

The results of this experiment are compared in Table 7 with those obtained a patch of stimulus intensity five in the previous experiment. The duration of the first patch visit with oviposition was greater than that with no oviposition. This difference was significant for patch times calculated using the 14 sec criterion (row 1, $p < 0.05$) and for patch times using the one minute criterion (row 2, $p < 0.025$). A similar increase was observed in the time spent on the patch and the time spent probing on the patch over the hour.

To look at this latter change in more detail, the average duration of successive patch visits and interpatch intervals was calculated. This data is presented in Figure 15, where it is compared with the data from Experiment 2 for stimulus intensity 5. In contrast to the effect of increasing the patch stimulus, oviposition increased only the duration of the first patch visit. Subsequent patch visits did not differ in

TABLE 7. The effect of oviposition on the time *Nemeritis* spends on a patch.

Ave. time in minutes ± 95% confidence limits	No oviposition on patch of stimulus intensity 5	One oviposition upon entering patch of stimulus intensity 5
Time until walking (or flying) off patch for 14 sec.	12.81 ± 3.84	22.70 ± 8.29
Time until off patch for one minute	13.75 ± 3.57	27.92 ± 10.60
Total time spent on patch over one hour	26.83 ± 5.83	37.31 ± 7.35
Total time spent probing	10.90 ± 3.71	19.40 ± 7.01
Average duration of patch visits (not including first visit)	3.29 ± 1.02	2.92 ± 0.62
Average duration of inter-patch intervals	3.84 ± 0.61	2.40 ± 0.33

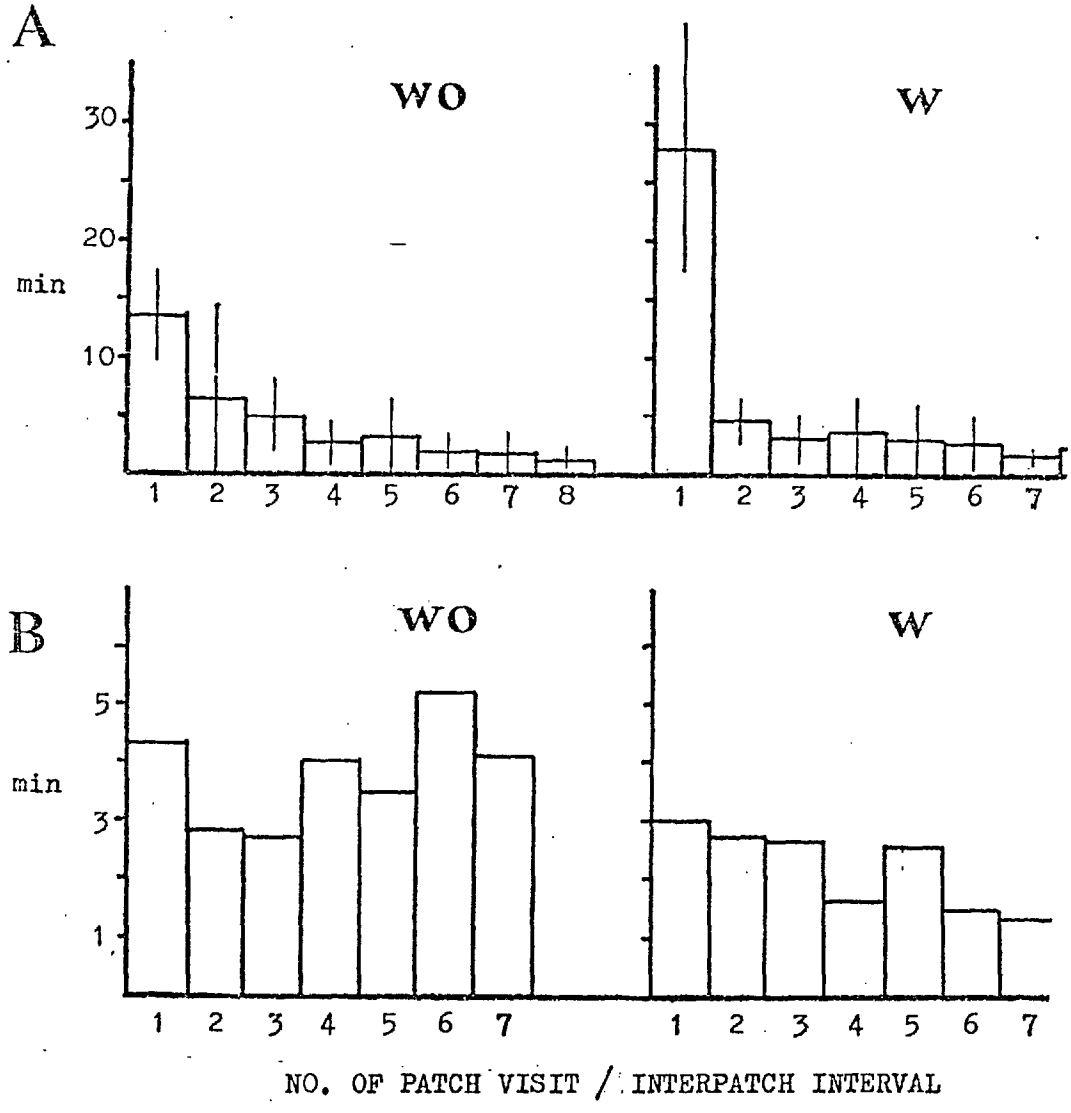


Figure 15. A. Average duration of successive patch visit (with 95% confidence intervals) with (W) and without (WO oviposition at start of first visit (patch stimulus intesity = 5). B. Average duration of successive interpatch intervals with and without oviposition.

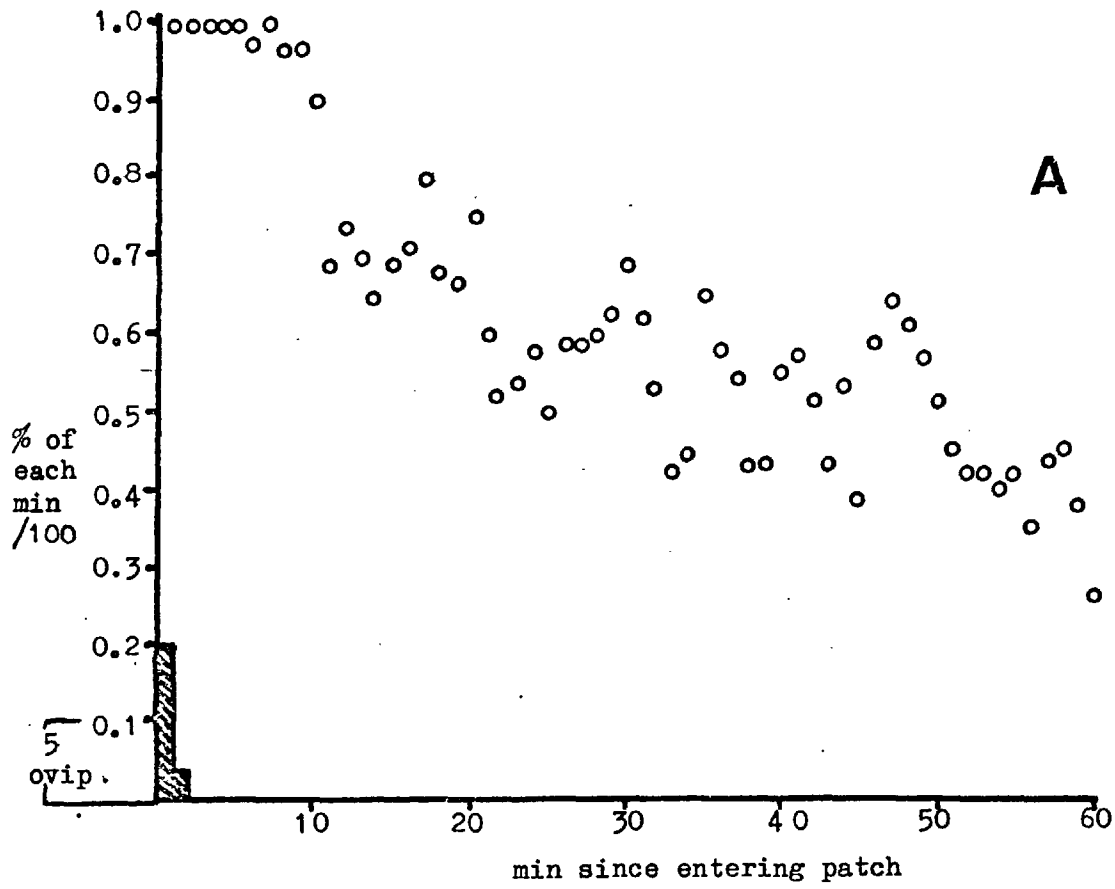
duration from those obtained with no oviposition in Experiment 2. The interpatch interval decreased markedly throughout the hour relative to the experiment with no oviposition. This may be the result of an increased attractiveness of the patch to the insect, or simply an increase in the overall activity of the wasp leading to more frequent random encounters with the patch.

The change in interpatch interval is reflected in the patch time probability function for one oviposition (Figure 16), which begins to decay later and remains higher over the hour than the corresponding function for no oviposition (Figure 12). These results may be compared to the predictions of the threshold rate hypothesis, which states that prey capture (oviposition) adds a discrete increment of time to the patch visit. This increased tendency to stay on a patch is clear from Figure 15, where it is also apparent that it does not carry over into subsequent patch visits. Oviposition, however, does affect patch time over longer periods by altering the tendency to return to a patch. Such long term effects are not considered in the threshold rate model.

DISCUSSION

While this experiment demonstrated that oviposition increased the duration of a patch visit, the mechanism involved is not clear. It seems most reasonable to conclude that oviposition slows the decay of the klinotactic edge response to patch odour, as it has already been demonstrated that a patch will be abandoned only when this response disappears. An alternative mechanism, however, is that oviposition elicits its own response, such as area restricted search, which is independent of the response to the patch edge but, by its localization of searching movements, tends to increase patch time. In fact, no such change in walking behaviour within the patch was observed following cocking, but as this

Figure 16. A. Fraction of each minute spent by an average wasp on a patch of stimulus intensity 5 with one oviposition upon entering the patch. Darkened bars represent the cumulative distribution of ovipositions (in this case 12) over the first few min. B. Fraction of each minute spent probing.


A
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0.9
0.8
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% of each min /100
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10
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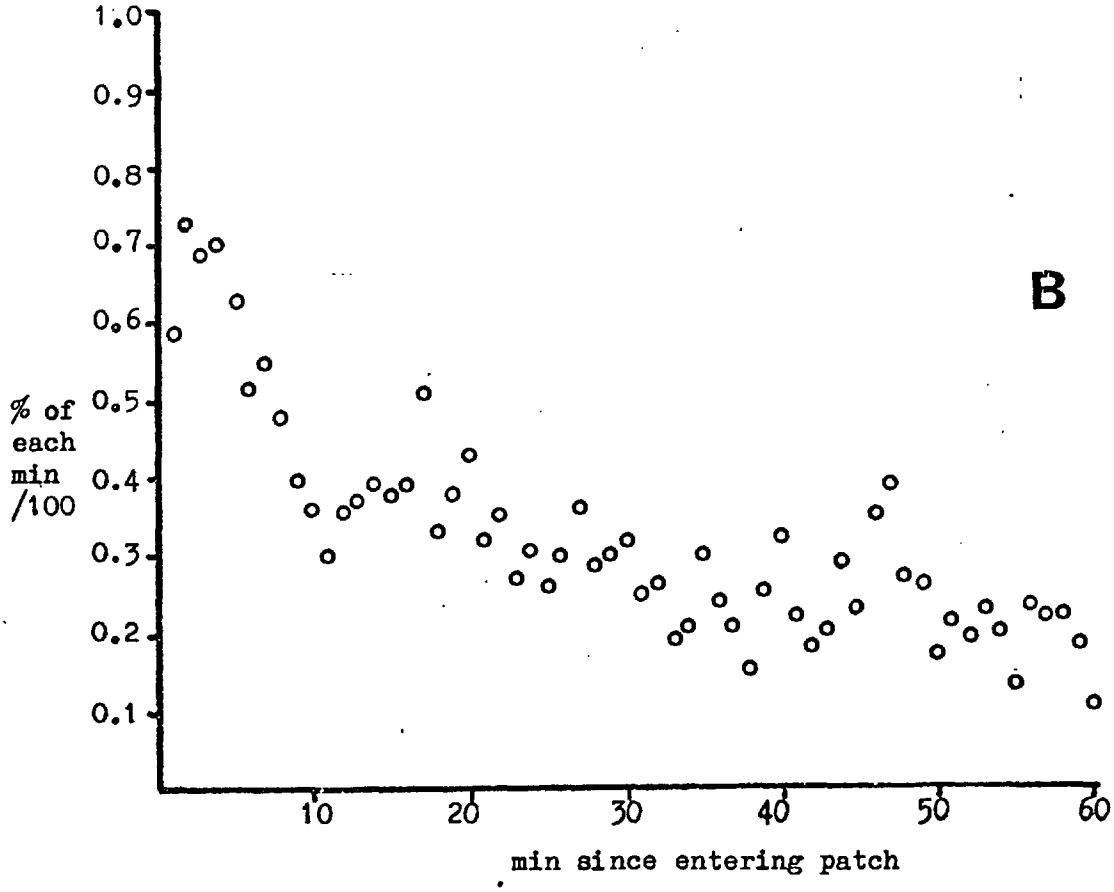
min since entering patch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% of each min /100
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20
30
40
50
60
min since entering patch

observation would be difficult to quantify, an experiment was designed to test whether the oviposition response was independent of the response to patch stimuli.

EXPERIMENT 4: THE MECHANISM OF THE OVIPOSITION RESPONSE

MATERIALS AND METHODS

For this experiment the apparatus illustrated in Figure 4c was used. The patch was made as in Experiment 1, only in this case, 15 fifth instar *Plodia* larvae were confined between the screens for only three hours. As before, the lower of the two screens was used, and this was raised beneath the floor of the experimental chamber stretched over a dish (B), either with (trial 1) or without (trial 2) the 15 larvae underneath. A standard wasp was placed in the chamber and dish B was raised until it was barely touching the chamber floor. The time was recorded from when the wasp walked on the patch area and executed either one "burst" of probing (trial 2) or one oviposition and cock (trial 1). The dish was then immediately lowered, removing the patch stimulus, and the time measured until the wasp left the patch area and climbed onto the walls of the experimental chamber. After several minutes, this experiment was repeated on the same wasp with the other trial. Six wasps were tested in all, three with trial 1 first, and three with trial 2 first.

RESULTS

To test whether oviposition increased the time spent search the surface after removal of the patch stimulus, the times spent searching for both trials were paired for each wasp and the data was subjected to a paired t-test. No significant difference was observed in the time elapsed, with and without oviposition, between the removal of the patch stimulus and movement onto the walls of the chamber, which was inter-

preted as the termination of search ($\bar{D}$ = 2.37, n = 6, $p < 0.4$). The average time spent searching was actually greater without oviposition (4.19 min) than with oviposition (1.82 min). In both trials, probing stopped with, or soon after, the removal of odour, and the amount which did occur did not differ significantly between trials ($\bar{D}$ = 0.07, n = 6, $p < 0.4$).

These results suggest that oviposition alone does not increase the tendency to stay in an area (except, of course, by adding increments of handling time), and support the hypothesis that oviposition increases patch time by affecting the decay of responsiveness to patch stimuli and, in particular, the turning response at the patch edge.

DISCUSSION

In natural patch situations, *Nemeritis* will often make a number of ovipositions over varying intervals of time. How might the effects of sequential ovipositions interact and influence patch time? The simplest mechanism one could propose for the effect of a series of ovipositions on patch time is that individual ovipositions effects are additive. In such a situation, each oviposition would add an increment of time to total patch time. An alternative mechanism is suggested by the threshold rate model discussed in Chapter 4. These models, based on the rate of prey capture (oviposition), assume that the effect of an oviposition on patch time decreases with a decrease in time between it and the previous oviposition. In the words of the threshold rate model, the forager's clock is reset with each capture such that, at high capture rates, clocks are set back to zero before they run their maximum time per oviposition, S (see p. 54). Figure 17 compares the patch time predictions of the additive hypothesis and the threshold rate hypothesis as oviposition number and rate are varied. For simplicity's sake, this figure treats

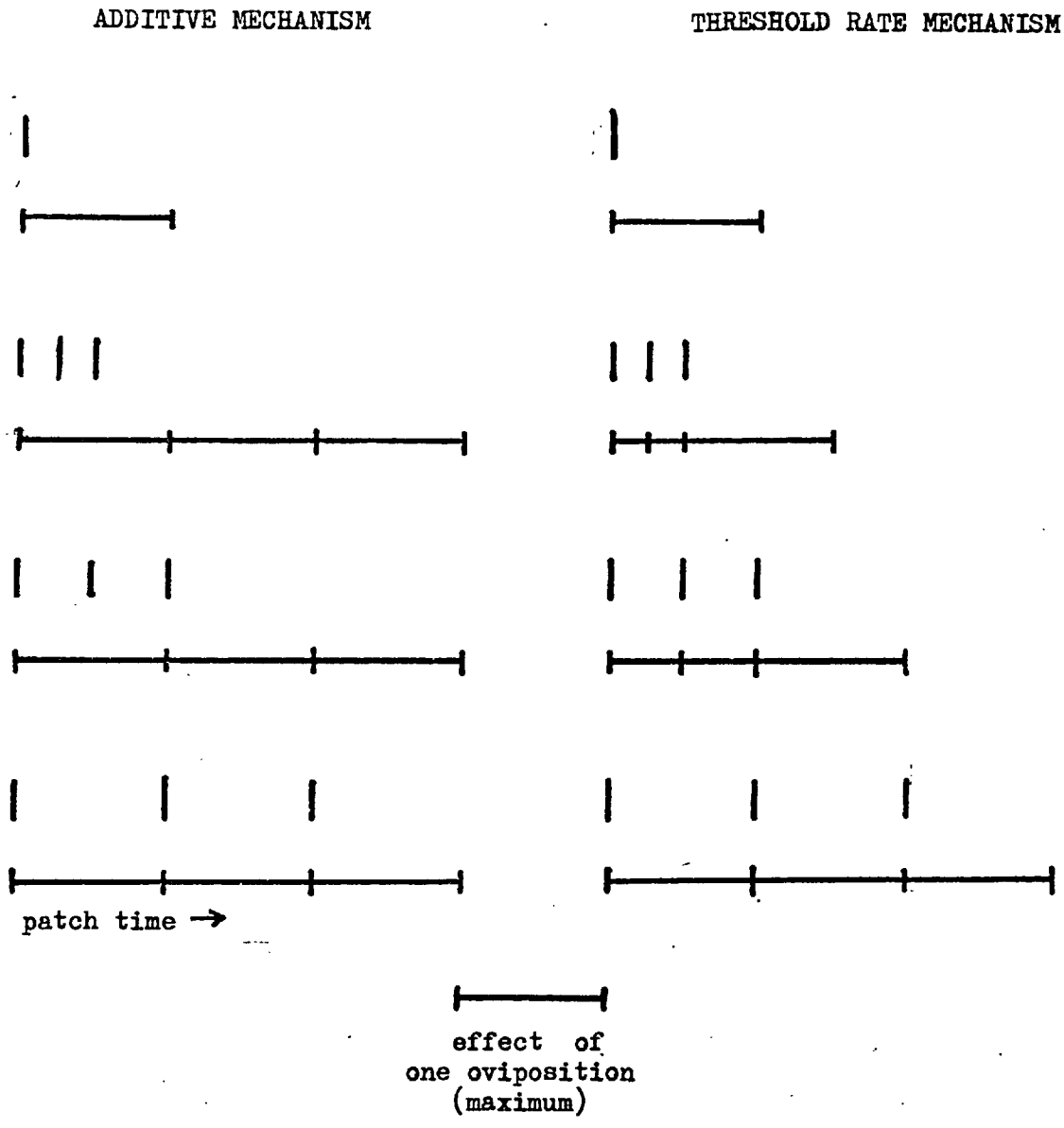


Figure 17. A comparison of different mechanisms for the effect of sequential ovipositions on patch time. Time proceeds from left to right, vertical bars represent the timing of oviposition, the lines below them represent patch time. See text for explanation.

the oviposition effect as a unit increment in patch time. Experiment 3 has shown that, for *Nemeritis*, oviposition may actually have a more prolonged and complex effect on patch time.

These two mechanisms represent hypothetical extremes in the possible interaction of the effect of one oviposition with another, and therefore make good models against which the response of *Nemeritis* (measured in terms of time on patch) to sequential ovipositions can be tested.

EXPERIMENT 5: THE EFFECT OF SEQUENTIAL OVIPOSITIONS ON PATCH TIME

MATERIAL AND METHODS

Using a procedure identical to that in Experiment 3, wasps were given 5 ovipositions within the first few minutes of patch time by leaving the dish with larvae below the middlings patch until 5 cockings were observed. The dish was then replaced with an empty dish and activity of the wasp was recorded over the rest of the hour as in previous experiments. This experiment was replicated 12 times. In another treatment, wasps were given 5 ovipositions spaced at roughly 3 minute intervals by alternating the larvae-covered dish with an empty one. As above, the activity of the wasps was recorded over this oviposition period and for the rest of the hour afterwards. Twelve replicates were run. The timing of ovipositions in these two treatments is shown clearly in Figures 18 and 19.

RESULTS

If oviposition effects are additive, patch time should not differ between the two treatments. Furthermore, patch time for both treatments should be greater than that found for one oviposition in the previous experiment. If, at the other extreme, ovipositions interact as in the threshold rate model, more time should be spent on the patch by wasps

given 5 ovipositions over 15 minutes than by those given 5 ovipositions in rapid succession (over about 3 minutes). This assumes, of course, that the time spent in unrewarded search before a patch is abandoned, S, is greater than 3 minutes. Furthermore, we might expect the time spent on the patch by wasps given 5 ovipositions in rapid succession to be similar to that of wasps given oneoviposition, as the timing of the last oviposition in both cases would be similar.

The results obtained from this experiment are presented in Table 8, along with comparable measurements from Experiment 3. Their interpretation depends on the criterion used to evaluate patch time. If the criterion in Row 1 is applied (14 seconds walking off the patch), neither hypothesis is fully supported. The data contradicts the additive hypothesis in that no difference was observed between one and 5 ovipositions. The threshold rate hypothesis is not supported because no difference is observed between 5 ovipositions in rapid succession and 5 ovipositions at 3 minute intervals, although this does not rule out some form of rate-dependent mechanism. If the criterion in Row 2 is applied (1 minute off patch), a significant difference ($p < 0.025$) is observed between the two 5 oviposition treatments, and the values obtained for 5 rapid ovipositions and one oviposition are not significantly different. These are the results predicted by the threshold rate hypothesis. It should be noted, however, that the hypothesis predicts as well that time should be greater for 5 ovipositions over 15 minutes than for one oviposition. The difference obtained is, in fact, not significant due largely to the high variance in patch time with one oviposition.

If one analyses the total time spent on the patch over the hour, the data obtained again tends to support the threshold rate hypothesis. As can be seen from the patch time probability functions in Figures 18

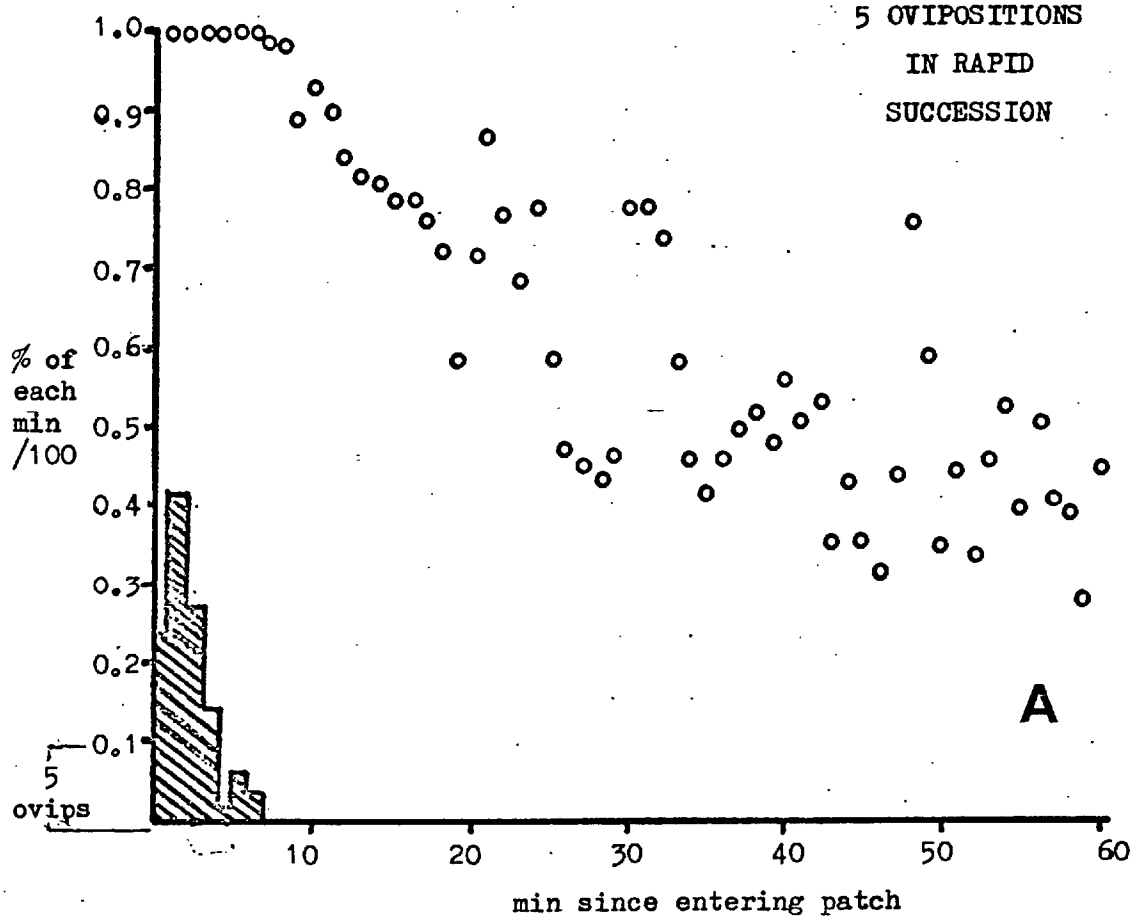
TABLE 8. The effect of oviposition rate on patch time.

	One oviposition upon entering patch	Five ovipositions upon entering patch	Five ovipositions over first 15 minutes
Time until walking (or flying) off patch for 14 sec.	21.45 ± 8.52	21.43 ± 6.12	22.69 ± 6.22
Time until off patch for one minute	26.81 ± 10.59	22.79 ± 6.23	34.92 ± 8.70
Total time spent on patch over one hour	37.31 ± 7.35	38.09 ± 6.05	44.86 ± 3.86
Total time spent probing on patch over one hour	19.40 ± 7.01	18.25 ± 4.76	24.60 ± 4.08

Figure 18. A. Fraction of each minute spent by an average wasp on a patch of stimulus intensity 5 with five ovipositions in rapid sequence upon entering the patch. Darkened areas represent timing of ovipositions as in Figure 16. B. Fraction of each minute spent probing

Figure 19. A. Fraction of each minute spent by an average wasp on a patch of stimulus intensity 5 with five ovipositions spread out over 15 min (at approximately 3 min intervals. Darkened areas represent timing of ovipositions as in Figure 16. B. Fraction of each minute spent probing.

FIGURE 18
5 OVIPOSITIONS IN RAPID SUCCESSION



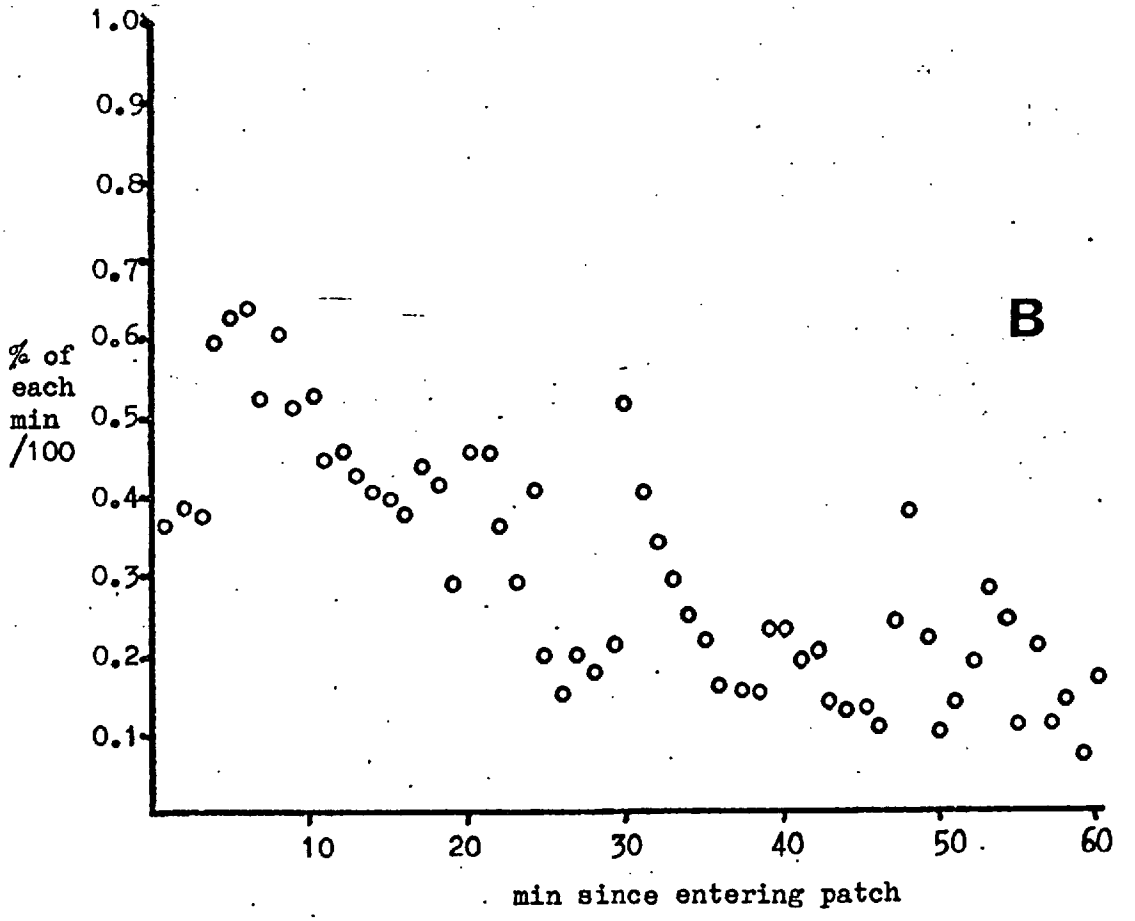
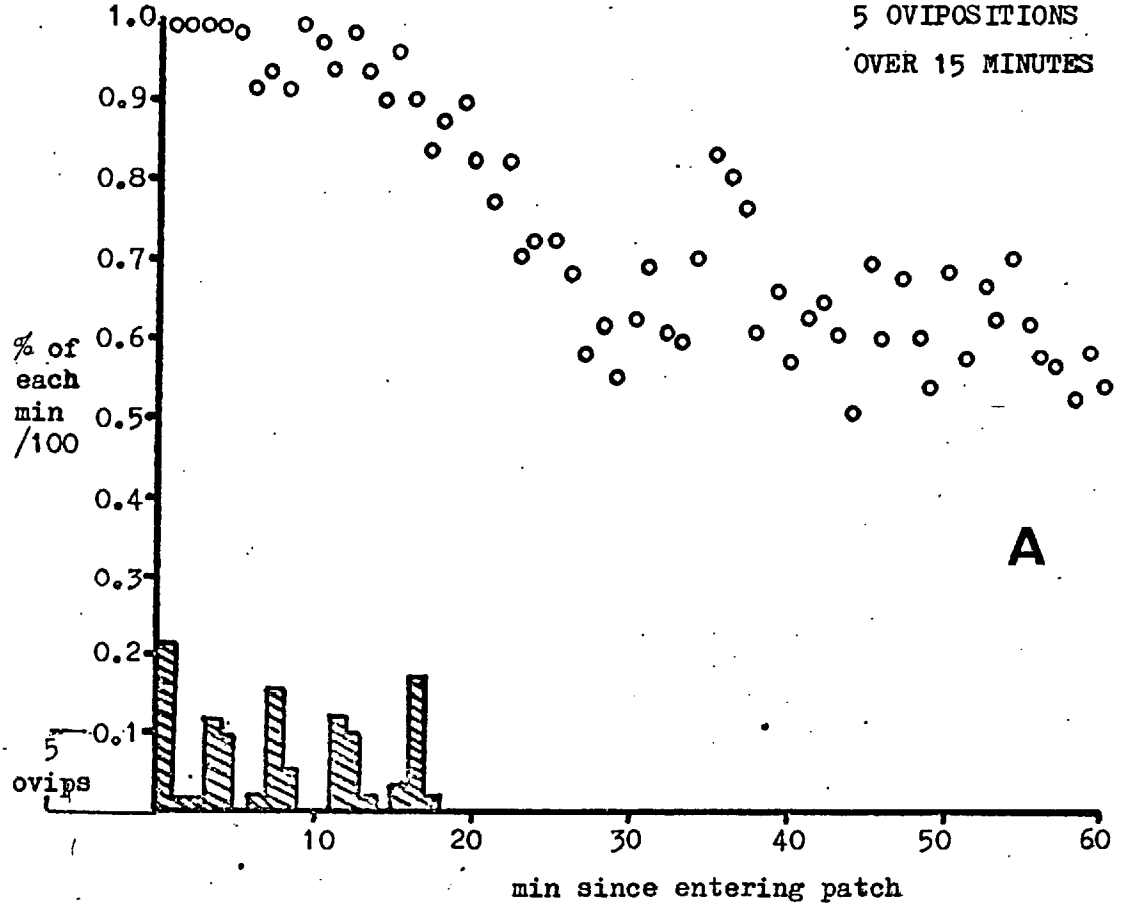
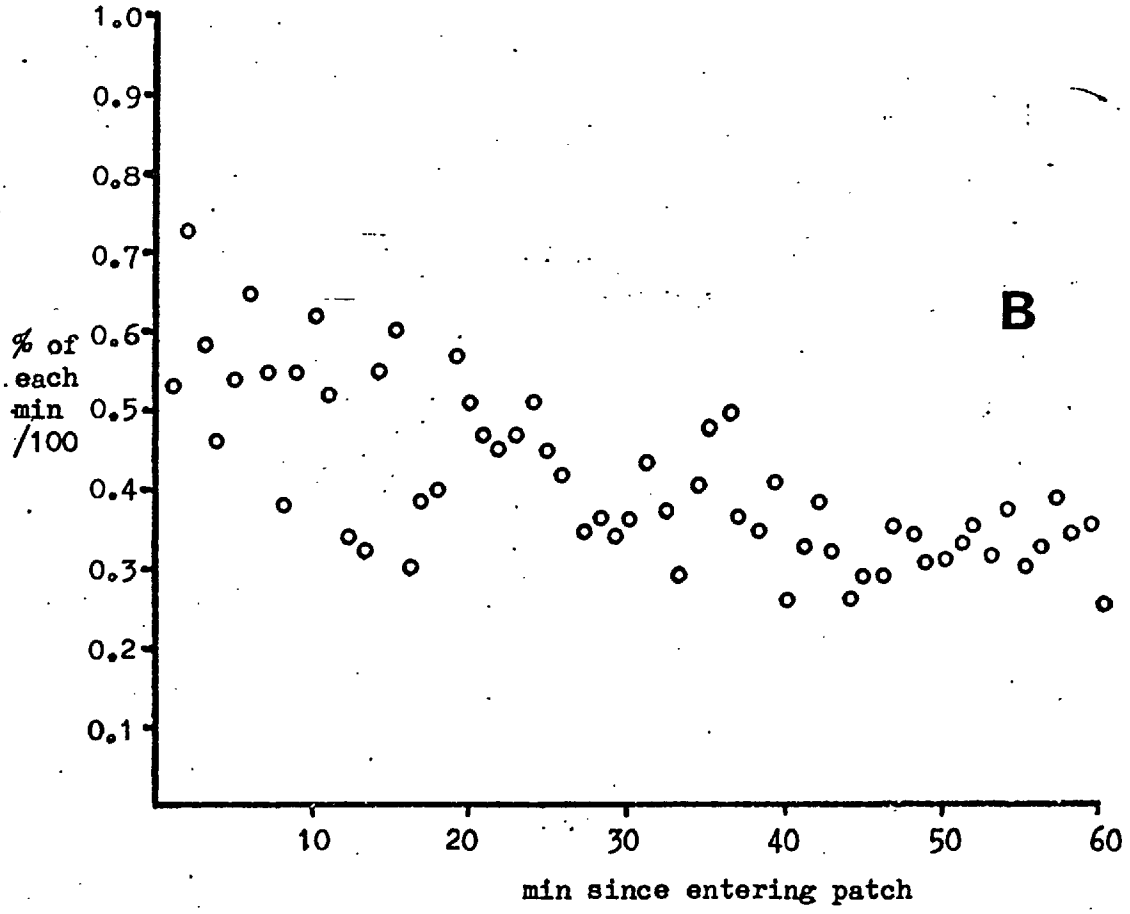


FIGURE 19
5 OVIPOSITIONS
OVER 15 MINUTES





and 19, this arises from a higher probability of being on the patch throughout the hour, and therefore represents a more complex situation than the evaluations of the first patch visit made above.

DISCUSSION

From this experiment we may conclude that (1) the additive hypothesis is not supported by the data, and (2) the threshold rate hypothesis is supported by some of the results, but not conclusively, and more complex processes are suggested. Thus, the effect of sequential ovipositions observed in *Nemeritis* approaches that predicted by the threshold rate hypothesis, but a more complex interaction of the timing and rate of ovipositions is suggested.

6.4 GENERAL DISCUSSION

The experimental findings of this chapter may be summarized as follows:

I. *Nemeritis* responds to chemical patch stimuli by exhibiting a complex orthokinetic response involving stopping, slowed walking and probing. Increased turning on the patch is also observed.

II. In response to the removal of the chemical patch stimulus, as would occur at the patch edge, *Nemeritis* exhibits a klinotactic turning response which keeps it in the patch. Leaving the patch is the consequence of the disappearance of this response.

III. Increasing the chemical patch stimulus increases the time spent on the patch and affects the duration of subsequent visits to the patch and the time between them.

IV. Oviposition on the patch increases the time spent before leaving and influences the tendency to return to that patch. Oviposition

apparently retards the decay of the patch edge response.

V. The effect of successive ovipositions on patch time is not additive, but probably depends on the rate and timing of their occurrence. It resembles somewhat the effect predicted by the threshold rate model.

The response of *Nemeritis* to the removal of the patch stimulus appears to be the major factor in the determination of patch time. Similar klinotactic responses to the removal of an odour deposited on a substrate have been observed in other insects. Blowflies (*Phormia regina*), for instance, follow streaks of sucrose solution spread on a substrate and make sharp, 180° turns when they come to the end of streaks where the stimulus disappears (Dethier, 1976). Larvae of the butterfly, *Danaus plexippus* L., when allowed to walk on a screen suspended directly over the surface of a leaf of their host plant (*Asclepias* sp.), make casting movements and turns when the leaf edge is crossed which lead the insect along the edge or back over the leaf (Dethier, 1947b). Tropotactic response to chemicals volatilizing off a trail on a surface have been shown in ants and moths (see Kennedy, 1977).

In parasitoids, turning at the edge of an airborne odour stimulus has been observed in walking *Nasonia vitripennis* in response to a plume of odour produced by infested host medium (rotting meat) (Edwards, 1954). This response, however, may have an anemotactic component, and therefore is not directly comparable with turning responses to chemicals deposited on a substrate. More convincing evidence of klinotactic responses is provided by observations on *Cardiochiles nigriceps* (Vinson and Lewis, 1965) which turns sharply when it reaches the end of a streak of host chemical made on a substrate. While no other distinct response to the edge of a chemical patch has been recorded for any parasitoid, except

for *Nemeritis* in the present study, it seems likely that the turning responses elicited in parasitoids by contact chemicals (see Table 1) may prove, upon closer examination, to be responses to the disappearance of the contact chemical at the patch edge.

The decay of the patch edge response in *Nemeritis* determines the time spent on the patch. This decay may result from two possible processes, (1) a decrement in the responsiveness to the patch stimulus or its removal, or (2) a response to a deterrent chemical, such as the trail odours found by Price (1972) in *Pleolopnus basizonus*, which is deposited as the wasp searches and which causes the wasp to leave the patch when a certain concentration has been reached. This latter hypothesis is difficult to test, as its predictions are so similar to those of a decrement in responsiveness. No clear marking behaviour, however, was observed by *Nemeritis* on patches. Furthermore, fairly complex mechanisms would have to be proposed to explain the observed effects of increasing stimulus intensity and oviposition using a deterrent chemical theory. Therefore, this hypothesis will be put aside of the moment in favour of the former one. The existence of a deterrent chemical will be considered in later chapters in the context of the detection of already visited patches.

The favoured hypothesis is that wasps leave a patch as a result of a waning of the responsiveness to the patch edge with time and/or repeated encounters. The primary question here is whether this waning is peripheral, that is, due to an adaptation of the chemoreceptors in the antennae, or whether it involves a central process of habituation.

In an interesting set of experiments on the probing response of *Nemeritis* to host secretion, Corbet (1973) concluded that a peripheral

mechanism was responsible for changes in responsiveness to the host secretion over time. She demonstrated that previous exposure of *Nemeritis* to host odour below the threshold concentration for probing affected the strength of a probing response elicited subsequently with higher stimulus concentrations. Exposure first to very low concentrations increased the tendency to probe later (as measured by the number of probing bursts over a period of time) while somewhat higher concentrations, still below the probing threshold, were inhibitory. These changes in responsiveness were interpreted as the result of sensory adaptation of antennal chemoreceptors. Specifically, Corbet proposed a complex process by which enzymatically inactivated stimulant molecules blocked a changing fraction of the receptor sites as the airborne concentration of molecules changed.

Another possible interpretation of Corbet's results would be that changes in responsiveness reflect central processes of habituation and sensitization. Such an interaction of incremental and decremental processes in the central nervous system has been demonstrated in a number of experimental systems (Hinde, 1970). This latter interpretation is simpler, but from the available data it is impossible to support one interpretation over the other.

The edge response is elicited by a lower chemical concentration than the probing response. Several lines of evidence point to its decrement as being the result of habituation rather than peripheral adaptation. Raising the patch stimulus intensity both decreases the rate of encounter with the patch edge (due to probing, see Figure 5b) and steepens the chemical gradient at the patch edge. The effect of these changes is to increase patch time with increased stimulus intensity. This effect may be likened to a decrease in the rate of decay of a response with (1) increasing stimulus strength and (2) decreasing present-

ation rate, a common property of habituation. Applying Corbet's hypothesis to this situation, we might conclude that higher stimulus concentrations would lead to more rapid blocking or adaptation of chemoreceptors, resulting in less time being spent on higher density patches - the opposite of what is observed.

Habituation is supported more convincingly by observations, to be presented later in this study, which indicate that wasps walking off one patch onto another patch of lower or higher stimulus intensity regain their "entire responsiveness" to the stimulus on this new patch and spend as much time there as if it were the first patch visited. This suggests that a waning of responsiveness to a patch stimulus is specific to the patch or stimulus intensity. With sensory adaptation we would expect this waning to be non-specific and decrease responsiveness to any stimulus intensity on any patch, and therefore these results support a habituation hypothesis.

The patch specific behaviour observed in *Nemeritis* has been seen to be in some ways similar to that predicted by the threshold clock model discussed in Chapter 4. One major difference is the effect of the patch stimulus, which elicits a fixed period of search time, S, at all patch densities in the threshold rate model, but clearly has a density dependent effect in *Nemeritis*. The effect of patch experience on further visits to the patch, which has been seen to be rather complex for *Nemeritis* is also not considered by the threshold rate model.

An interesting model, similar in some ways to the threshold rate model, is suggested by the experiments in this chapter. It should be stressed that the structure of this model, although incorporating behavioural elements, is designed for convenient representation and not as an accurate description of neural processes.

Consider patch time as being determined by the interaction of two incremental processes, the response to patch stimuli and the response to oviposition stimuli, and one decremental process, the habituation of the patch edge response. The intensity of the patch stimulus, perceived as the wasp enters the patch, sets some hypothetical level of responsiveness, r. This responsiveness subsequently decays as the insect habituates, until some level, r*, is achieved at which the insect no longer responds to the patch edge and leaves the patch. For simplicity's sake, this decay will be considered linear, although the decay of responsiveness due to habituation often takes an exponential form. A linear function may, in fact, be a satisfactory description of an exponential trend over a short period relevant to the decay of the edge response.

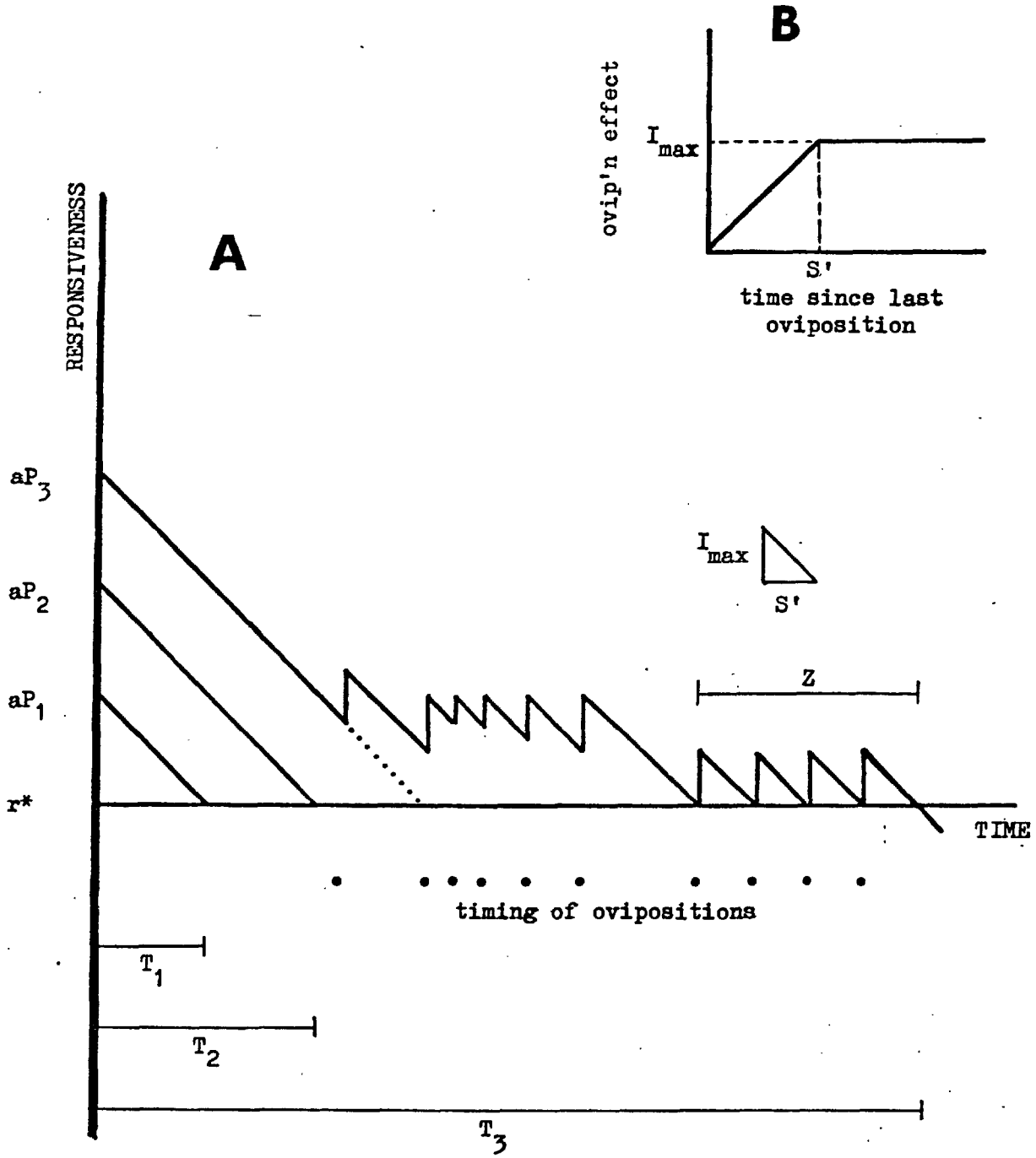
An oviposition on the patch affects the decay of responsiveness by adding an increment I to the value of r, thereby shifting the decay curve I units upward and increasing patch time. Incorporating varying responses to successive ovipositions, in the manner postulated by the threshold rate hypothesis, make I a variable which ranges in magnitude between zero and some value, I_{max}, as the time since the last oviposition ranges between zero and a value, S'. This latter value represents the time period over which an oviposition increment of I_{max} would decay to the same level of responsiveness as before oviposition. This relationship may be seen more clearly in Figure 20 a, b.

The patch time model just described is illustrated graphically in Figure 20a and mathematically by the equation:

$$r = (aP + \sum_{i=1}^{n} I_i) - bt \qquad (1)$$

where r is the level of responsiveness, b the slope of the decay of responsiveness and t the time since entering the patch. The constant,

Figure 20. Graphical representation of patch-time model incorporating the effect of patch stimuli (aP) and oviposition stimuli (I). The patch times T_1, T_2 and T_3 are shown for patches of initial density P_1, P_2 and P_3, respectively. See text for explanation.


B
ovip'n effect
I_{max}
S'
time since last oviposition
A
RESPONSIVENESS
aP_3
aP_2
aP_1
r*
I_{max}
S'
Z
TIME
timing of ovipositions
T_1
T_2
T_3

a, relates the patch stimulus intensity, P, (a function of the number of hosts) to some initial level of responsiveness. The summation term represents the effect of ovipositions while on the patch, where I_i, the effect of the i^{th} oviposition, is dependent on the time since the last oviposition, I_{i-1}. When this time equals S', I_i equals I_{max}, as explained above and in Figure 20b. As can be seen over region Z of Figure 20a, S' becomes similar to S, the giving up time of the threshold clock model, when $r = r^*$, in that the forager stays on the patch as long as the oviposition rate remains above $1/S'$. It should be remembered, though, that S' describes the time of decay of responsiveness and not a fixed increment of time on the patch. Furthermore, the effect of oviposition here is affected only by the timing of an oviposition relative to the immediately previous one. In a more realistic and complex model it might be affected as well by the timing of all ovipositions on the patch and the total time since entering the patch.

From Equation 1, the time spent on a patch before leaving, T, may be easily computed by dividing the total increment of responsiveness on that patch by the rate of decay of responsiveness. Thus,

$$T = (aP + \sum_{i=1}^{n} I_i - r^*)/b \qquad (2)$$

To learn how T varies with host density in a patch (the aggregative response) a computer simulation was devised with the help of Dr. H. Comins. The complete program is presented in its entirety in Appendix A. A random predation model was used to compute the total time to the next oviposition (including handling time for the previous one). During this time the responsiveness decayed at a fixed rate. For simplicity, the initial responsiveness was set equal to the number of hosts in the patch. When an oviposition occurred, an increment was added

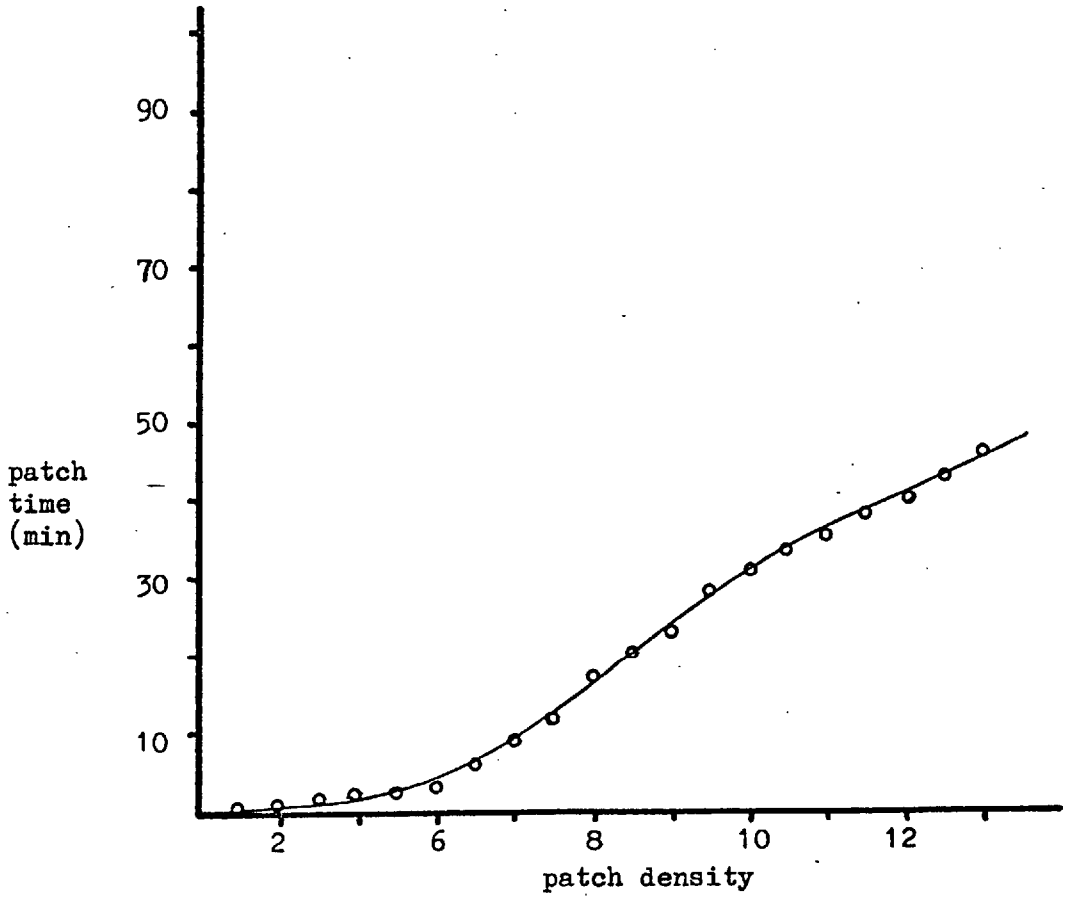
to the responsiveness, the value of which was determined (as described above) by the time since the last oviposition. When responsiveness fell below zero, the patch was left.

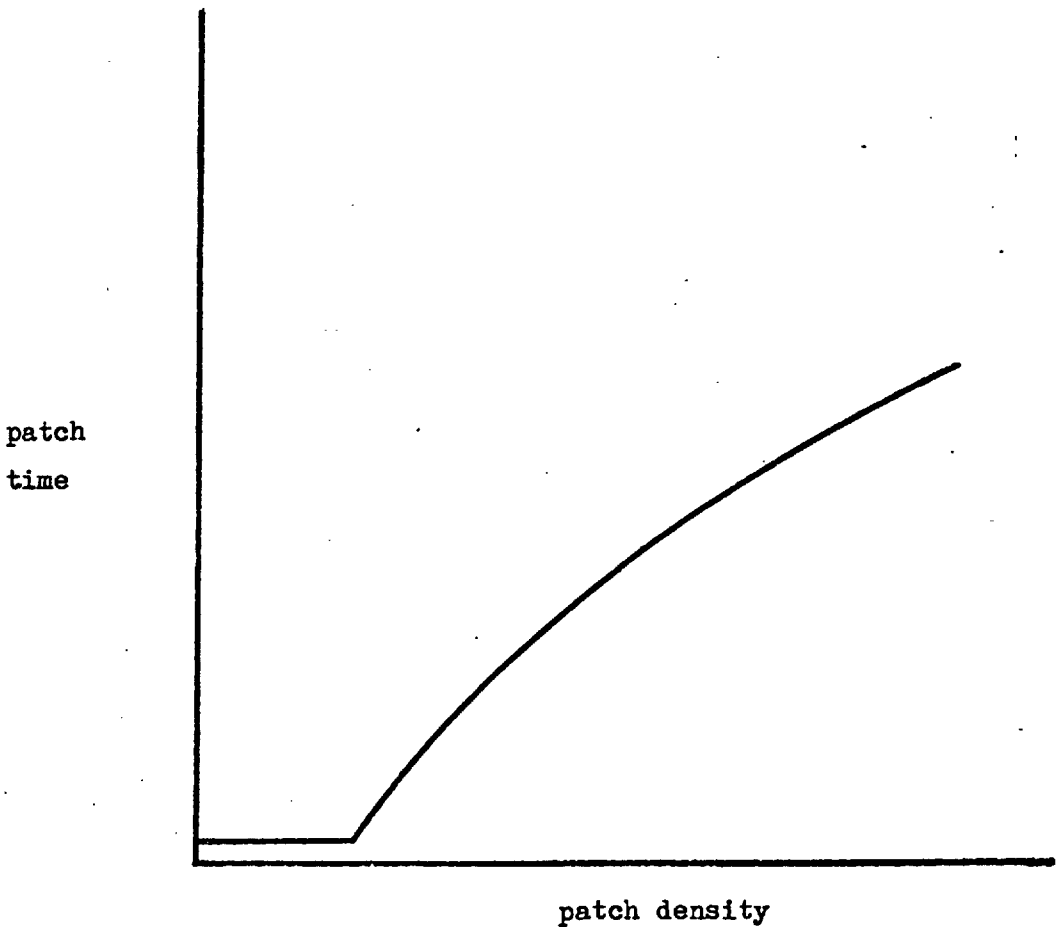
Figure 21a shows an aggregative response produced by this simulation. It resembles closely the response predicted by the threshold rate model of Hassell and May (1974), which is shown in Figure 21b. Both curves possess an initial lag period during which patches are left before any prey are found, but in the former, the subsequent acceleration of the function is smoothed by the increasing effect of patch stimulus with increasing host density. Both curves are sigmoid in form, although in the threshold rate model the deceleration at high densities is lost when handling time is greater than zero.

In Figure 22, the magnitude of two parameters of the present model are varied; the rate of decay of responsiveness (a) and the effect of the oviposition stimulus (b). Increasing the magnitude of the initial response to the patch stimulus has a similar effect on the model as decreasing the rate of stimulus decay.

Although the aggregative response curves of the threshold rate model and the present model can be similar, there are important differences in the mechanisms involved. In the former model, for instance, the giving up time (time between the last prey capture and leaving the patch) is constant for all densities. In the present model it is variable, as shown in Figure 23. If one considers a more long term measure of oviposition rate, such as the number of ovipositions in the last several minutes on the patch, the predictions of the two models appear more similar. The initial and terminal oviposition rates over a period of 5 and 10 minutes for the curve in Figure 21a are shown in Figure 24. While

Figure 21. Graphs of patch-time versus patch density predicted by (A) computer simulation of the model presented in the text (Chapter 4), and (B) the patch-time model of Hassell and May (1974). Both models would lead to an aggregative effect on the population level.


90
70
50
30
10
patch
time
(min)
2
6
8
10
12
patch density


patch
time
patch density

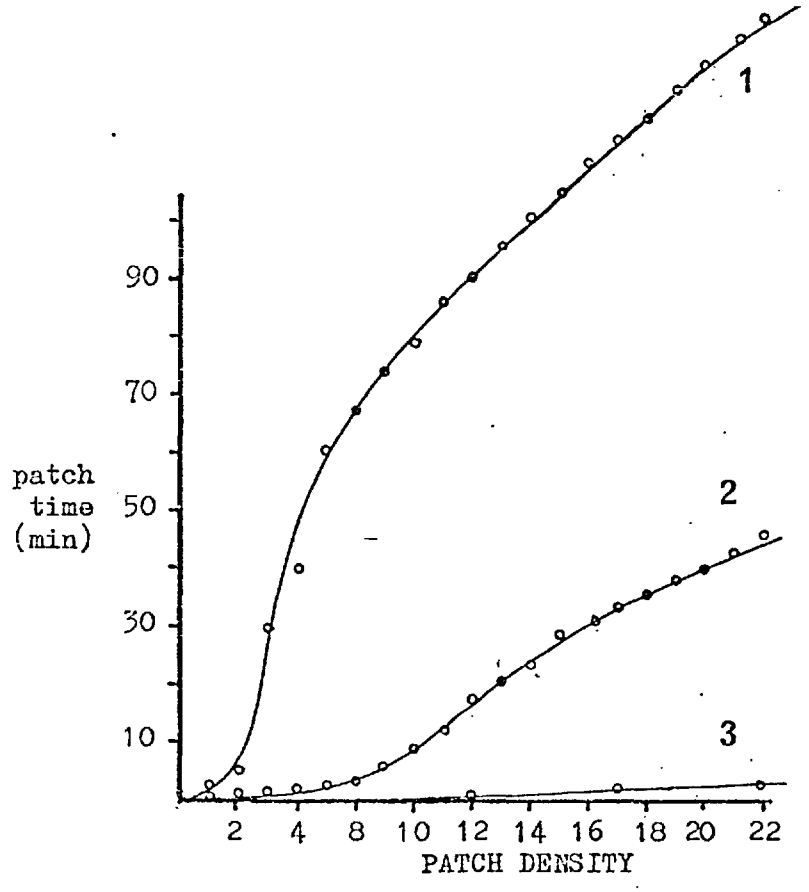
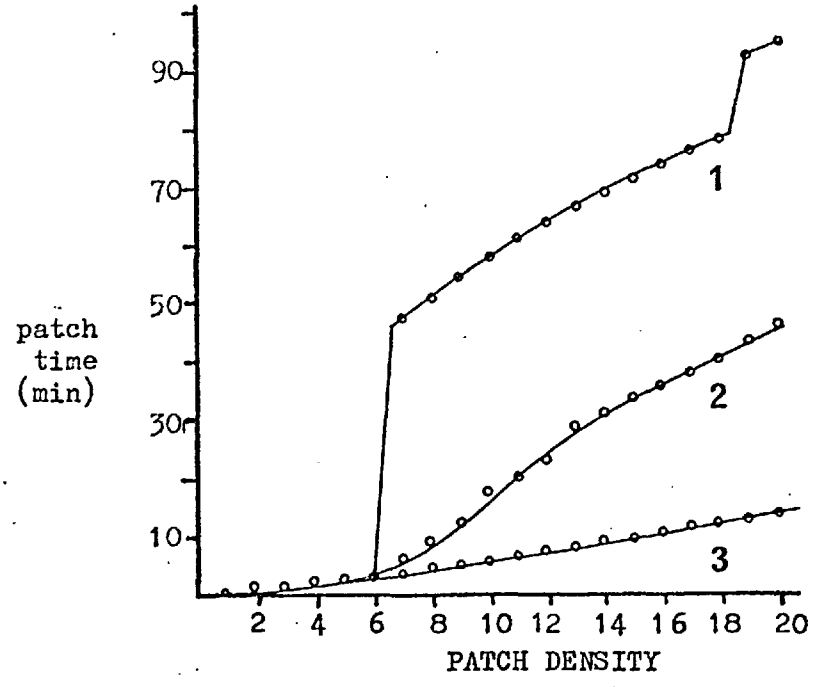


Figure 22. A. Patch-time simulation model with varying decay rate (b). Curve 1, b=0.4 curve 2, b=2.0, curve 3, b=10.0



B. Simulation model with varying oviposition effect (I). Curve 1, I=25, curve 2, I=5, curve 3, I=1

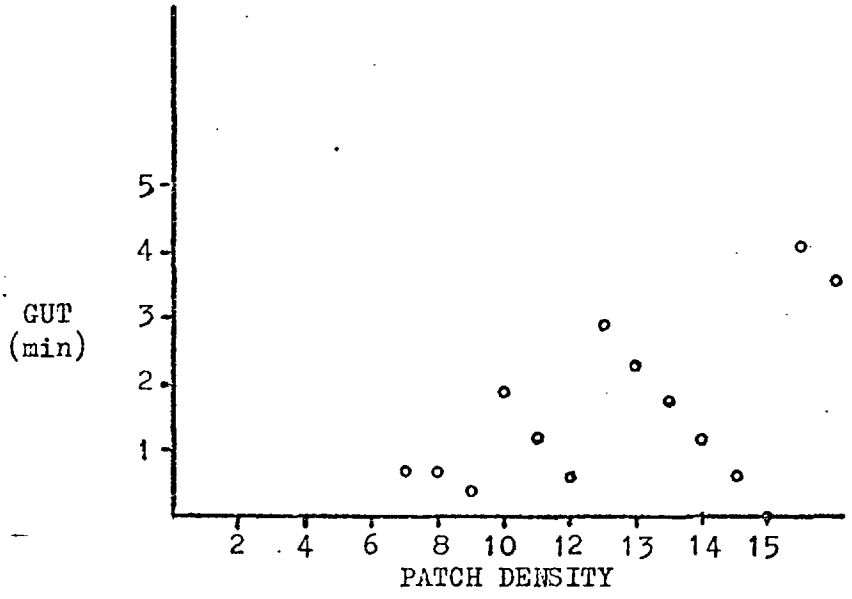


Figure 23. Changes in giving up time (GUT), the time between the last oviposition and leaving the patch, with changes in patch density

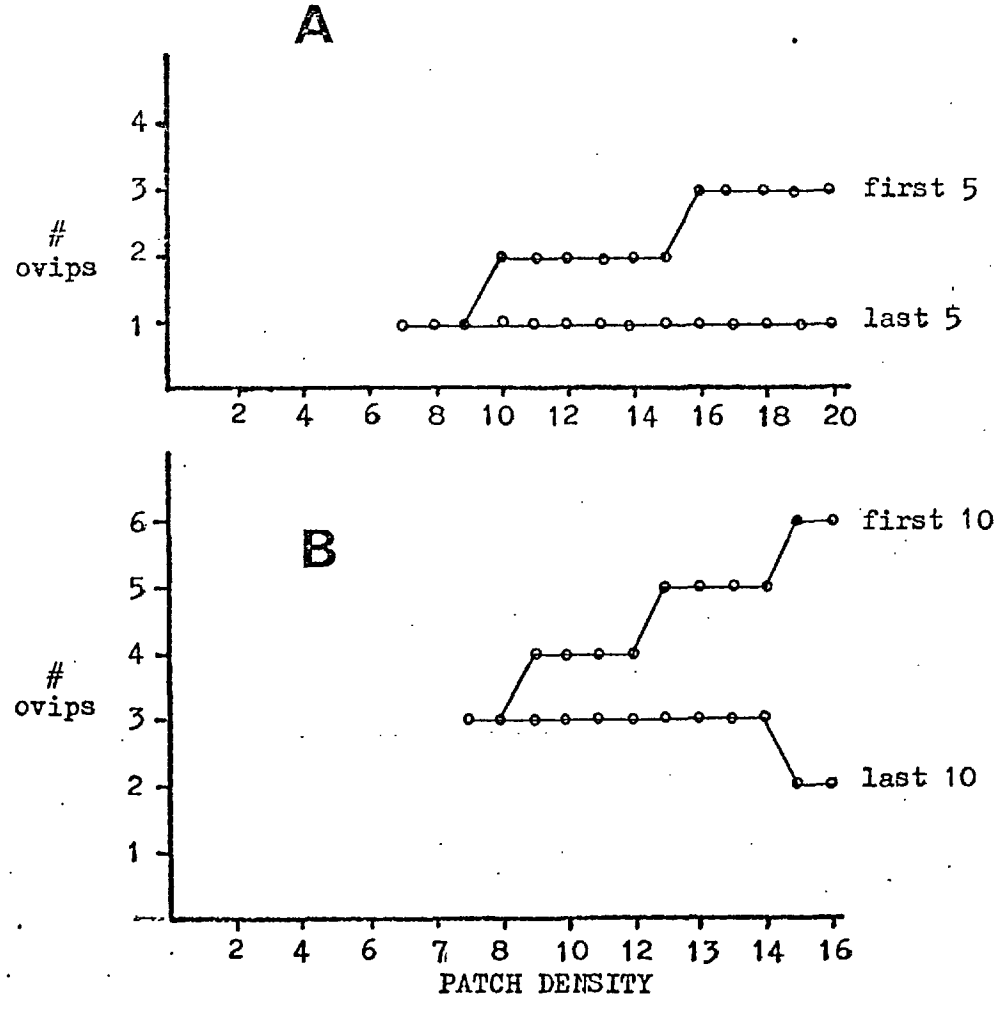


Figure 24. Changes in the number of ovipositions in the first and last 5 (A) and 10 (B) minutes on the patch as patch density is increased.

the initial oviposition rate increases with host density, patches of all densities are left at about the same rate of oviposition, which is what would be predicted by the threshold rate model. In the next chapter, further comparisons of these two models will be made in relation to the actual aggregative response of *Nemeritis*.

The appeal of the model presented above is that it incorporates observed responses to chemical patch stimuli, which are probably general in parasitoids, and relates patch time, albeit simplistically, to behavioural processes in the central nervous system of the forager. It is a minimal model, which includes all factors which are known to influence patch time in *Nemeritis*, and in this sense it is an improvement over the fixed rate models for this system, and probably for all parasitoid systems. Nonetheless, the model has a number of disadvantages. Firstly, it does not take into consideration the effect of experience on subsequent patch visits. Secondly, it is not a deterministic model, and can only be examined by simulation. Finally, the large number of parameters, for which it would be difficult to obtain realistic values, complicate the application of this model to experimental systems. Further studies of parasitoid behaviour will, hopefully, provide material for testing and improving the representation of the patch time processes in this model.

CHAPTER 7

THE DISTRIBUTIONAL RESPONSE OF *NEMERITIS* TO PATCHES OF DIFFERENT PREY DENSITY

7.1 INTRODUCTION

The experiments of the previous chapter demonstrated that various factors are involved in determining the time spent on a patch (e.g., chemical patch stimuli, oviposition rate). To establish this, particular factors were studied in isolation, while holding all other factors constant. In this chapter, the effect of various patch specific stimuli will be considered together, as would occur in nature. The purpose of this approach is to (1) learn if certain factors are clearly more important than others in determining patch time and to (2) examine how these patch specific behaviours relate to the ecological concept of aggregation.

Aggregation is an inappropriate term for describing the tendency to be attracted to and/or stay in a particular place, particularly if one is dealing with individual foragers which, of course, cannot aggregate. In the present context, aggregation by an individual forager is taken to mean the differential allocation of foraging time between different patches. It is therefore used in an ecological sense as a form of distribution response by a forager to patches of different prey density. From the findings in the last chapter, we anticipate that changes in patch stimulus intensity and oviposition rate will influence aggregation. Another factor, yet unconsidered, could be of major importance in determining patch time. This is the response to the contact, with the ovipositor, of already parasitised hosts, and it will be briefly discussed now.

Rogers (1972b) has demonstrated that the probability that *Nemeritis*

will reject an already parasitised host rises with the time since the previous oviposition in the host from zero to 0.80 (see Figure 29). This change of probability is probably attributable to a chemical change in the host haemolymph, detected by the ovipositor. The method employed by Rogers, however, does not completely rule out the possibility that *Nemeritis* learns to recognize parasitized hosts, thereby improving with experience. The role of learning in the avoidance of superparasitism has been demonstrated in *Pseudocoila bochei* by van Lenteren and Bakker (1975). *P. bochei* will accept the first host it is offered, even if parasitised, and subsequently rejects hosts which have had more eggs laid in them than this first one. Presentation of a host with less parasitoid eggs (or none) lowers the rejection criterion to this new level.

The complexity of this process of avoidance complicates the testing of its effects on patch time. First of all, one confronts the difficulty of deciding whether a host has been rejected at all (remember that in the previous experiment, cocking was used as the indicator of host contact). More importantly, though, the evaluation of host contact responses poses problems. If a wasp has at best only an 80% probability of rejecting a particular parasitized host, we might anticipate that ovipositions, which occur 20% of the time in such circumstances, would have a different effect on patch time than ovipositions in unparasitized hosts, which occur 100% of the time. Unfortunately, we have no way to distinguish oviposition in parasitised and unparasitised hosts, as the only criterion we can measure is acceptance or rejection. In the previous chapter, only parasitism of previously unparasitised hosts was considered, and this problem did not arise.

Assuming, for simplicity's sake, that oviposition under any cicumstances increases the tendency to stay on a patch, what value is

to be placed on rejection? Presumably, it is either zero or negative, that is, that it has no effect on the tendency to leave a patch (responsiveness to the patch edge) or that it increases the tendency to leave a patch (lowers responsiveness). The predictions of these two hypotheses may, under experimental analysis, give very similar results. Rogers (1970), for instance, found that *Nemeritis* spends considerably less time on a patch of all parasitised hosts than all unparasitised hosts. Is this simply because the decay of responsiveness on the former patch was not arrested by as many ovipositions, or because it was accelerated by the effect of encountering parasitised hosts? The effect of encountering parasitised hosts on patch time will be taken into consideration in the analysis of the experiments to follow.

In the first experiment on the distribution of foraging time by *Nemeritis* on different density patches, one potentially important factor will be omitted. This is the effect of previous patch experience on future patch time allocation. As this is an important effect in many hypothetical foraging models, it is interesting to see, as a sort of null case, to what extent *Nemeritis* aggregates in the absence of previous patch experience, and compare this later to an experiment which includes experience.

7.2 THE DISTRIBUTION OF FORAGING TIME BETWEEN PATCHES BY *NEMERITIS*

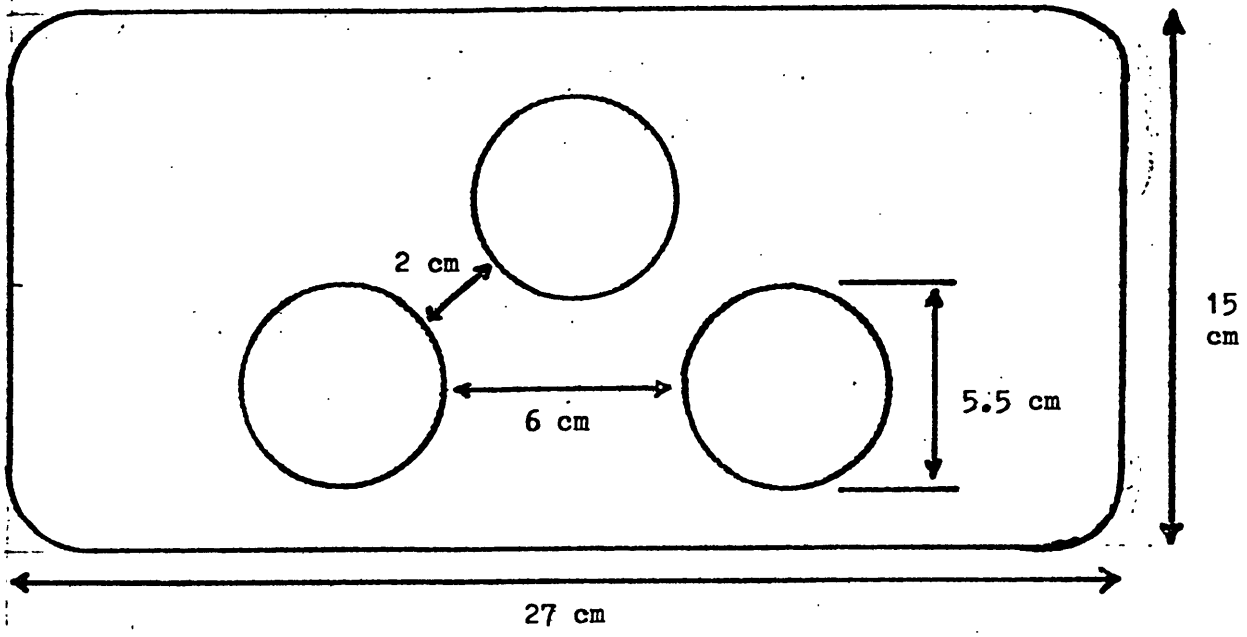
EXPERIMENT 6: THE DISTRIBUTIONAL RESPONSE OF *NEMERITIS* IN THE ABSENCE OF PREVIOUS PATCH EXPERIENCE

MATERIALS AND METHODS

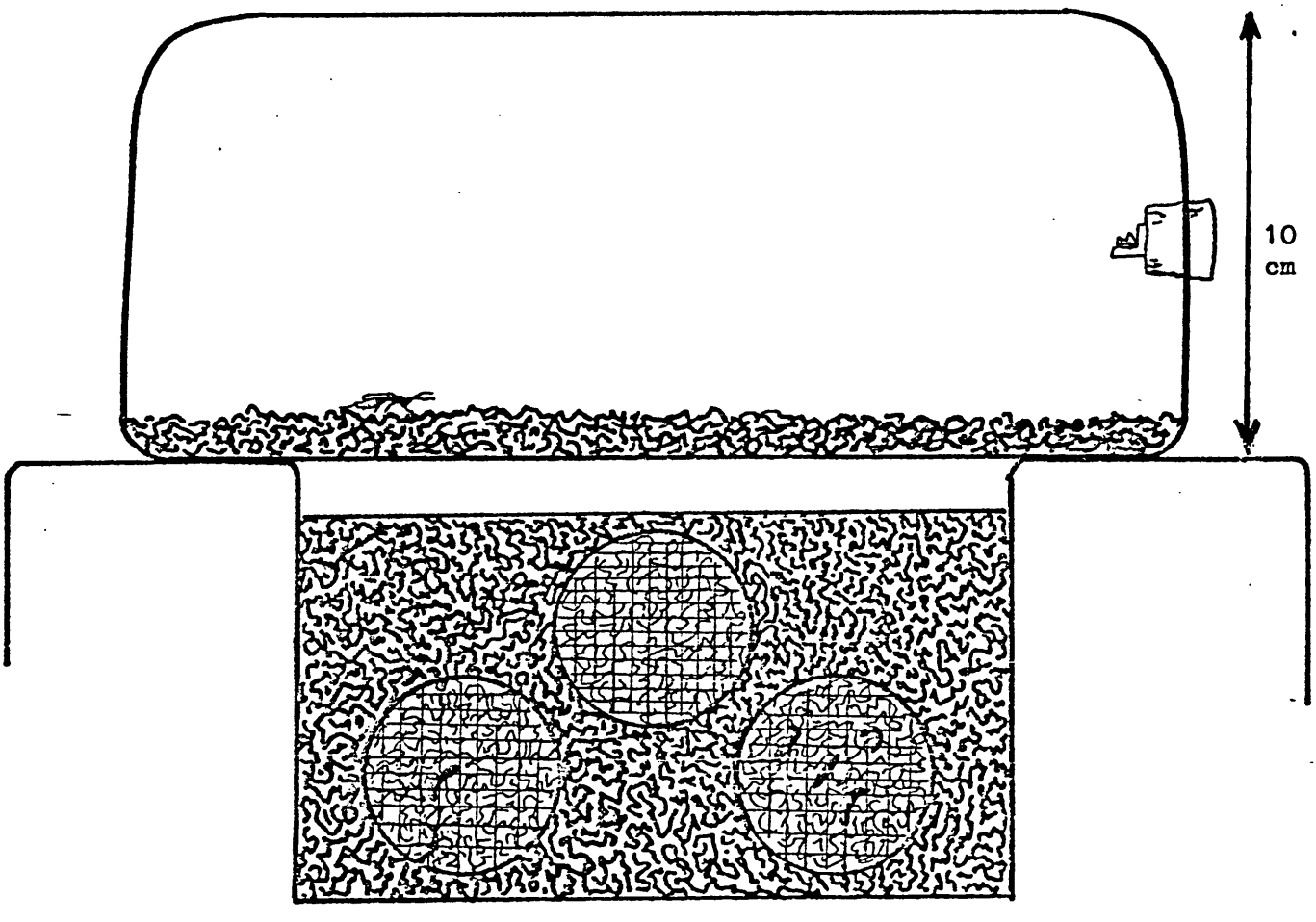
The experimental chamber used is illustrated in Figure 25. It consisted of three patches set flush with a substrate of host medium. The central patch was always empty, consisting of a 5.5 cm diameter dish

Figure 25. Experimental set-up for Experiment 6 and 7. A. Distribution of the three patches on the chamber floor. The right hand patch always had 4 hosts, the center 0 hosts, and the right 1, 4, 8 or 16 hosts. B. A side view of the chamber, showing the mirror beneath for the observation of host contacts.

A



B



with a terylene net stretched over it, on top of which was scattered 0.3 g of host medium. One of the other two patches always contained 4 *Plodia* larvae between the dish and net, while the other contained either 1, 4, 8 or 16 larvae, depending upon the replicate. These two patches were made as follows: the appropriate number of *Plodia* larvae were contained for 15 hours between two terylene screens (as in Figure 3a) with 0.3 grams of middlings. Just before the experiment, the top screen was taken off and the larvae removed from the contaminated medium and placed under the lower screen on top of the plastic dish. This produced a patch with contaminated medium above the screen and hosts beneath it and served to confine the larvae to the patch area, in which they moved more or less randomly.

The purpose of the patch with a constant density of 4 larvae will become apparent in Experiment 7.

For the present experiment wasps, standardized and transferred in the manner described in Experiment 2, had to find the patch with variable density (1, 4, 8 or 16) first, within 12 minutes. If they did not, they were removed from the chamber and a new wasp was added. The original criterion for having left the patch was the entering of one of the other two patches. Since the direction in which the wasp left the patch was random and greatly influenced the probability of finding another patch, the criterion used previously of 14 seconds walking or flying off the patch was adopted.

The floor of the experimental chamber below the medium was clear plastic, and a mirror placed below this permitted observation of the wasp and larvae on the patch from beneath (Figure 25). By such observation, the contact of a larva with the ovipositor could be established with

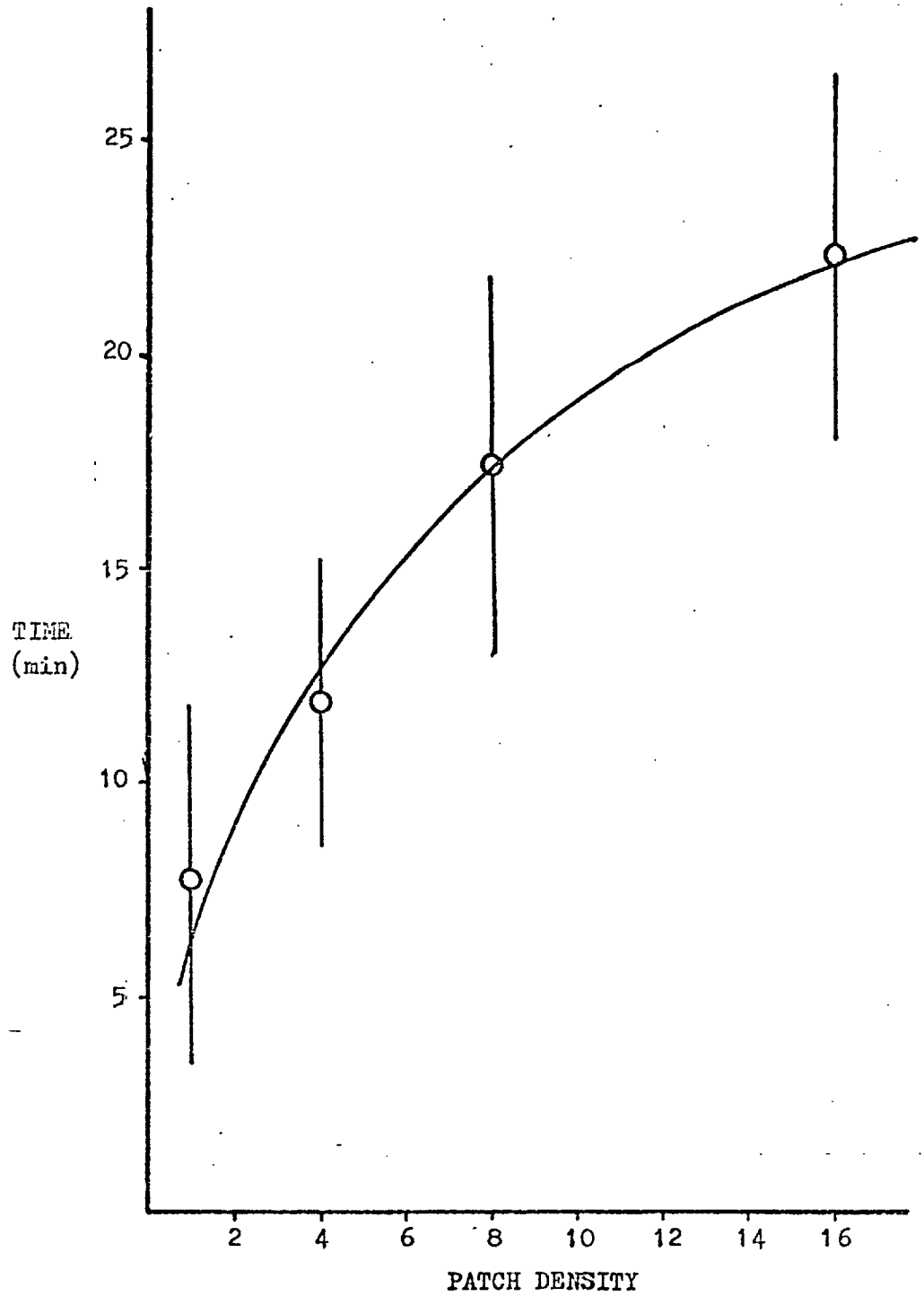
certainty and, therefore, both host acceptance (contact with subsequent cocking) and rejection (contact without subsequent cocking) could be recorded. The activities recorded on an 8-channel Rustrak recorder were as follows: presence on a particular patch, probing, contacting a host with the ovipositor, cocking, resting, flying and presence on the side of the chamber. All observations were made through a red plastic screen which, as before, was necessary so as not to disturb the wasp. Recording commenced when the wasp walked on to the first patch (1, 4, 8 or 16 hosts) and continued until it abandoned the second patch (4 hosts) for 14 sec. Twelve replicates were run for densities 1, 4 and 8, and 16 were run for density 12.

RESULTS AND DISCUSSION

The average duration of patch visits at different densities is presented in Figure 26. These durations were quite variable, but a clear tendency to spend more time on higher density patches appears, which may be slightly decelerating at higher densities. We may think of this curve as the distributional response of *Nemeritis* if the parasitoid was in no way affected by previous patch experience and responded to each patch found as if it were the first patch visited. Patch time here is influenced only by the responses to stimuli from the patch the wasp is on. At a population level, such a response would clearly lead to aggregation.

The form of the response obtained is similar to that predicted by both the threshold rate model and the model of the previous chapter at intermediate densities. That this should occur at low densities in this experiment is of little concern here, as the rate of oviposition for these low densities was often quite high, owing (1) to the ease with which hosts could be contacted through the screen and (2) the fact that hosts were often parasitised several times before rejection built up. We

Figure 26. The distributional response of Nemeritis in the absence of previous experience. Average time spent on a patch (time before walking or flying off patch for 14 sec) with 95% confidence intervals at different patch densities. Curve fitted by eye.


25
20
15
10
5
TIME
(min)
2
4
6
8
10
12
14
16
PATCH DENSITY

would expect to find the low density response predicted in the models, where patches are left before any hosts are found, in *Nemeritis* searching in natural patches. In piles of grain or fallen fruit, for instance, hosts are more concealed and may be able to move out of the reach of the ovipositor after one oviposition.

The variability observed in the time spent on a patch has two sources. Firstly, there is the innate variability of the insect; that is, the variability which causes two insects to respond differently to the same stimulus. But even if all wasps had identical responsiveness and behaved according to the patch-time models mentioned above, considerable variability would arise from differences in the experience of each wasp on the patch. Patches of the same density may, for instance, vary in the intensity of the chemical stimulus. More importantly, perhaps, the number and timing of successive ovipositions and rejections will vary between replicates because the wasps contact hosts effectively at random. Fitting the behaviour of a particular forager to a patch time model is complicated by this problem of distinguishing variability predicted by the model from innate variability of the forager.

While the form of the distributional response obtained resembles that predicted by the threshold rate model, factors other than oviposition rate may be important. As we have already seen, the increase of patch stimulus intensity with host density could, itself, lead to aggregation, even in the absence of oviposition. The importance of oviposition rate in patch time determination deserves closer scrutiny.

In Figure 27, initial and terminal oviposition rates for different patch densities are given. These were obtained by counting the number of ovipositions which occurred in the first and last 3 minutes on the patch.

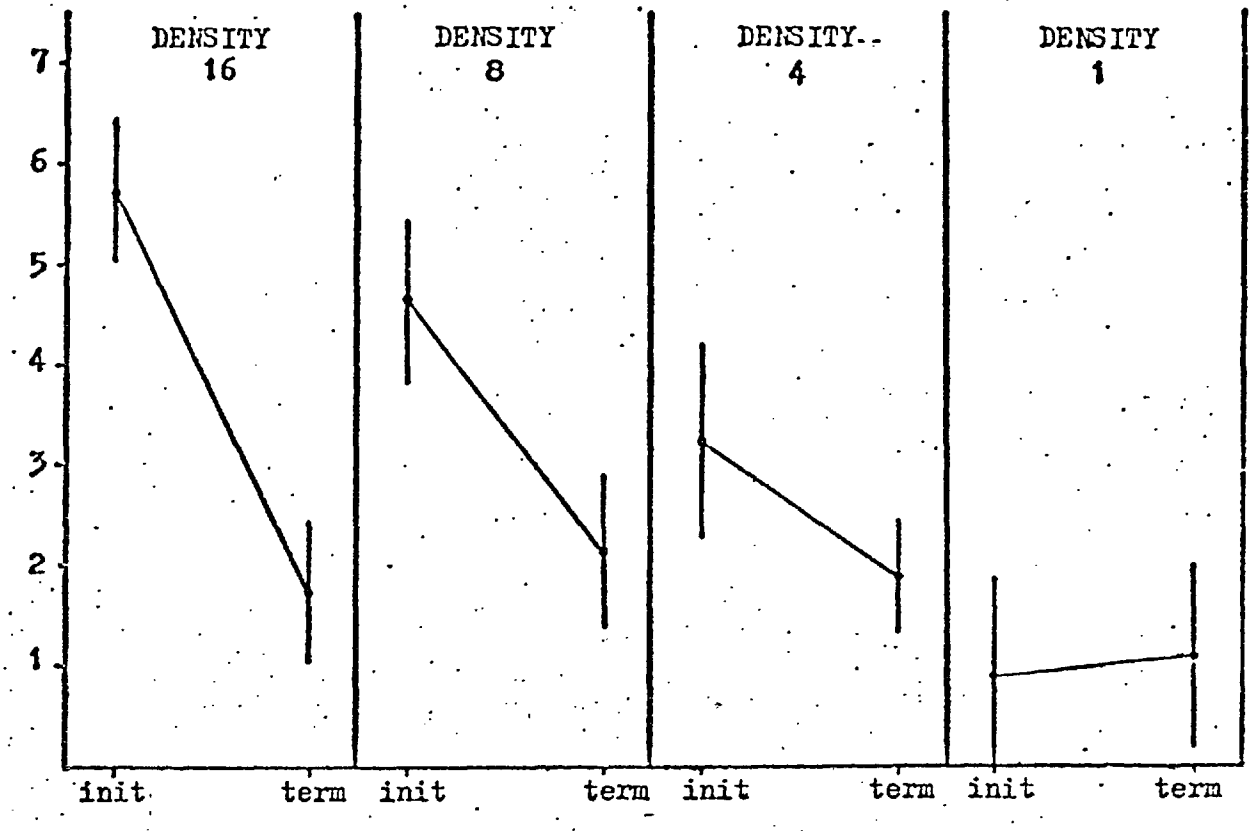


Figure 27. Initial and terminal oviposition rates at different patch densities. Ordinate = ave. no. ovipositions (± 95% C.I.) over three minute period.

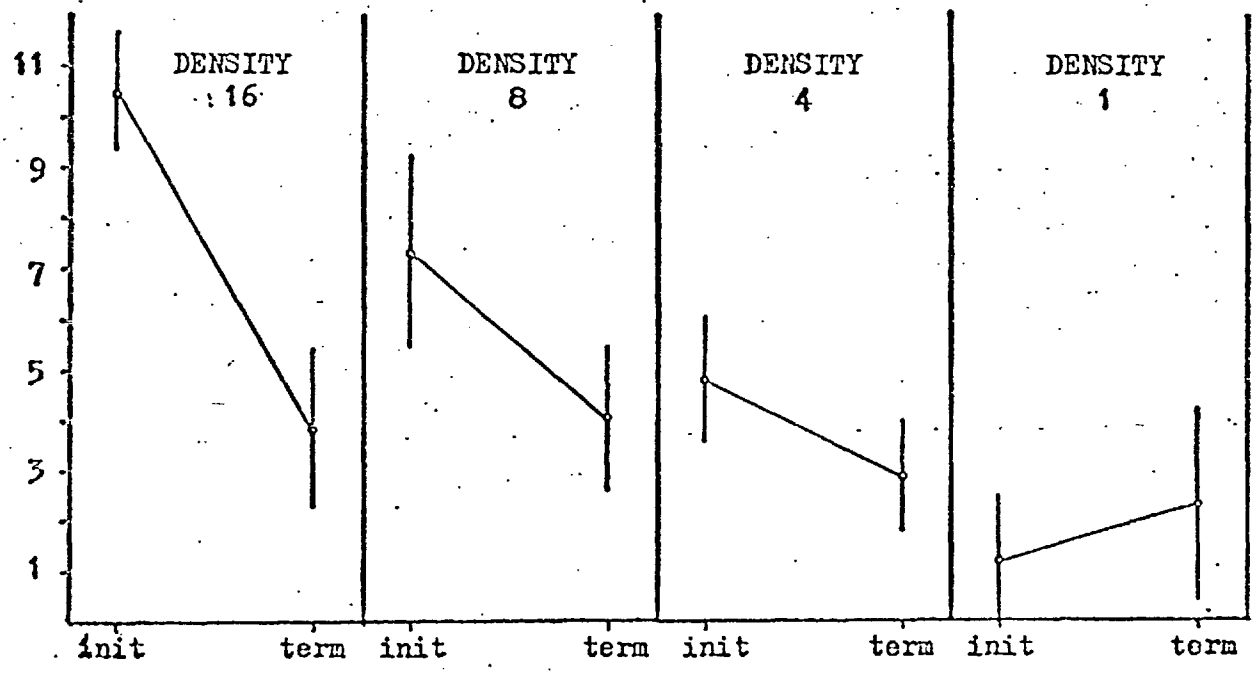


Figure 28. Initial and terminal oviposition rates at different patch densities. Ordinate = ave. no. ovipositions (± 95% C.I.) over three minute period <u>searching</u> on patch (i.e., not including T_h and $T_{resting}$)

At densities 1 and 4, some wasps left the patch before 3 minutes had elapsed and these replicates were not included in the calculation. Rejection of already parasitised hosts was ignored.

As one would anticipate, the initial oviposition rate increased markedly with patch density. With the possible exception of density 1, the terminal rates of oviposition are nearly identical. These results are just those predicted by the threshold rate model (and by the Marginal Value Theorem for a particular habitat), namely, that the profitability (rate of prey capture) will be lowered to a particular level, whereupon the patch will be abandoned, leaving all patches, eventually, at the same profitability. The results presented in Figure 27 are also compatible with the model presented in the previous chapter.

Before proceeding further, it should be observed that the threshold rate models apply to searching time on the patch, while the data presented in Figure 27 describes total time, that is, a total period of three minutes, including both searching and handling time. If the number of ovipositions over three minutes searching on the patch are calculated (i.e., total time - time spent handling parasitised and unparasitised hosts - time spent moving off the patch for less than 14 sec), similar results to those in Figure 27 are obtained, as shown in Figure 28. By contrast, the model described in the previous chapter applies to total time.

Although a threshold rate mechanism is compatible with the results obtained, a model based on instantaneous capture rates (the time since the last oviposition or the average rate for the last few ovipositions) may not be valid for *Nemeritis* foraging. Implicit in models based on instantaneous capture rates is the assumption that the terminal rate on

a patch is the lowest rate of capture which has occurred since the patch was entered. Similarly, if a giving-up-time criterion is used this time is assumed to be longer than any previous intercapture interval on the patch. Furthermore, these mechanisms assume that, immediately upon achieving this terminal rate, the patch will be abandoned. Thus, this terminal rate will not be maintained on the patch for any period of time.

These assumptions do not hold for the patch specific behaviour of *Nemeritis*, and are probably not valid, as well, for the behaviour of other foragers whose patch specific behaviour has been so modelled. To illustrate this for the present system, the time between each successive oviposition for each replicate in this experiment is presented in Appendix B. The abscissa of these graphs presents the oviposition number (first, second, third, etc.), while the ordinate value represents the total time on the patch. The slope of the line suggested by the points is the oviposition rate and the vertical distance between points represents the inter-oviposition interval, except for the last two points, where it represents the giving up time.

As can be seen from many replicates, the giving up time is often shorter than previous inter-oviposition intervals. Why, then, did not the wasp leave the patch at these earlier intervals? Even the rate of the last several ovipositions is often greater than previous rates, and the terminal rate, in many cases, appears to continue for several minutes before the patch is left. Clearly, short-term changes in capture rate do not, of themselves, determine patch leaving in *Nemeritis*.

If changes in oviposition rate do influence patch time, it would appear as though relatively long term trends must be involved. In other words, whether a wasp left a patch at time $\underline{t}$ would depend not upon the

time since the last oviposition, or several ovipositions, but upon the number and timing of many, if not all, previous ovipositions on the patch. This might occur, for example, if every oviposition affected some initial tendency to stay on the patch. Such a hypothesis is implicit in the mechanism of the model developed in the last chapter. Here, each oviposition increases an initial level of responsiveness, affecting patch time to a greater or lesser extent depending on the timing of previous ovipositions and, of course, on their number, which determines how far the responsiveness is, at the moment of oviposition, from the threshold level. With this model, there is no oviposition rate, per se, below which the patch will be abandoned. There is, however, a rate (1/S'), above which the forager will stay on the patch and below which the forager will eventually leave. It is at this critical rate that responsiveness begins to decay faster than it is increased by oviposition effects. As shown in Figure 24, this model predicts similar terminal capture rates when, like the threshold rate model, the rate of oviposition decreases regularly with time and exploitation. Unlike the threshold rate model, however, the model in Chapter 6 does not require that successive interoviposition intervals be always of increasing duration.

The rate of encounter of parasitised hosts is another factor which changes markedly during the patch visit and may affect patch time. As mentioned previously, we can measure this rate only in terms of acceptance and rejection, which does not consider the effect of oviposition in parasitised hosts and could, therefore, lead to inaccurate interpretations. As more time is spent on a patch, more parasitised hosts are encountered. Similarly, as patch density increases, the rate of rejection is observed to increase. Table 9 shows the average number of rejections per patch visit for the different densities. It is clear

TABLE 9. A comparison of the occurrence of host rejection on patches of different density.

	PATCH DENSITY			
	1	4	8	16
AVERAGE NUMBER OF HOST REJECTIONS PER PATCH VISIT (± 95% conf. lim.)	0.00 ± 0.00	1.08 ± 0.96	4.85 ± 2.57	7.67 ± 3.53
TERMINAL HOST REJECTION RATE ON PATCH (average number in last 3 min ± 95% conf. lim.)		0.54 ± 0.47	1.58 ± 0.84	2.56 ± 0.72
$\frac{\text{HOST REJECTIONS}}{\text{HOST REJECTIONS + OVIPOSITIONS}}$ DURING LAST 3 MIN ON PATCH (average ± 95% conf. lim.)		0.22 ± 0.20	0.36 ± 0.16	0.61 ± 0.14

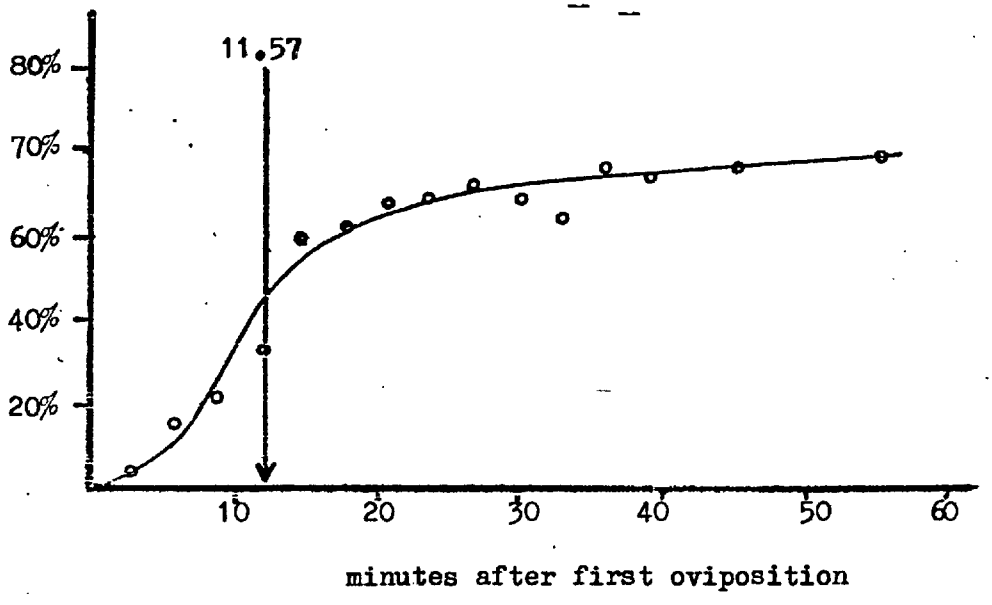
from this data that host rejection does not influence patch leaving at a density of 1, where the patch is left before any rejections occur. This is because the duration of the period necessary for the development of the rejection response to a parasitised host is greater than the average time spent on the patch. This period, the time between entering a patch and rejecting a host for the first time, has been calculated for host densities 4, 8 and 16, and is shown in Table 10. Despite changes in host density, the time till the first rejection of a parasitised host on a patch is nearly identical for all treatments. Interestingly, the average of all values obtained, when compared to Roger's (1972b) graph of changing rejection probabilities with time (Figure 29) falls precisely where the probability of rejection is increasing most rapdily.

Terminal rejection rates on patches of different density are shown in Table 9. These vary more than terminal oviposition rates and increase with host density. There appears to be no clear correlation between patch leaving and a particular rate of rejection. Another hypothesis is that some ratio of rejection and oviposition rates may determine the time when a patch is left. Although this could not apply, of course, at low densities, where the patch is left before rejection (an in some cases oviposition) occurs, it could be involved in patch leaving at higher densities. In Table 9, the per cent of encounters in the last three minutes on a patch which are rejections are presented. A per cent measure, rather than a simple ratio, is necessary because zero values are occasionally encountered both for terminal oviposition and for terminal rejection rates. There appears to be no particular combination of rejection and oviposition rate at which the patch is abandoned. Rather, this terminal ratio appears to increase with patch density.

TABLE 10. Average time until first host rejection at different patch density.

		Average time between entering patch and rejecting first host	
PATCH DENSITY	4	12.50 ± 2.66	(n = 6)
	8	11.00 ± 2.75	(n = 12)
	16	11.67 ± 0.47	(n = 16)
	average of all densities	11.57 ± 1.26	(n = 34)

Figure 29. Change in per cent avoidance (rejection) of hosts with time since the last oviposition. Data from Rogers (1972b) for Nemeritis attacking Cadra cautella, curve fitted by eye. Arrow indicates average time from entering patch to first host rejection in Experiment 6. See Table 10 and text for explanation.



The data presented here are inconclusive regarding the role in patch leaving of encountering parasitised hosts. It is clearly not the sole factor affecting patch time, nor is there a fixed rate of rejection or ratio of rejection rate to oviposition rate which can be associated with patch leaving. A number of times during the experimental observations, the rejection of a host was followed immediately by a brief walk off the patch (usually less than 14 sec), suggesting some negative effect on patch time and responsiveness to the patch edge. Nonetheless, the hypothesis that rejection has very little or no effect on patch time, but simply serves to reduce the rate of oviposition, remains appealing and cannot be ruled out.

As one might expect, the time spent searching per prey capture and prey rejection has been seen to change both with patch density and time on the patch. More surprisingly, the other major component of patch time, the handling time, also changes with density and time. Such a change is not anticipated by the models for patch time determination, where T_h is considered constant. In fact, if one calculates the handling time for the different host densities in this experiment by averaging the values for the initial 7 to 10 ovipositions per replicate, handling time is seen to decrease significantly with increasing host density (Table 11). It is tempting to speculate that this is caused by the higher excitatory state, due to patch and oviposition stimuli, of wasps on high density patches which competes with, and reduces, the duration of the refractory state following oviposition.

Changes in handling time over the period of a particular patch visit are observed as well. This is most clearly shown from Experiment 8 to follow, where handling time sometimes increased markedly as different patches were visited over a period of two hours (Figure 36). This

TABLE 11. Differences in initial handling times on patches of different densities.

	PATCH DENSITY			
	1	4	8	16
Handling time (min.)	0.38 ± 0.10	0.38 ± 0.03	0.27 ± 0.02	0.27 ± 0.02
Time taken to handle rejected hosts (min.)	-	0.10 ± 0.04	0.13 ± 0.03	0.09 ± 0.01

increase is almost certainly attributable to the gradual depletion of mature eggs in the oviducts. As handling time increases for a wasp, a distinct "resting period" following the usual post-oviposition grooming appears and increases in length. During this period, the wasp remains motionless, occasionally starting to tap the substrate with the antennae as if initiating search, but quickly returning to the motionless rest position. Short "flexes" of the ovipositor are sometimes observed, suggesting aborted cocking responses. Finally, often after several minutes, the ovipositor is cocked and searching commences. Wasps dissected after exhibiting handling times in excess of five minutes were found to contain few or no mature eggs in the oviducts.

While discussing handling time, it is worth mentioning the time taken to reject hosts, which must enter into considerations of total patch time. Patch time models which incorporate the Random Predator Equation (Rogers, 1972a), such as the threshold rate model of Hassell and May (1974) and the model in the last chapter, assume there to be no time taken rehandling already captured prey (as they have been consumed). For parasitoids which reject already parasitised hosts but re-encounter them as well, a certain amount of time is taken in determining that they are parasitised before search is recommenced. This time for *Nemeritis* is shown in Table 11. Rejection time was measured as the time between host contact and the resumption of probing, and therefore differs in measurement from the handling time, which is terminated by cocking, although probing usual follows this immediately. Rejection time is much shorter than handling time and does not appear to vary with patch density.

The results of the present experiment reveal the complexity of processes determining patch time. Mechanisms relating patch time to one factor, such as chemical stimuli, rate of oviposition or rate of rejection

are clearly too simple. In particular, threshold rate models, which assume patch time to be determined by short term changes in the rate of oviposition or capture, do not appear applicable to the *Nemeritis* system. Relatively long term changes in oviposition rate, on the other hand, may be important in determining patch time, as predicted by the model in Chapter 5. The effect of chemical patch stimuli on patch time is suggested by the substantial time spent on patches of density 1, where the initial oviposition rate was lower than the terminal rate for higher density patches. A critical rate of rejection of parasitized hosts, or some ratio of rejection to oviposition, does not appear to be closely correlated with patch leaving, but it remains unclear whether rejection has a negative effect on patch time or no effect. As changes in the rate of rejection are reflected directly in the rate of oviposition, the hypothesis that rejection has a zero effect on patch time is simpler and somewhat more appealing, but more experimentation is necessary before any conclusions may be drawn.

Experiment 6 was also designed to examine the effect of experience on previous patches upon the time spent on a patch of a particular density. This part will now be described as a separate experiment.

EXPERIMENT 7: THE EFFECT OF PREVIOUS PATCH EXPERIENCE UPON PATCH TIME

MATERIALS AND METHODS

Experiment 6 was terminated when the wasp walked off the first patch for 14 sec. This experiment begins when the wasp walks onto the second patch (of constant density 4), which usually occurred immediately after the first patch was left. Sometimes, the wasp returned to the first patch for a few minutes before moving on to the second patch. In the present experiment, recordings were made as in Experiment 6, until the wasps walked off the patch for 14 sec. In some replicates, this second

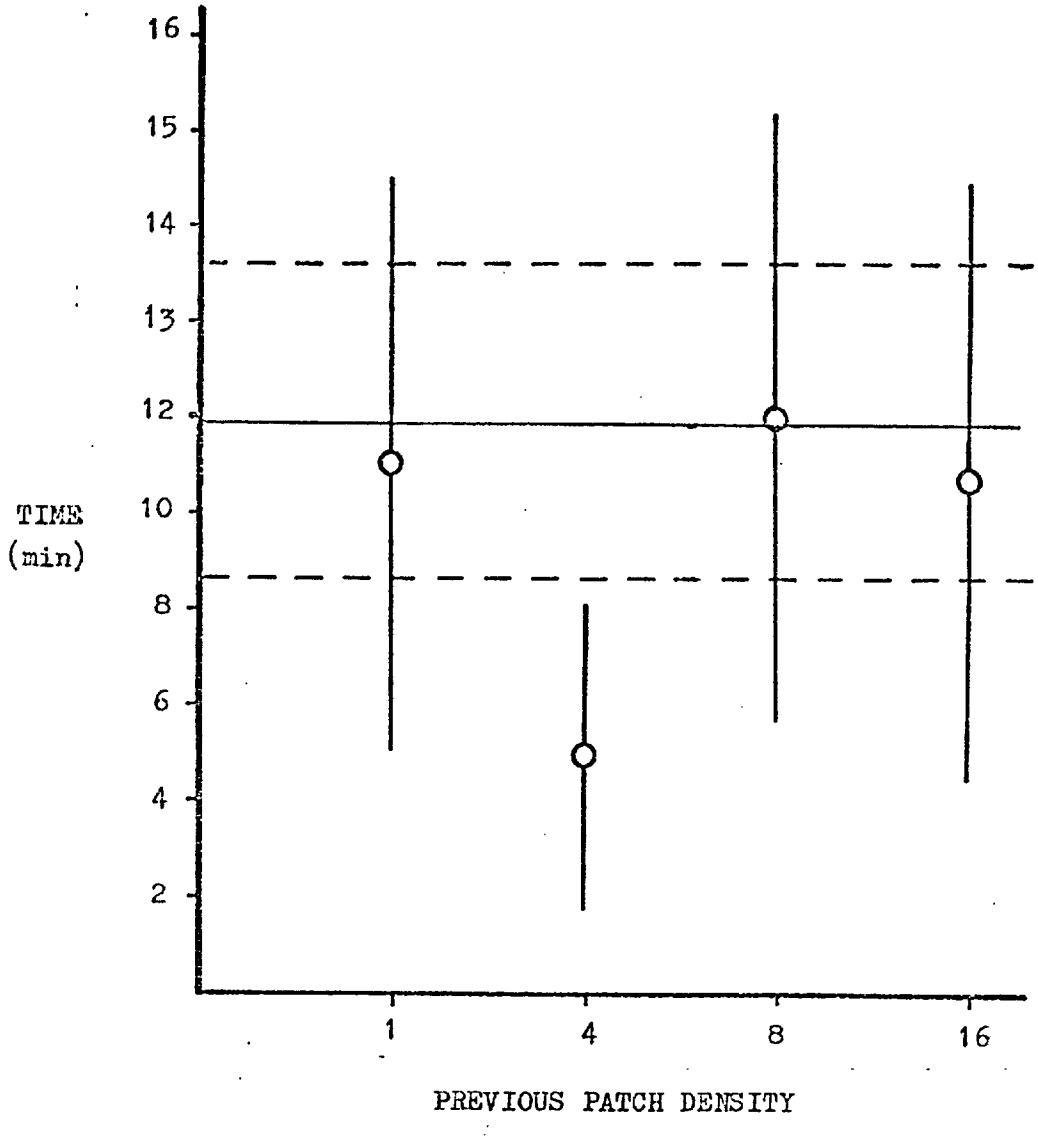
visit was not recorded, such that only 10 replicates were obtained in this experiment for each patch density.

RESULTS AND DISCUSSION

If experience on a previous patch affects present patch time, we might expect differences in patch time between, say, wasps coming from a patch of 16 and wasps coming from a patch of 1. This experiment compares the time spent on a patch of 4 by wasps coming from patches of 1, 4, 8 or 16. If, as suggested by the Marginal Value Theorem for movements from habitat to habitat (Charnov, 1976), wasps adjust some threshold oviposition rate as a consequence of experience on previous patches (lowering the rate with high densities and raising it with low densities), we might expect wasps coming from a patch density of 1 to spend more time on a subsequent patch of density 4 than wasps coming from a patch density of 16. Another hypothesis yielding the same prediction might presume that wasps leaving a patch have become habituated to patch stimuli of concentrations equal to or lower than those on that patch. This process would make wasps coming from a patch of density 16 less responsive to a patch of density 4 than wasps coming from a patch of density 1.

The average patch times for wasps on a patch of 4 coming from patches of different density are presented in Figure 30, and compared there to the time spent on a patch of 4 when it is the first patch visited, this value being taken from Experiment 6. The variability of these patch times is very high. This may reflect the compounding of the effect on patch time of innate and experimental variability by the variability of experience on the previous patch, if, indeed, this does affect the present patch time.

Figure 30. Time spent on a patch of host density 4 by wasps coming from a patch of density 1, 4, 8 or 16. The horizontal solid and dashed lines represent the mean and 95% confidence limits, respectively, of the time spent on a patch of 4 when it is the first patch visited.


16
15
14
13
12
10
8
6
4
2
TIME
(min)
1
4
8
16
PREVIOUS PATCH DENSITY

On average, the time spent on a patch of density 4 coming from patches of densities 1, 8 and 16 are very similar to each other and also to the average value for a first visit to a patch of four. When a wasp, however, moves from a patch of density 4 onto a patch of the same density, patch time on the second patch is much reduced. An intriguing hypothesis which would explain this result is that the insect has become, while on the first patch, habituated specifically to the stimulus intensity of a patch of 4, and therefore possesses lowered responsiveness to the second patch. In more anthropomorphic, and less accurate, terms, it might be said that the wasp treats this patch as if it were the patch just left. Although this is a rather loose representation of the mechanism suggested, it does indicate its selective advantage, namely, in avoiding patches already visited. In natural situations where patches are likely to be widely spaced, this behaviour would facilitate the abandonment of already exploited areas and the selection of and movement to new areas. This habituation mechanisms suggests that the decay of responsiveness to the patch edge, examined in Chapter 6, is specific to the difference in stimulus intensity across that edge. Higher or lower intensities would evoke responses unaffected by the visit to the previous patch.

The results of this experiment are too variable to draw any definite conclusions, but it can be said that the duration of a patch visit does not appear to be affected by previous visits to patches of higher or lower density, at least in the short term. This might be taken as evidence against the predictions of the Marginal Value Theorem, but this model predicts different effects depending on what one calls the habitat, and so presents problems in comparison. An immediately previous visit to a patch of the same density appears to decrease time spent on a patch.

This may reflect specific habituation to the intensity of the patch stimulus on the first patch which is carried over to the second.

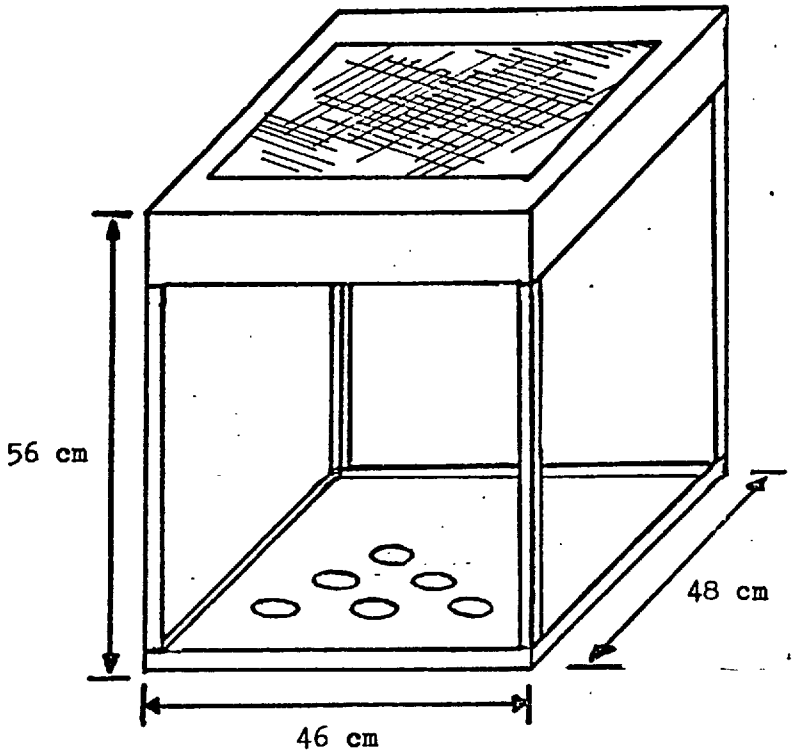
In the next experiment, the effect of experience on patch time is examined in a more natural context. Here, the allocation of patch time will be considered between a set of patches of different densities over a relatively long period of time.

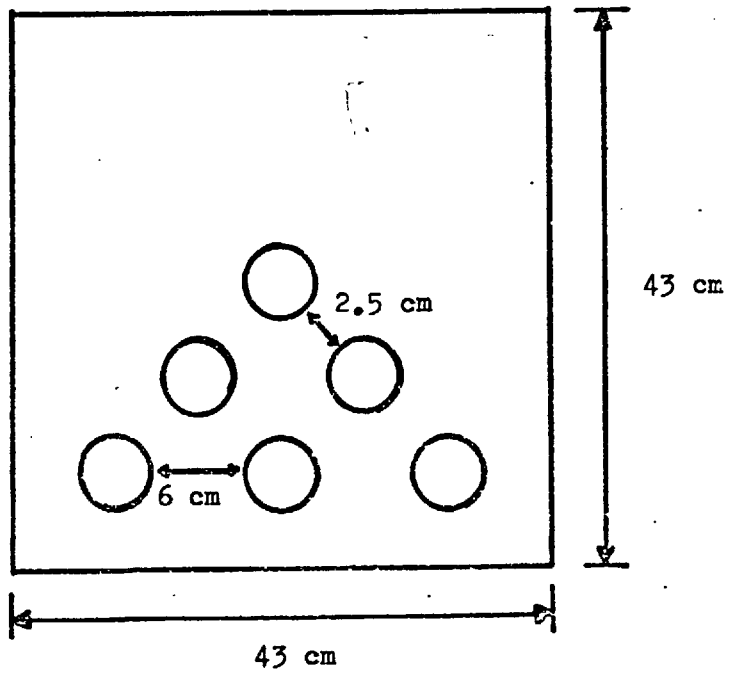
EXPERIMENT 8: FORAGING BY *NEMERITIS* IN A SET OF PATCHES OF DIFFERENT HOST DENSITIES

MATERIALS AND METHODS

In this experiment, a single standardized *Nemeritis* was allowed to forage for 2½ hours on six patches. These patches were made in an identical manner to those in Experiment 6, and placed in a triangular array on the floor of a large cage. The exact placement of the patches and the dimension of the cage are illustrated in Figure 31. Of the 6 patches, two were of host density 8, two of host density 4 and two of host density 1. Their positions in the array were allocated randomly at the beginning of each replicate. These patches were sunk flush with the pasteboard floor of the cage, which was covered with a thin layer of middlings. The wasp was introduced into the back of the cage in a vial, out of which it would soon fly, thus starting the experiment. Its movements were observed through a red plastic screen and the following activities were recorded on an 8-channel Rustrak event recorder; presence on any of the 6 patches, walking, resting, probing, flying, possible contact of host by the ovipositor (while probing) and cocking. Because the hosts could not be observed from below as in the last experiment, only host contacts ending in cocking (ovipositions) could be recorded with certainty.

Figure 31. A. Experimental chamber for Experiment 8. The four sides of the chamber were glass, the top was muslin. B. Distribution of the six patches on the floor of the chamber. The wasp was released at the back of the chamber (top of the illustration) from a glass vial.


56 cm
48 cm
46 cm


2.5 cm
6 cm
43 cm
43 cm

Fourteen replicated were run. A few wasps apparently ran out of eggs after about two hours, and in one case, the recorder broke down after 100 minutes. Therefore, calculations to follow were made from recorded observations over the first 120 minutes of each replicate, except for one replicate, where observations were made over 100 minutes only.

RESULTS AND DISCUSSION

The purpose of this experiment is to examine the overall distributional response of *Nemeritis* to a set of patches of different density. In particular, we want to consider (1), for the first time, the selection of patches by the wasp, (2) the time spent on patches of different densities and (3) the effect on this time of previous experience on the same, and on different, patches.

It is possible that *Nemeritis* acts selectively in the manner in which it exploits host patches. This selectivity might arise from differential attraction to patches of different density and/or preferences developed as a result of experience. In this experiment, patches were close together, and this may have interfered with selective attraction to any one patch density. Wasps usually flew from their release point to the patch areas, landing at the border of the triangular array and walking onto the nearest patch. In Table 12, the order in which different patches were discovered is presented for the 14 replicates. As shown in Table 13a, selection of the first and subsequent patches appears random and no significant bias occurs. By comparison, if the wasps foraged in the optimal manner suggested by Royama's (1971a) model (in a sequence from highest to lowest patch density), the distribution of successive patch visits would be as shown in Table 13b.

TABLE 12. Experiment 8. The order in which patches of different density were exploited in each replicate of 150 min (return visits not included)

		PATCH EXPLOITED					
		1st	2nd	3rd	4th	5th	6th
REPLICATE NUMBER	1	1	1	8	4	4	8
	2	8	1	1	4	4	8
	3	1	4	8	4	1	8
	4	4	1	8	4	8	1
	5	8	8	-	-	-	-
	6	1	4	4	8	1	8
	7	4	1	8	8	-	-
	8	8	8	4	1	1	4
	9	9	4	1	1	8	4
	10	8	8	1	4	1	4
	11	4	1	8	4	1	8
	12	4	1	1	8	4	
	13	8	4	1	1	8	4
	14	1	8	8	1	4	4

TABLE 13. (a) Analysis of the order in which different density patches were exploited.

(b) A hypothetical optimal order of exploitation by the same set of wasps.

(a)

		PATCHES OF EACH DENSITY WHICH ARE EXPLOITED						
		1st	2nd	3rd	4th	5th	6th	
	8	6	4	6	4	3	5	
DENSITY	4	4	4	2	5	4	5	
	1	4	6	5	4	5	1	
	CHI-SQUARE	0.57	0.57	2.00	0.15	0.50	2.91	(none significant)

(b)

		SEQUENCE OF PATCH EXPLOITATION SUGGESTED BY OPTIMAL FORAGING MODEL OF ROYAMA (1971a)					
		1st	2nd	3rd	4th	5th	6th
	8	14	14	0	0	0	0
DENSITY	4	0	0	13	13	0	0
	1	0	0	0	0	12	11

This method of analysis does not consider the possibility that experience on a particular patch might affect the subsequent selection of other patches. In Table 14, the data is analyzed to indicate the probability of exploiting next a patch of density 1, 4 or 8 having just exploited a patch of any of these densities. Once more, no bias is observed, and patches appear to be visited at random. From this we may conclude that, in the present foraging situation, no patch selection occurs and the probability of visiting a patch is independent of it's host density.

As in Experiment 6, the time spent of patches of different densities shows a clear aggregative effect. Figure 32a presents the duration of the first visit to a patch of density 1, 4 or 8, and Figure 32b the total time spent on a patch type over the observation period. The distributional response is very similar to that observed in naive wasps which have had no patch experience (Figure 26). The exact form of the averaged distributional response in Figure 32b appears linear or slightly decelerating, but this averaging conceals a great variability in the forms of the aggregation curves for individual insects. To illustrate this, the percentage of total time spent in each patch type is shown in Appendix C for each of the 14 replicates. Two observations are worth making regarding these data. Firstly, all wasps exhibit 'aggregation' (i.e., they spend more time on patches of higher density). Secondly, different wasps exhibit very different patch time distributions ranging from curves which are accelerating (#s 2, 6, 8, 13, 14) through linear curves (#s1, 7, 9) to decelerating and even dome-shaped curves (#s 3, 4, 5, 10, 11, 12). Thus, a distributional response suggesting (on a population level) aggregation is characteristic of each and every wasp, but any particular <u>form</u> of response is characteristic of only some individuals,

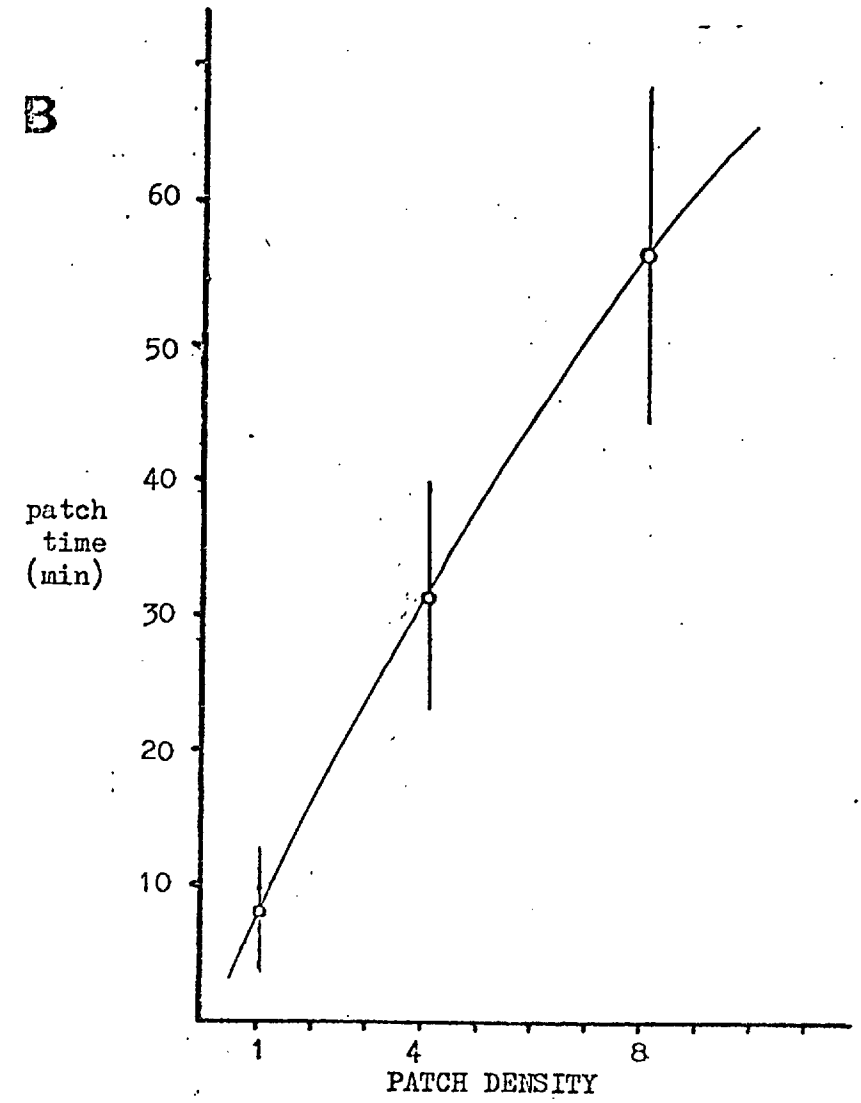
TABLE 14. Probability of entering an unexploited patch of a particular density (X) having just exploited a patch of another density (Y). Return visits not considered.

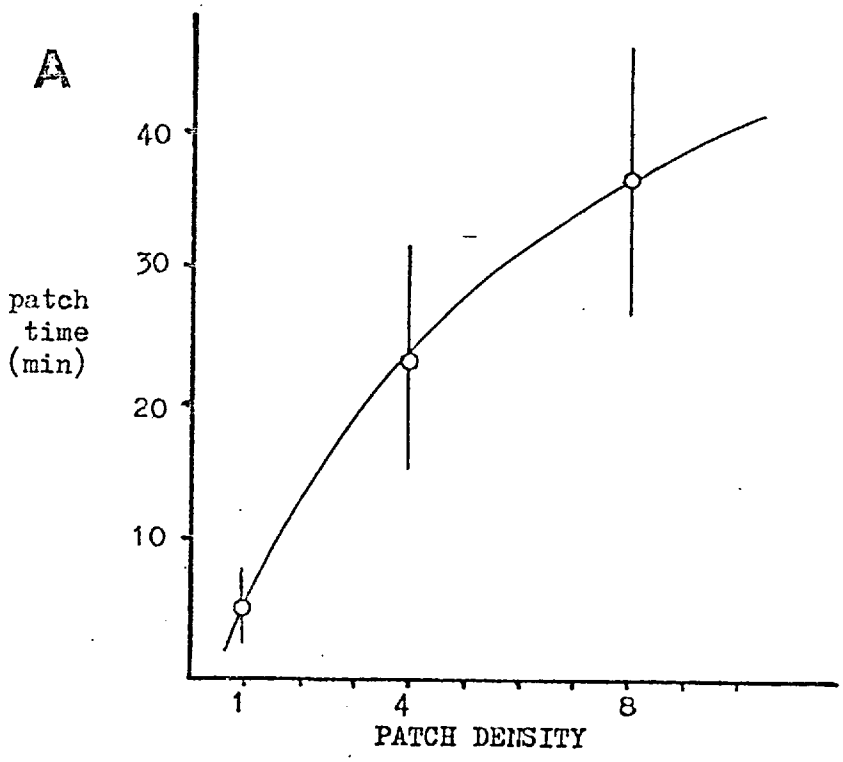
		Patch coming from (Y)		
		1	4	8
patch going to (X)	1	6	10	5
	4	7	4	10
	8	10	5	5

CHI-SQUARE NOT SIGNIFICANT

$p < 0.25$

Figure 32. A. Average duration for all replicates of first patch visit to patches of different density (with 95% confidence intervals). Curve fitted by eye. B. Average time per replicate spent on patches of different densities (with 95% confidence intervals). Curve fitted by eye.


B
60
50
40
30
20
10
patch
time
(min)
1
4
8
PATCH DENSITY


A
40
30
20
10
patch
time
(min)
1
4
8
PATCH DENSITY

or of the population as a whole.

It is interesting to ask, once a patch has been visited, what part of subsequent foraging time is allocated to revisiting it. At one hypothetical extreme, implied by some foraging models, the first visit to a patch may be a short 'sampling' visit (a part of the habitat sampling process), to be followed later by a longer 'exploitation visit'. Whether or not such preliminary sampling occurs, most foraging models assume that a patch is only exploited once and is not revisited after this. While this is clearly a convenience for mathematical modelling, it may also be a realistic strategy for the forager. In *Nemeritis*, return visits to a patch are observed, but they tend to be of much shorter duration than the first visit. The time spent on a return visit is influenced by the intensity of the chemical patch stimulus (see Figure 12). The effect of oviposition stimuli does not appear to carry over to subsequent patch visits (see Figure 15).

Figure 33 presents the durations of the first ten patch visits to patches of 1, 4 and 8 hosts. Within 3 or 4 visits, the duration of visits falls to essentially the same lever for all patch densities. This probably reflects both habituation to the chemical patch stimulus and reduction of the rate of oviposition to the same level on all patches. This latter process is illustrated in Figure 34, where the average oviposition rate (ovipositions/min) for successive patch visits are compared.

The response of *Nemeritis* upon encountering a previously visited patch is more complex than suggested by previous experiments. These would predict that a completely unresponsive wasps would walk across and out of an already visited patch without changing its speed or its path tortuosity. In fact, in many instances, wasps encountering an already

Figure 33. Average time spent in successive visits to one patch, with 95% confidence intervals. Data include patch rejections as visits of 0.00 min duration. Initial patch densities as given.

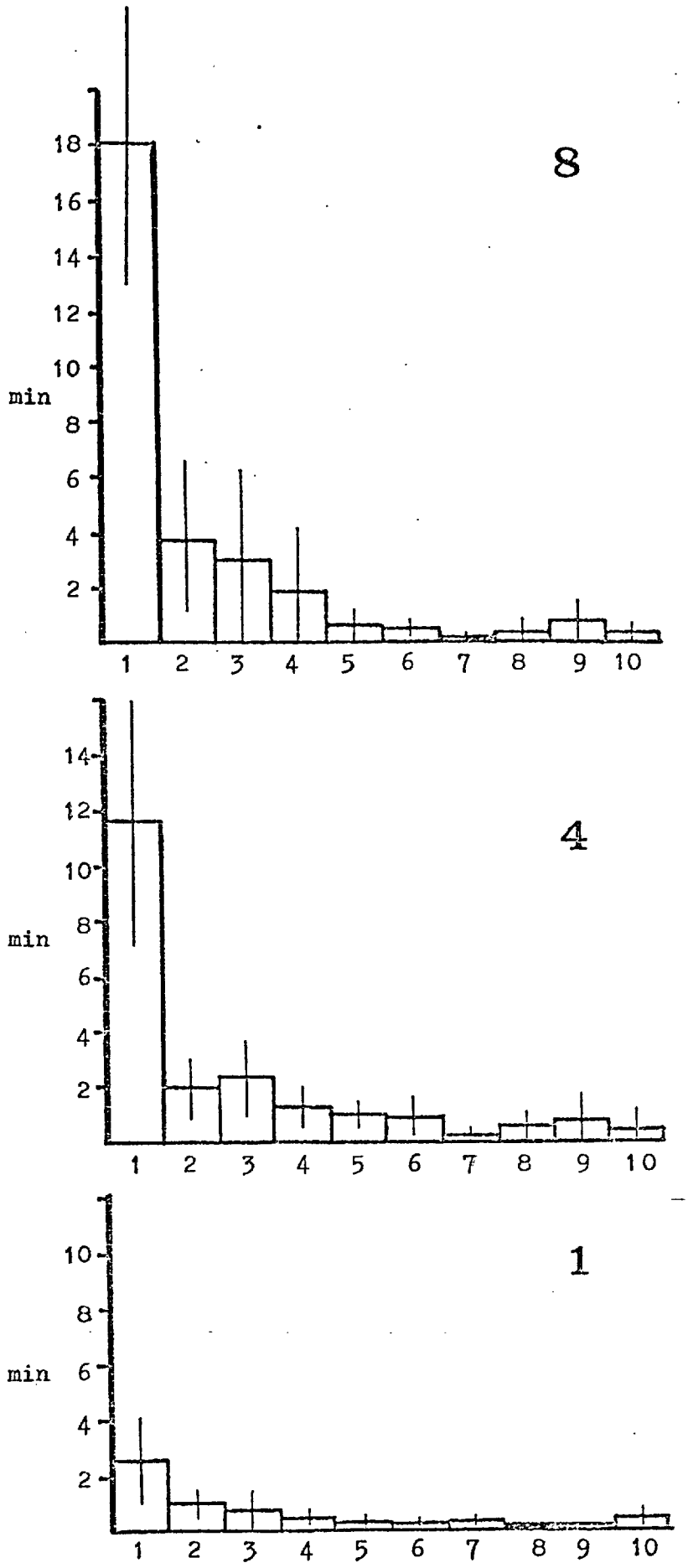
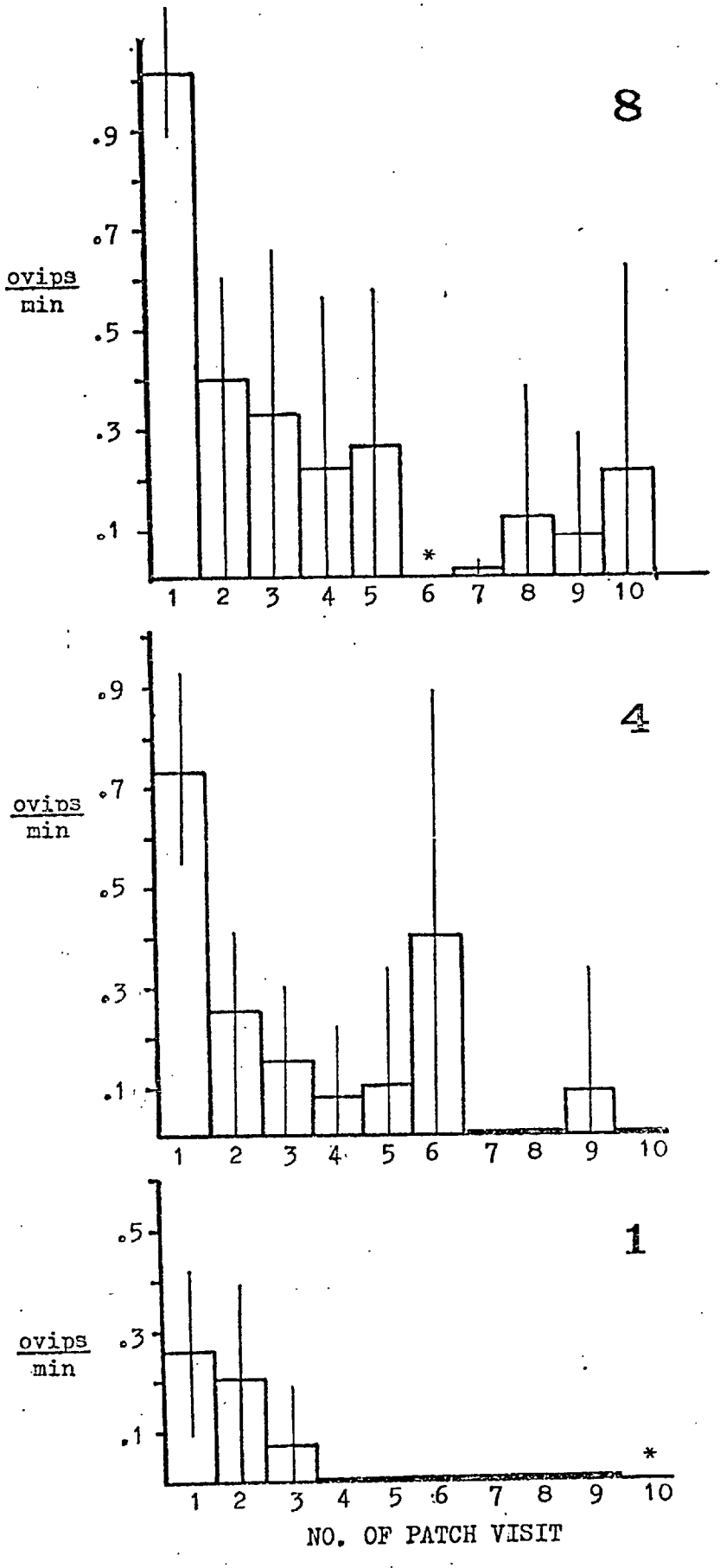

8
18
16
14
12
10
min
8
6
4
2
1 2 3 4 5 6 7 8 9 10
4
14
12
10
min
8
6
4
2
1 2 3 4 5 6 7 8 9 10
1
10
8
min
6
4
2
1 2 3 4 5 6 7 8 9 10
NO. OF PATCH VISIT

Figure 34. Average number of ovipositions per minute for successive patch visits, with 95% confidence intervals. Patch rejections (visits of 0.00 min duration) are not included in the calculations. Starred (*) visits were not included because less than five replicates were available.


8
ovips
min
.9
.7
.5
.3
.1
*
1 2 3 4 5 6 7 8 9 10
4
ovips
min
.9
.7
.5
.3
.1
1 2 3 4 5 6 7 8 9 10
1
ovips
min
.5
.3
.1
*
1 2 3 4 5 6 7 8 9 10
NO. OF PATCH VISIT

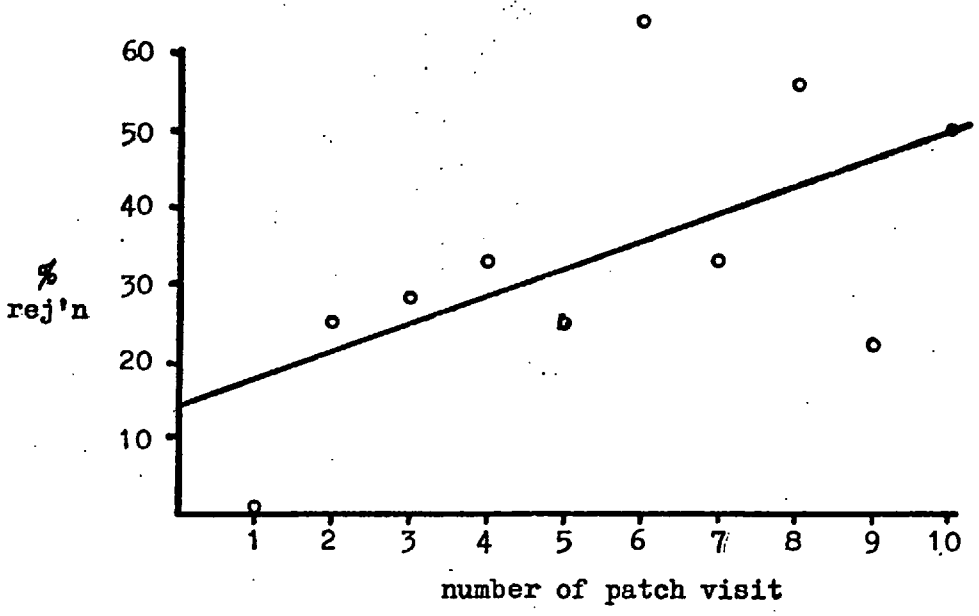
visited patch made a distinct turn away from the patch at the patch edge. This appears to be a response to a chemical stimulus at the patch edge, although some subtle visual stimulus associated with the patch cannot be ruled out. If a chemical is involved, it must be either the patch stimulus itself (here eliciting turning with the presentation of the stimulus - the opposite of the response described earlier) or a deterrent chemical deposited by the wasp during previous visits. With the information available, it is impossible to choose between these two possibilities. If this 'patch rejection response' is elicited by the patch stimulus, it may be related to the patch specific habituation suggested in Experiment 7.

During the course of the experiment, the frequency of the patch rejection response increases in a more or less linear fashion (Figure 35). It is interesting to note that, when this trend is fitted to a linear regression for each patch density, the slope of these regressions do not differe significantly. Thus, it seems that the rejection response is affected by the number of visits made to a patch and not by the density of the patch or the duration of the visit.

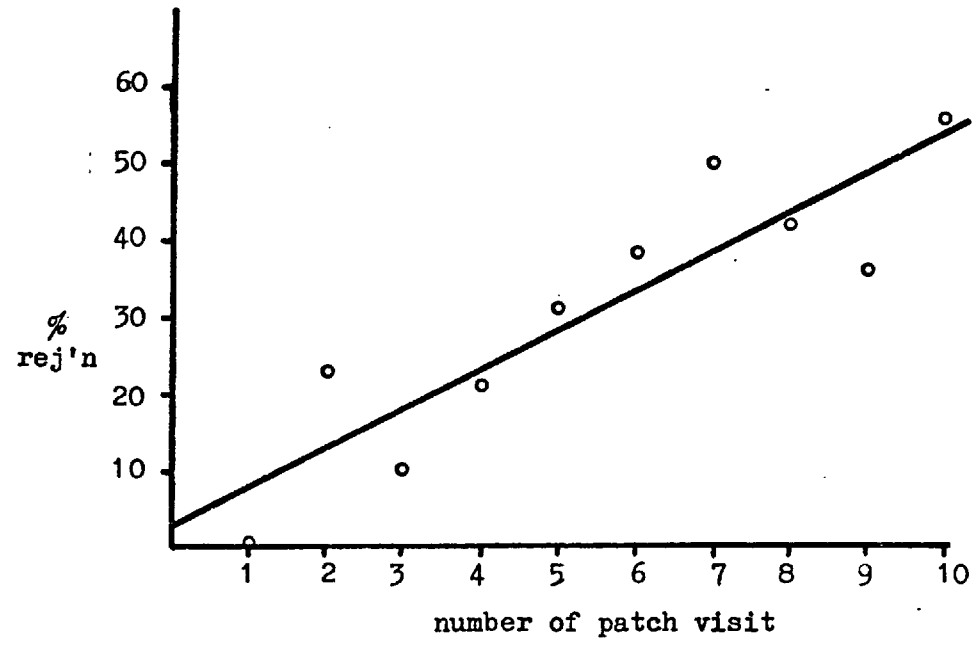
We turn now to the effect on patch time of previous visits to other patches. The interesting results of Experiment 7 suggest that patch time is decreased by previous experience on patches of the same stimulus intensity, but not by previous experience on patches of greater or lesser stimulus intensity. Some form of intensity specific habituation is suggested by the data. As mentioned previously, another hypothesis might predict that wasps habituate to patch stimulus intensities such that responsiveness is decreased to intensities equal to or lower than those previously experienced. According to this mechanism, wasps coming from high density patches would spend less time on a particular patch than

Figure 35. Changes in the percentage of patch encounters which are rejections with successive patch visits to patches of different densities. Regressions for curves:

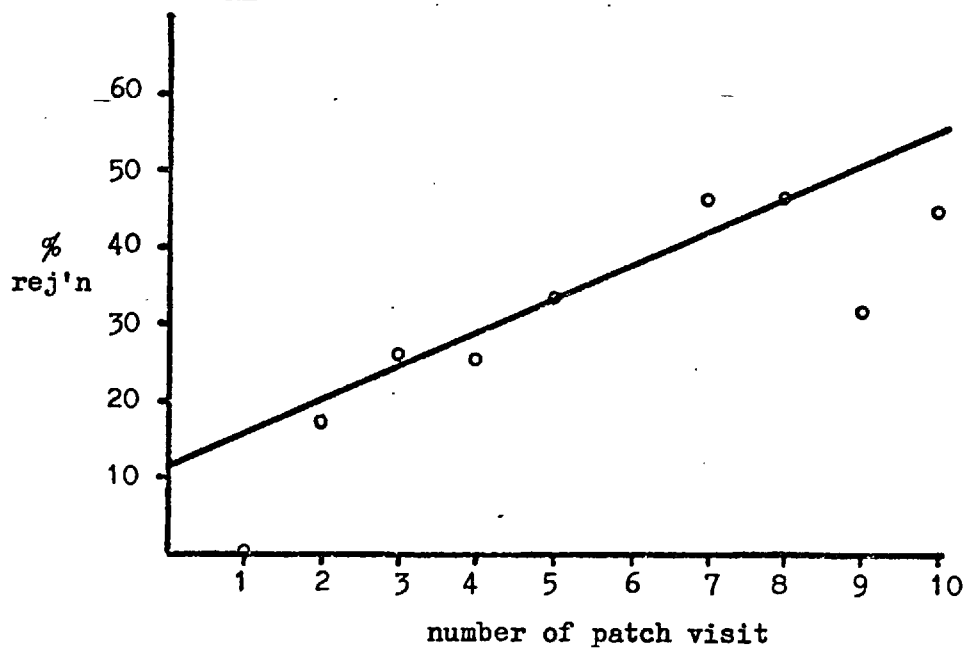
patch density 1	$y = 3.60x + 13.70$
patch density 4	$y = 5.14x + 2.40$
patch density 8	$y = 4.28x + 11.53$


60
50
40
30
20
10
% rej'n
1 2 3 4 5 6 7 8 9 10
number of patch visit

1


60
50
40
30
20
10
% rej'n
1 2 3 4 5 6 7 8 9 10
number of patch visit

4


60
50
40
30
20
10
% rej'n
1 2 3 4 5 6 7 8 9 10
number of patch visit

8

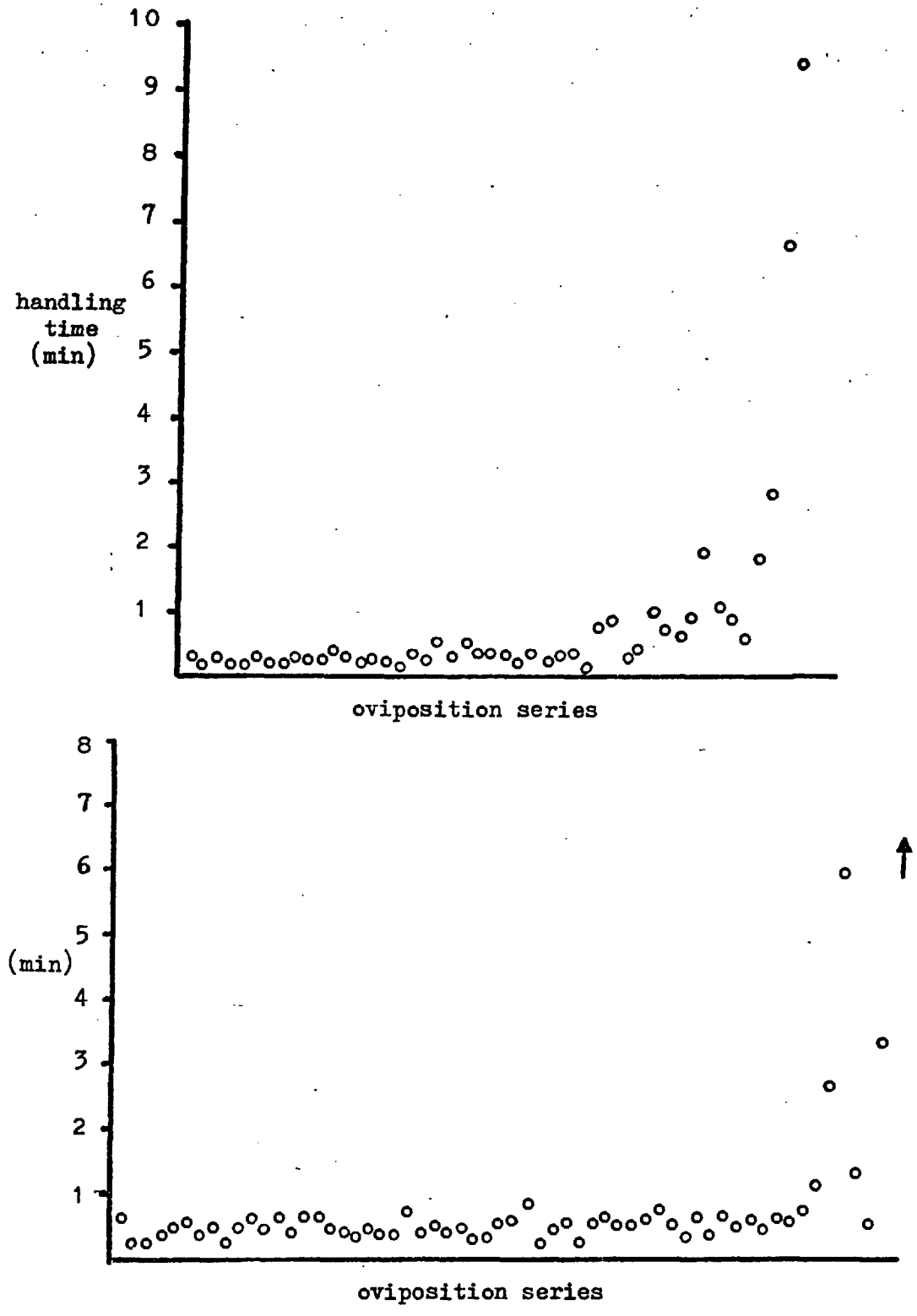


Figure 36. Some representative changes in handling time with successive ovipositions. Both trends resulted from egg depletion. Data from Experiment 8 (rejected replicates)

wasps coming from low density patches. A similar effect, resulting from oviposition stimuli rather than patch stimuli, is suggested by the optimal foraging model described by Krebs, et al. (1974). In rich habitats (relatively high density patches) wasps would decrease their giving up time (or increase some terminal capture rate), while in poor habitats (relatively low density patches) wasps would increase their giving up time. By this mechanism, time spent on a particular patch by a wasp coming from high density patches would be less than time spent by a wasp coming from low density patches. In the present experiment we may look at the effect of experience in a more realistic context than in Experiment 7 and test the predictions of these different mechanisms.

To learn how patch time might be influenced by previous experience on other patches, if, indeed, it is at all, correlations were made between the duration of the first visit to a patch and various indices of previous experience. Arriving at a satisfactory index of experience poses many problems. An effect of experience might only appear from patch to patch, or it might appear only after several days. We may characterize all such effects by four parameters:

1. the duration of the effect, i.e., the period over which it will influence subsequent patch time.

2. the intensity of the effect, which may change over its duration.

3. the specificity of the effect, i.e., changes in its intensity dependent upon the density of the present patch.

4. the interaction of the effect with other effects from previous patches visited.

The number and potential variability of these parameters illustrate how

complex the effect of experience may be. At any one moment, the number of previous patch visits affecting patch time will be determined by the duration of previous effects and the time since these patch visits, and the effect itself will be some interactive function of their present intensities and specificity.

A somewhat different, and simpler, way of looking at the effect of experience is to imagine the forager has a 'memory window', that is, a period of time stretching back from the present over which any previous patch visit will exert an effect on present patch time. Visits 'outside' this window (before this fixed period) will not affect patch time. A memory window may be described in units of patches rather than time, such that a forager has a memory window of, say, four previous patches.

To represent the maximum range of experience which might affect patch time within the limits of the present experiment, three indices of different lengths were chosen. Virtually every patch visit in this experiment has unique 'history' of times and durations of previous visits. This made comparison of patch experience more difficult than in Experiment 7, and in some cases experience has been generalized to make different visits more comparable. This undoubtedly obscures finer differences in experience which could have an important effect.

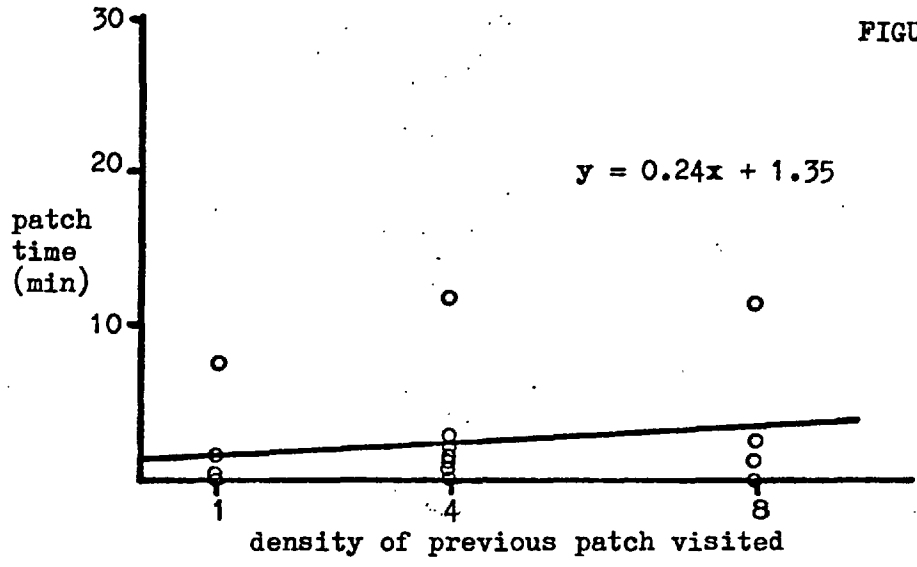
In Figure 37, the time spent on a patch is compared with the density of the patch visited immediately previously. This previous visit may have been a revisit, and thus of short duration. The first visits in each replicate were, of course, not included. The data is highly variable and no significant correlation or difference is apparent between patch time and the density of the previous patch.

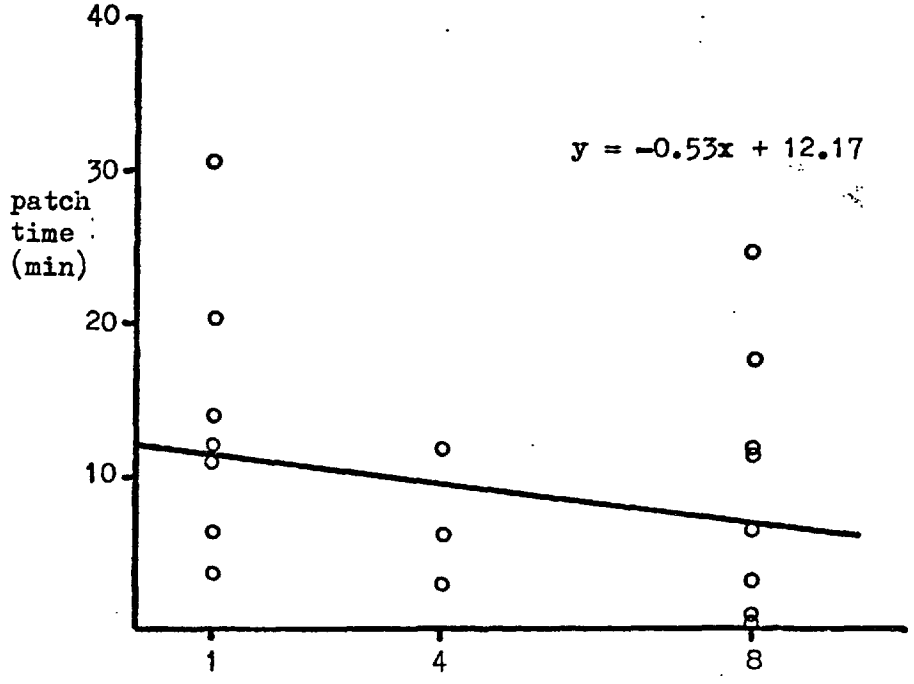
Figure 37. Correlation of duration of first visit to a patch with the density of the previous patch visited

Figure 38. Correlation of duration of first visit to a patch with the average density of patches already exploited (i.e., visited one or more times) See text for explanation.

Figure 39. Correlation of duration of first visit to a patch with the total time already spent on previously visited patches. The first patch visited in the experiment is included here with previous patch time of 0.00. See text for explanation.

FIGURE 37


30
20
10
patch time (min)
y = 0.24x + 1.35
1
4
8
density of previous patch visited


40
30
20
10
patch time (min)
y = -0.53x + 12.17
4
1
4
8

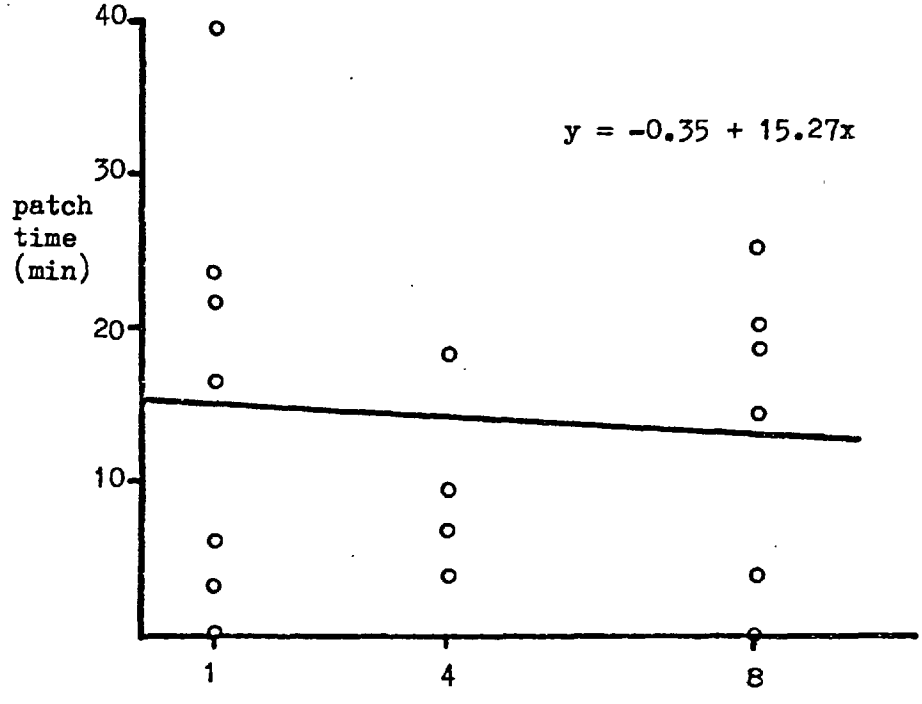
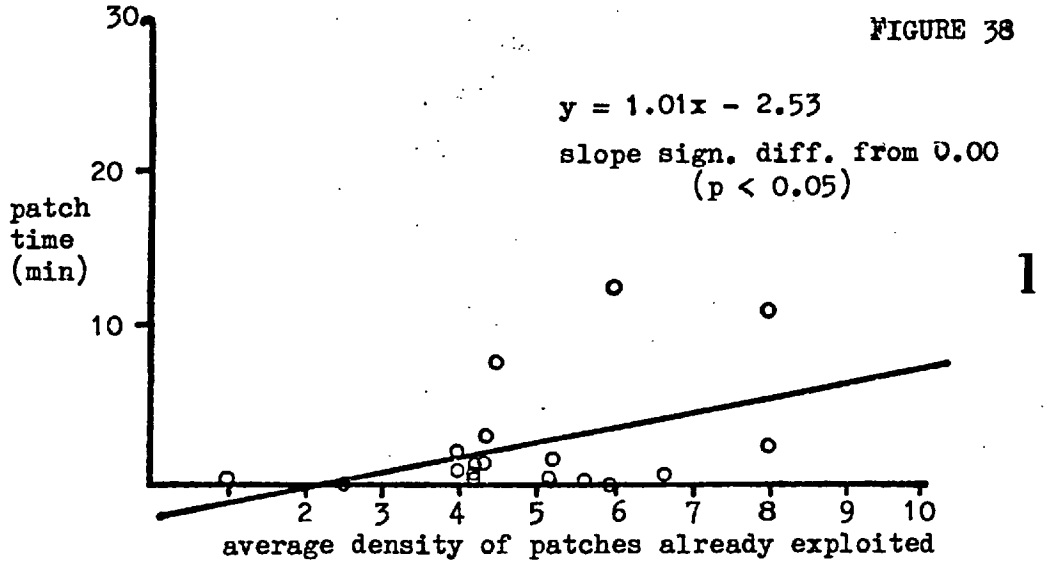
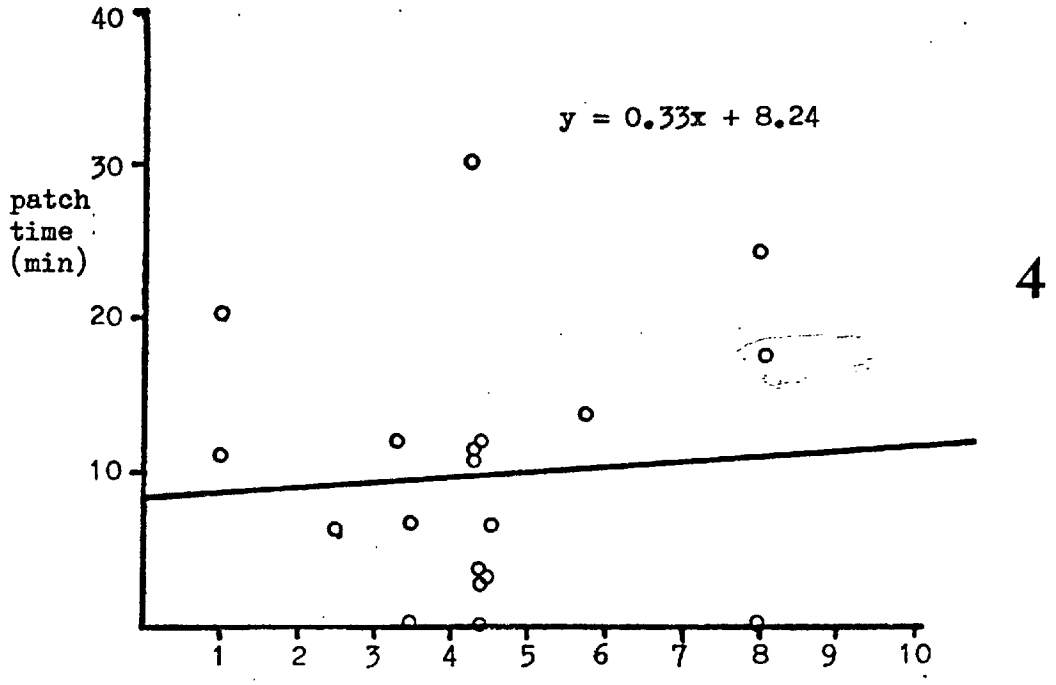

40
30
20
10
patch time (min)
y = -0.35 + 15.27x
8
1
4
8

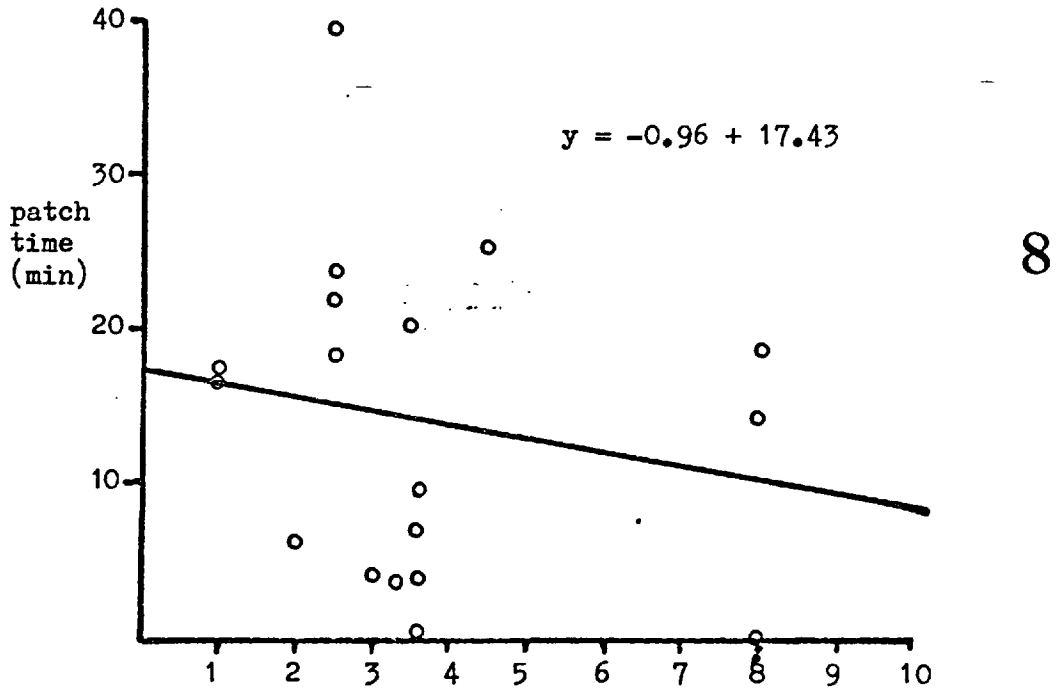
FIGURE 38



1

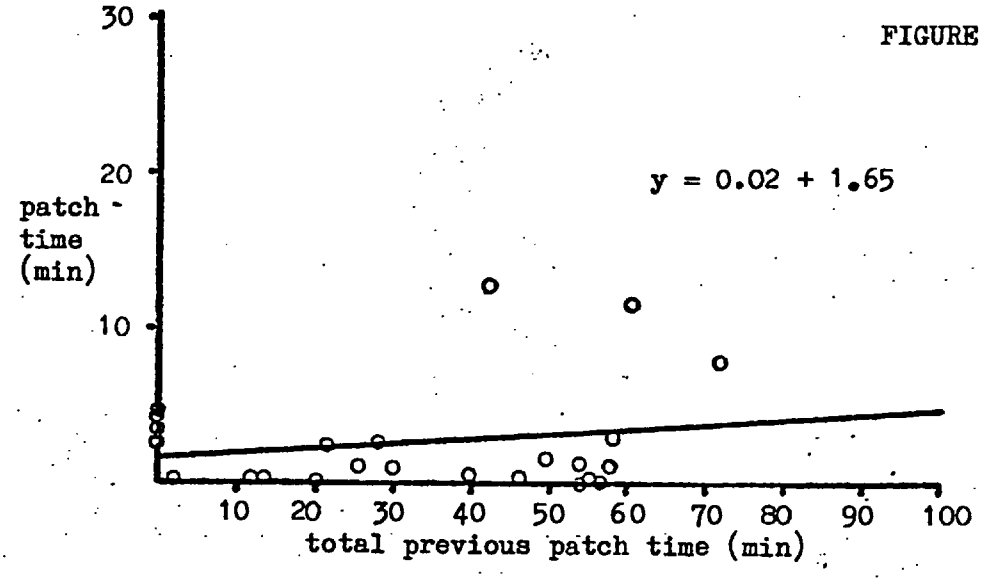


4

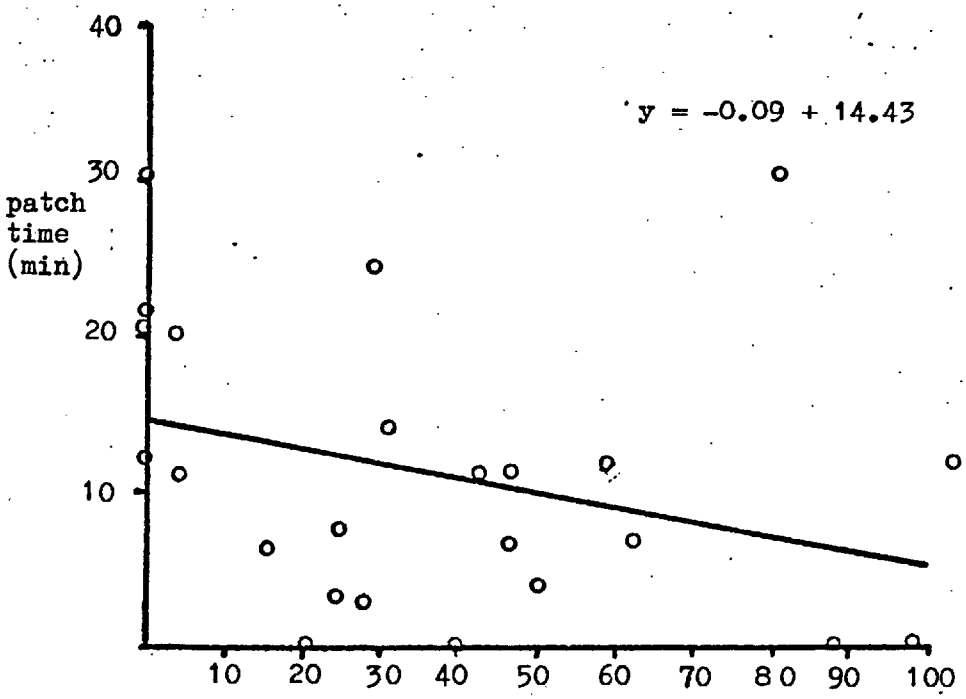


8

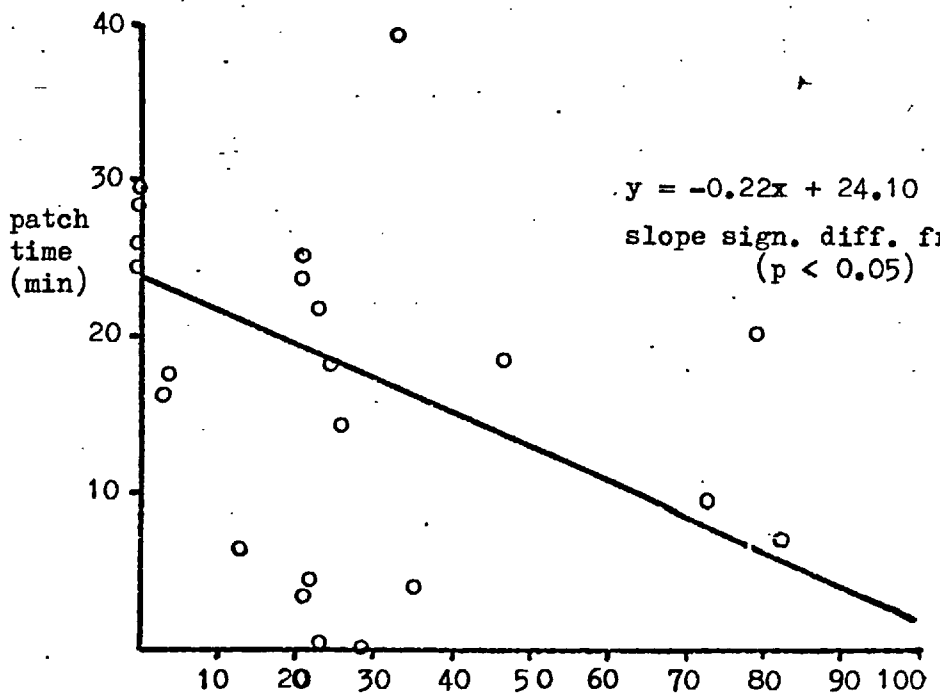
FIGURE 39



1



4



8

To investigate the other extreme, an index was used which was the average density of all patches (of the set of six) which had already been discovered and exploited. This was the average patch density which the wasp had experienced before entering the patch in question, from which it could build an impression of habitat richness. High average densities indicate experience on high density patches (e.g., (8 + 8 + 4)/3 = 6.67) and low average densities experience on low density patches ((1 + 4)/2 = 2.5). Again, the first visits in each replicate were not included.

As seen in Figure 38, the slope of the regression of this index against the duration of the patch visit is not significantly different from zero for densities 8 and 4. For a patch density of 1, patch time increases as the average density of previous patches visited increases. These results do not support the mechanisms proposed above in which experience on higher density patches tends to decrease patch time.

A similar index of total previous experience is made by comparing the total time spent previously on all patches with the duration of the present patch visit. Total time will be higher if previous patches are of higher density, and so this index bears similarities to the previous one. Previous patches visited, however, are weighted according to the time spent on them, rather than their density, and this may be more representative of the exact experience of the wasp. Furthermore, the first visits in the replicates are included in this data, being assigned a total previous patch time value of zero. As shown in Figure 39, no significant trend is seen for patches of density 1. A downward trend, although not significant, is suggested for density 4, and a significant downward trend is observed for density 8. This suggests that the time spent on high density patches decreases with increasing experience on high density patches. While this supports the optimal foraging mechanism

described above, the absence of this effect at density 1, where it should be more apparent, contradicts this mechanism.

From these analyses we may conclude that experience on previous patches does affect patch time, apparently with some specificity. The predictions derived from an optimal foraging type hypothesis, that time on patches will decrease with increasing experience on high density patches is not supported by the data, in fact, the opposite trend is observed in one analysis. It should be stressed, though, that the data is highly variable and the indices chosen represent just some of the many possible. Furthermore, they represent the effect of experience over a short period of at most two hours, and the effect of experience over longer periods may be very different.

An interesting interpretation of these results arises if we look at the difference between the durations of the visits to the first patch and second patch of a particular density. From Experiment 7, we might anticipate that experience on a patch of density n will decrease time spent on the next patch of density n, and ascribe this to habituation specific to the patch stimulus intensity. Such a decrease in patch time is, indeed seen in all densities, as shown in Table 15. This effect may explain the trends seen above. In Figure 38, wasps entering a patch of densities 4 or 8 after a long period of previous patch time had probably already visited a patch of these densities, while wasps with little or no previous patch experience were probably visiting patches of density 4 or 8 for the first time. This association will not be as apparent with a density of 1, as previous visits to patches of 1 do not affect total patch time considerably, and so it is not surprising that no correlation is seen here. In Figure 39, however, previous visits to patches of density 1 influence significantly the value of the average patch density

TABLE 15. Comparison of the duration of the first visits to the first and second patch found of the same density.

	PATCH DENSITY		
	1	4	8
Mean duration of first patch visit	3.82	12.98	21.72
Mean duration of visit to second patch	1.44	4.75	10.21
t statistic for paired t test	2.38*	2.61*	3.28**

* $p < 0.05$

** $p < 0.01$

visited, thus making low values more indicative of situations where a patch of one has already been visited and high values of situations where this has not occurred. Consequently, we would expect the duration of visits to patches of density 1 to increase with increasing average patch density, and so they do.

The tendency to spend less time on a patch if a patch of the same density (patch stimulus intensity) has already been visited is, therefore, supported by the data, corroborating the findings of Experiment 7. This behaviour, which is presumably associated with intensity-specific habituation to the patch stimulus, explains most, if not all, of the effect of previous experience observed in this experiment.

7.3 ASSOCIATIVE LEARNING AND PATCH TIME

As mentioned above, the effect of experience considered in Experiment 8 applies to only short term changes. Long term effects of experience on foraging in *Nemeritis*, involving conditioning, have been demonstrated by Arthur (1971) and Thorpe and Jones (1937). In Arthur's experiment, wasps conditioned to the odour of geraniol mixed with host-infested flour were subsequently observed more often on patches of geraniol mixed with uninfested flour than on patches uninfested flour alone. The traning period was six days. The aggregation data involve counts of the number of *Nemeritis* (there were ten in all) on the patches at two minute intervals over an hour. This means that they probably reflect longer patch visits by individual wasps on patches containing geraniol, but it might reflect, as well, an increased tendency to return to patches with geraniol which, even if all visits were of the same duration, would give data suggesting aggregation.

The results of Thorpe and Jones (1937) and Thorpe (1938) are part-

icularly interesting in that they suggest experience may affect the choice of host species and, consequently, lead to host race formation. These authors showed that *Nemeritis* reared on the lesser wax moth, *Achroia grisella*, exhibited a slight but significant attraction to the odour of this host in a Y-tube olfactometer, while wasps reared on *Anagasta kuhniella* showed no such response. This effect could also be produced if wasps, newly emerged from *Anagasta* were conditioned for one week with the odour of *Achroia*. Subsequently, Thorpe (1938) showed that this conditioning decayed over a period of about 5 to 10 days. From these experiments it is difficult to draw any conclusions about how experience over long periods with different hosts might affect foraging time allocation in *Nemeritis*, although increased attraction to patches of *Achroia* seems a possible consequence of conditioning.

To examine how conditioning might affect the aspects of foraging behaviour investigated in this study, a patch time experiment was conducted with *Nemeritis* reared on *Achroia* and *Plodia*.

EXPERIMENT 9: THE EFFECT OF OLFACTORY CONDITIONING ON PATCH TIME

MATERIALS AND METHODS

Patches of medium contaminated with *Achroia* larvae were made in the same manner as *Plodia* patches in previous experiments. Ten larvae of *Achroia* (approx. 10 mm in length), which had been reared on *Plodia* medium, were contained for 15 hours with 0.3 g of *Plodia* medium. Such a patch without larvae was placed, as in Experiment 6, flush with a layer of *Plodia* medium in the bottom of a plastic tray. Standardized wasps were transferred to an experimental chamber identical to the one in Figure 3c, which was then placed over this middlings surface, with the 5.5 mm diam. patch in the centre. Event recorder records were made of time on the patch and probing on the patch. Patch time was determined as the time

from entering the patch until leaving it for more than 14 seconds of flying or walking. Six wasps were tested which had been reared on *Achroia*. These wasps were removed from cultures within several hours of their emergence and tested the following day, after standardization. Five wasps reared on *Plodia* were also subjected to the identical test.

RESULTS AND DISCUSSION

Wasps reared on *Achroia* spent significantly more time on their first visit to a patch of *Achroia*-contaminated medium than wasps reared on *Plodia*, as shown in Table 16. The average duration of the patch visit was 3 or 4 times greater for the *Achroia*-reared wasps. This suggests that experience, such as conditioning, which is obtained over relatively long periods, can significantly affect the foraging time allocation of *Nemeritis*. The implications of such phenomena for parasitoid ecology and evolution will be discussed in the next chapter.

TABLE 16. Comparison of patch visit duration in wasps reared on *Plodia* and *Achroia*.

		DURATION OF VISIT (min) TO PATCH OF *ACHROIA* ODOUR FOR WASPS	
		REARED ON *ACHROIA*	REARED ON *PLODIA*
WASP NUMBER	1	4.47	3.92
	2	15.94	8.65
	3	18.61	0.37
	4	12.82	13.33
	5	33.57	5.14
	6	24.45	
	mean	17.08	6.28

$t = 2.24$ (df = 9) $p < 0.05$

CHAPTER 8

SUMMARY AND DISCUSSION

In this final chapter I shall summarize in general terms what has been learned about *Nemeritis* foraging and discuss to what extent the mechanisms suggested may be common to all parasitoids. The ecological and evolutionary implications of the results obtained for *Nemeritis* will also be discussed.

BEHAVIOURAL IMPLICATIONS

The foraging behaviour of *Nemeritis* was studied in and between 'patches' characterized by the presence of a host secretion. A chemical in this secretion elicits an orthokinetic response by *Nemeritis* upon entering a patch, including a probing response whereby hosts are contacted in the medium beneath. The removal of this chemical stimulus, as at the patch edge, elicits a klinotactic response (turning back into the patch) which keep the wasp on the area of host secretion. The patch is finally abandoned when this patch edge response wanes and the wasp crosses out of the area of secretion without turning back.

Oviposition while on the patch influences the waning of this response and increases the time spent on the patch. The effect of a series of ovipositions on patch time is determined by the rate at which these ovipositions occurs.

Previous experience on a patch can influence the duration of subsequent visits to that and other patches. *Nemeritis* spends less time on a patch containing a particular concentration of chemical stimulus (density of hosts) if it has previously visited patches of the same stimulus concentration. Return visits to patches, presumably because of this effect, decrease sharply in duration and may even involve rejection of the patch as soon as the edge is contacted.

Rearing *Nemeritis* on an alternate host increases the tendency of adult wasps to remain on patches of that host. Thus long-term changes in responsiveness due to learning (here, preimaginal conditioning) may affect the foraging behaviour of *Nemeritis*.

To what extent might these findings for *Nemeritis* be generalized to other parasitoid-host systems? The model of patch-localized behaviour presented in Chapter 5 recognizes two sorts of parasitoid responses, the response to chemical patch stimuli and the response to host contact stimuli, particularly oviposition. The first response is common to all parasitoids which react to some contact chemical produced by the host (Table 1 and others). Whether the exact mechanisms of these responses are the same as for *Nemeritis* in not certain. Orthokinesis seems a general response to contact chemicals. In addition to *Nemeritis*, a klinotactic response to contact of the patch edge has been observed in *Cardiochiles nigriceps*, which exhibits a 180° turn when it comes to the end of a linear streak of host chemical (Vinson and Lewis, 1965).

With regards to patch leaving, the waning of responsiveness to a chemical stimulus produced by the host has been observed in *Cardiochiles nigriceps* (Vinson and Lewis, 1965) and *Microplitis croceipes* (Lewis and Jones, 1971). In *Microplitis*, in fact, individuals not only became unresponsive with time to a spot of host chemical on filter paper, but began as well to avoid the contaminated area. This patch rejection behaviour is similar to that observed in *Nemeritis* in Experiment 8.

Responses to host contact stimuli and their effect on patch time have not been studied in parasitoids other than *Nemeritis*. Some inferential evidence is, however, available. Hafez (1961), for instance, made observations on a female *Diaeretiella rapae* confined in a glass

vial with hosts over a six hour period. He found that the oviposition rate in the host area decreased with time while periods of oviposition began to alternate with ever increasing periods of rest or walking outside of the host area. There was, however, no evidence that oviposition rate fell due to the rejection of already parasitized hosts. Thus, although we may conclude that *D. rapae* tends to leave a host area as oviposition rate decreases, such movements may not be caused by a change in the rate of encounter of acceptable hosts. Some perceived decrease in the suitability of encountered hosts may be involved, but one cannot rule out other possible causes of emmigration from host areas, such as fatigue, short-term egg depletion or waning of responsiveness to host contact stimuli.

More convincing evidence for an effect of changing oviposition rate on patch time is found in the experiments of van Lenteren (1976) with *Pseudocoila bochei*, a parasitoid of *Drosophila* spp. He exposed 25 host larvae in their food medium to a single female wasp for 6 hours. The larval medium was spread on the bottom of a petri dish and the movements of the wasp on the medium and on the sides and top of the dish were recorded. *P. bochei* rejects already parasitised hosts, and this led to a rapid decline in the oviposition rate over the first hour. As this rate decreased, the tendency to leave the medium increased rapidly. That this increasing emmigration tendency was the result of decreasing oviposition rate (or increasing rejection rate) was confirmed by a control experiment where hosts were removed immediately after parasitism and replaced with healthy hosts. In this series, the rate of oviposition did not decrease over the 6 hours and the tendency to leave the patch remained very low and constant throughout the period.

Further studies of parasitoid behaviour are required to evaluate the generality of the responses to patch stimuli and host contact stimuli in parasitoids and their effect on patch time. However, there is one form of response documented for parasitoids which has not been considered in this study and should be mentioned. This is a deterrent response to a chemical produced by parasitoids during foraging. As mentioned in Chapter 3b, such chemical deterrents are known to be produced by *Pleolophus basizonus* (Price, 1972) and *Orgilus lepidus* (Greany and Oatman, 1972). A similar deterrent may be produced by *Nasonia vitripennis* (DeBach, 1944) but the evidence for this is not conclusive. Parasitoid-produced stimuli deposited in or on already parasitised hosts might elicit, besides host rejection responses, movement away from the area of the host.

Matthews (1974) has suggested that parasitoid-produced deterrent stimuli, which he calls 'search deterrent substances' (SDS) influence the oviposition behaviour of parasitoids by increasing their restlessness and encouraging emigration from areas which they have occupied for a prolonged period. Were such the case, the time spent in a particular foraging area would, presumably, be determined by the balance between the tendency to emmigrate, which is constantly increasing as more SDS is deposited, and the tendency to remain, maintained by arrestant patch stimuli.

It appears as though search deterrent substances may have an important role in the foraging of some parasitoids. For *Nemeritis*, however, no deterrent effect has been associated with the encounter of parasitised hosts (though one may occur) and avoidance of already searched areas has been identified only at the patch level, where it appears to be elicited by the patch stimulus rather than by some parasitoid-produced

marker. Thus, differences may exist between parasitoid species in the exact mechanism by which previously visited patches are avoided, although avoidance of previously visited patches is probably a general phenomenon.

Long-term changes in behaviour affecting patch-finding and patch time, as a result of learning, have been demonstrated in several parasitoids besides *Nemeritis* (see Chapter3c). Parasitoids probably vary in their ability to develop a learned preference for particular patches or patch types over time. This capacity can be related to at least three characteristics of the parasitoid's biology, it's longevity, the number of eggs matured per day and its host specificity.

Over the lifespan of a long-lived parasitoid, certain host areas may be available for repeated exploitation, due to renewal of the population of suitable hosts by immigration or development (i.e., continuous recruitment into the acceptable life stage). Such a situation would favour selection for the ability to learn the exact location of different patches so that they may be re-exploited. Short-lived parasitoids, whose life spans are less than or equal to some 'patch renewal time', would derive no benefit from the ability to relocate already exploited patches.

Some synovigenic parasitoids mature only a few eggs per day. *Pleolophus basizonus*, for instance, matures a meximum of 4 eggs daily over an average life span of 18 days, and has a maximum egg storage capacity of 8 mature eggs (McLeod, 1972). Presumably, daily egg complements are adapted to the average number of hosts encountered in a day's foraging. At one extreme, in high density areas, a parasitoid with a low egg complement may be unable to exploit fully the host population in one day's foraging. Such limitation could lead to selection for the ability to relocate and/or remain in profitable areas over a period of

several days or even weeks. Selective pressure to develop such learning abilities would be less intense in pro-ovigenic parasitoids or those with a high daily egg maturation which would be more capable to exploiting high density patches in a day's visit. Longevity and egg maturation rate are, of course, not independent characteristics and presumably interact in favouring the evolution of learning abilities in some parasitoids.

Host specificity could also be associated with the evolution of learning abilities in parasitoids. Arthur (1971) has suggested that learning host associated cues will be more useful to polyphagous parasitoids than to oligophagous species because the former search for different species of hosts in different habitats, while the latter can be guided directly to its host by innate responses. In support of this hypothesis, he demonstrated that the oligophagous *Nemeritis canescens* exhibited less retention time of a conditioned response (to an olfactory stimulus) than the polyphagous *Itoplectis conquisitor* (conditioned to a visual stimulus) (Arthur, 1967, 1971). Comparison of learning abilities between species using stimuli of different modalities presents certain difficulties, but a reasonable theoretical argument can be made for Arthur's hypothesis.

For specialist parasitoids, the many-tiered host finding process culminates in an innate response to stimuli from a particular host species. In generalists, by contrast, innate responses take the parasitoid to a higher level of the host finding process (e.g., responses to leaves, grass stems), where a variety of suitable host species may be encountered as a consequence of more or less random foraging. In this latter context, associative learning would facilitate the location of the most abundant host species (because stimuli associated with this species would be most frequently reinforced). This would permit the generalist to become a 'specialist' on areas of highest host density. Although

both specialists and generalists benefit from the ability to associate environmental stimuli with areas of high host density, the advantage that such learning confers on a forager would seem to be greater for a generalist to whom such learner associations are the primary means of host finding. We might expect, then, that generalist parasitoids would be capable of more rapid associative learning (with longer retention time) than specialists. More experimental studies of foraging and conditioning are required to test this hypothesis.

The above discussion has applied to learning as a consequence of previous foraging experience. Another form of parasitoid learning, pre-imaginal conditioning (or conditioning to host stimuli upon emergence and before commencement of foraging) might be related to rather different characteristics of parasitoid biology. Assuming that there is some advantage to pre-imaginal conditioning (i.e., that it is not an artefact of a learning process adapted to later foraging situations), what might be its function? The presumed effect of such conditioning is to direct a parasitoid's foraging activities towards the host species it was reared on. The majority of emerging parasitoids will be conditioned to the host species which was most abundant in their parent's generation. Pre-imaginal conditioning may therefore increase the foraging efficiency of a parasitoid <u>if</u> the host species vary little in relative abundance over the generation time of the parasitoid. This presumes that the population dynamics of the host species are more or less 'uncoupled' from those of the parasitoid. In such 'uncoupled' interactions, we might expect pre-imaginal conditioning to be particularly advantageous to short-lived parasitoids which, unlike the long-lived parasitoids considered above, cannot 'learn to find' the most abundant host species through conditioning over a prolonged period.

In summary, the conclusions drawn from the present study of *Nemeritis* behaviour may apply generally to many parasitoid species. Responses resembling those of *Nemeritis* to host chemicals and oviposition stimuli have been demonstrated in other species, as have similar long and short-term changes in responsiveness to such stimuli. Patch leaving and avoidance may have somewhat different mechanisms in different species. The importance of learning in foraging time allocation is also likely to vary between species as a result of differences in the parasitoid's biology.

ECOLOGICAL AND EVOLUTIONARY IMPLICATIONS

The ecological implications of the *Nemeritis* behaviour studied in previous chapters may be simply summarized. Individual wasps, in the experimental set-ups employed, (1) enter new, unexploited patches at random (independent of host density therein), (2) spend more time on patches of higher host density, (3) spend less time on or avoid already visited patches and (4) spend less time on newly discovered patches if patches of the same density have been exploited previously.

Extrapolating these results to the population level, we may conclude that the behaviour described leads to aggregation by *Nemeritis* in areas of higher host density. However, when we consider populations of wasps, we must also consider the effect of interactions between individual parasitoids. This interference effect can influence the allocation of foraging time between patches by individual parasitoids and may, indeed, oppose the aggregative effect (Hassell et al., 1976; Cook and Hubbard, 1977). Therefore, it should be remembered in the discussion to follow that aggregation is only one component affecting the foraging time allocation of parasitoids.

Aggregation on patches of high host density can arise through a tendency in individual parasitoids to select high density patches or to spend more time on high density patches or both. In Experiment 8, *Nemeritis* did not appear more attracted to high density than to low density patches. These results, however, might reflect the closeness of the patches involved and the relative absence of air currents in the experimental chamber. As there is some evidence that *Nemeritis* is attracted to hosts from a distance, it seems reasonable that intense odour sources (high density patches) will attract more wasps than weak odour sources, simply because their odour plumes will be longer (more easily intercepted) and denser (more easily followed). In natural situations, then, wasps might be selectively attracted to high density patches and thereby compound the aggregation effect brought about by their spending more time in high density areas.

Aggregation in patches of high host density has been demonstrated in several other parasitoid-host systems. In the laboratory, Noyes (1974) demonstrated the potential for aggregation in *Diadromus pulchellus* foraging for pupae of *Acrolepia assectella* (Zell.). Patches in this experiment were small (10 cm) petri dishes containing host pupae and placed closed together in a closed chamber. The time spent by individual wasps at each host density increased as patch density increased, tending to level off at higher patch densities. Judging from the experimental design and previous experiments in the study, patches were probably entered at random and the biased allocation of patch time was entirely attributable to orthokinetic and klionkinetic responses to an odour detected near the host and, perhaps, to a change in movement following oviposition.

Akinlosotu (1973) demonstrated a similar increasing relationship between patch density and time spent on patches by individual *Diaeretiella rapae* attacking *Brevicoryne brassicae*. The patches in this experiment were cabbage leaves and, as with *Diadromus*, the relationship between patch time and host density per patch tended to level off with increasing densities. Wasps entered patches at random and the increase of patch time with patch density appears to be solely the result of change in movement following host contact.

Aggregation by parasitoids has rarely been demonstrated in the field. Selective attraction to intense sources of host-associated odour is suggested by observations on *Diaeretiella rapae* (Read et al., 1970), *Spilocryptus extrematus* (Marsh, 1937) and *Pimpla bicolor* (Ullyett, 1953), but experimental data on attraction over a range of stimulus intensities is lacking. Hubbard (1977) has obtained clear evidence of aggregation by the parasitoid *Apanteles glomeratus*, which attacks larvae of *Pieris brassicae*. He recorded the number of parasitoids visiting cabbage plants of different host density over repeated observation periods. The relationship obtained, expressed as host density per plant versus total parasitoid hours per density, was clearly sigmoid in form.

By contrast, Weseloh (1973) found no correlation between the density of gypsy moth larvae and the number of their parasitoids captured or observed in 6 ha^2 forest plots. In fact, the number of *Apanteles melanoscelus* (Ratzeburg) collected on sticky panels and the number of the tachinid *Blepharipa scutellata* (R.-D.) observed flying in these areas decreased with increasing host density. Although these results suggest no aggregation by these parasitoids, they could also reflect a change in their foraging behaviour (e.g., less time flying and more time searching substrates) which would be commensurate with both aggregation and the

presence of less flying insects at high densities.

Field data on predation intensity in host areas of different density yield some information on aggregation by natural populations of parasitoids. Such information must be interpreted carefully, however, as it is often difficult to distinguish a number-eaten-per-patch relationship predicted by non-aggregation (a fixed time strategy) from that predicted by aggregation. Aggregation would be best supported by a relationship which was accelerating at low densities, suggesting the existence of a patch density below which patches were visited much less often or patch time was so low as to result in very little parasitism.

Varley (1941) found that the percentage parasitism on populations of the knapweed gall fly increased as the percentage of host infested flower heads increased in an area. This means that a suprapropportional number of ovipositions occurred on hosts in patches of flower heads with high densities of host, suggesting aggregation. Varley's observations on the foraging behaviour of the parasitoid suggest that such concentration of foraging time in high density patches is solely the result of changes in movement following oviposition. Similarly, Lathrop and Nickels (1932) have shown higher percentage parasitism of the blueberry maggot, *Rhagoletis pomonella* (Walsh), by *Opius melleus* Gahan in blueberry patches of high maggot density. Hassell (1968) has found that percentage parasitism of the winter moth, *Operophtera brumata* (L.), by the tachinid *Cyzenis albicans* (Fall.) increases with host density per tree. Aggregation in this case results from arrestment (orthokinesis and klinokinesis) elicited by a chemical (sucrose) produced by the hosts during feeding (Murdie and Hassell, 1973).

Khorkhordin (1975, 1976) has studied the foraging of *Pleolophus*

basizonus in the field by placing artificial patches of host pupae of different density in the forest leaf litter. His interesting technique permits not only the determination of parasitism in different density patches, but also an approximation of how many patches of each density were visited and how many parasitoids visited each patch. From this latter measurement, a somewhat sigmoid aggregative effect is observed. Because no patch boundaries were recognised by the parasitoid and long-range attraction to host stimuli does probably not occur in *P. basizonus*, aggregation here is probably attributable to area-restricted search elicited by host contact. In contrast to these examples, several field studies of parasitism on host patches of different density have given no clear evidence of aggregation (Viktorov and Guryanov, 1974; Gurianov, 1977).

The significance of aggregation by parasitoids in natural situations will be understood only after further careful field studies of parasitism in patches of different host density and, ideally, actual observations on the allocation of foraging time between patches.

We turn now to the evolutionary implication of the present study and in particular what the foraging behaviour of *Nemeritis* reveals about allocation of foraging time and the optimization models discussed in Chapter 4. There are two ways by which we might compare experimental observations on foraging with the predictions of optimization models. One is to compare the rate of prey capture obtained with the theoretically optimal rate calculated for the experimental situation. This gives us a measure of how successful the forager is at maximizing its rate of prey capture. To establish a relative scale, we might compare the data as well to the capture rate predicted by random foraging.

The other method of comparing experimental results with optimal predictions is to examine how an animal forages, relative to how it should forage to realize the optimal capture rate. Such an examination of foraging mechanisms is a more useful means of testing optimal models as it is not as restricted to a particular experimental situation as the comparison of capture rates. It is this method which has been emphasized in the present study.

Mechanisms for optimal foraging have been discussed in Chapter 4. Interpreted in a very strict sense, these mechanisms differ from that described for *Nemeritis*, as has been discussed at various points in the text. If we consider optimal foraging mechanisms in a broader sense, however, the behaviour of *Nemeritis* bears some resemblance to optimal behaviour. Firstly, of the various possible patch time mechanisms (Figure 2) *Nemeritis* exhibits a rate-dependent mechanism, as would be essential for optimal foraging. Different optimal foraging models make different predictions about patch selection, but the ability of *Nemeritis* to select high density patches for foraging, not demonstrated in this experiment but possible in natural situations, could only serve to increase the foraging efficiency of the wasp. Optimization models assume that patches are not revisited once they have been exploited. Although *Nemeritis* does, in fact, revisit patches, the time spent there on return visits is greatly decreased and patch rejection develops after only a few encounters.

The effect of previous patch experience on foraging in *Nemeritis* differs from that predicted by the optimal foraging models of Krebs et al, (1974) and Charnov (1976) but it should be remembered that only short term changes in foraging behaviour were investigated. Experience over longer periods of time may affect the responsiveness to the chemical

patch stimulus, and thereby patch time, in different ways. For instance, Williams (1951) has observed that *Nemeritis* which have not been allowed to oviposit for several days probe more readily in response to host odour than wasps which have recently oviposited. If this reflects an increased responsiveness to the host stimulus, which would also be expressed as increased patch time, we might conclude that wasps having low oviposition rates over several days tend to spend more time on patches than wasps with high oviposition rate. This prediction resembles that of optimal foraging models regarding experience in rich and poor habitats.

There are several reasons why we might not expect to find in *Nemeritis* and other parasitoids foraging behaviour which ensures the maximization of oviposition rate. First of all, examination of time allocation at one or two levels of foraging, as has been done here with *Nemeritis*, may not give a clear indication of the efficiency of the overall foraging process. As mentioned in Chapter 2, parasitoid foraging may be viewed as a series of steps, each characterized by a more or less discrete set of stimuli and responses. As we include higher and higher levels of patchiness in our calculation of oviposition rates, these rates will clearly decrease, as more and more foraging time is spent finding areas containing prey. Optimal rates will probably decrease, as well, as the foraging process is expanded. However, we might anticipate an even more rapid decrease in the oviposition rate predicted by random foraging, because of the enormous increase in the area to be foraged as higher levels of patchiness are included (e.g., leaves to whole plants to fields of plants). These changes suggest that the efficiency of a particular foraging behaviour, measured relative to the extremes of optimal and random foraging, might change as the number of levels of patchiness considered is changed. Furthermore, inefficient or random

foraging observed one level of patchiness may give a poor indication of the adaptedness of the foraging process as a whole.

In more general terms, we may ask to what extent the maximization of oviposition rate may truly be equated with the maximization of individual fitness. The search for hosts may be influenced by factors which make rate maximization and suboptimal strategy (Krebs et al., 1974). Price (1975) has shown that the fecundity of different parasitoids, rather than converging on some maximum value, shows great variability which is clearly correlated with the biology, in particular the survivorship, of their hosts. Such variations in fecundity and in the searching behaviour of different parasitoids suggests that, although parasitoids should be adapted to dispose of their entire egg complement, an instantaneous rate of oviposition might be an inappropriate measure of the success of this process.

Finally, it should be observed that parasitoids allocate time to other activities than host finding, and optimal overall time budgets may appear suboptimal with regard to any particular activity. Indeed, from a behavioural point of view, it is often impossible to distinguish activities so that their optimality can be evaluated. A flying parasitoid, for instance, may be receptive to stimuli from both host areas and areas of adult food resources. The manner in which it orients in flight may be a compromise between selective pressures to optimize responsiveness to both sets of stimuli. Besides host finding, parasitoids allocate their active time to mating activities and, as just mentioned, foraging for adult food resources. Female parasitoids spend little time in mating activities, as it is males which generally assume the task of mate finding. Foraging for food is, however, probably a major component of the time budget of female parasitoids. Adult feeding on

plant pollen and nectar and on hosts has been shown to increase both the longevity and the fecundity of parasitoids (Leius, 1961a, b, 1963), which clearly contributes to overall fitness. Parasitoids which host feed enjoy the economy of combining time spent host finding with time spent finding food and exploit, as well, an ideal food source.

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APPENDIX A

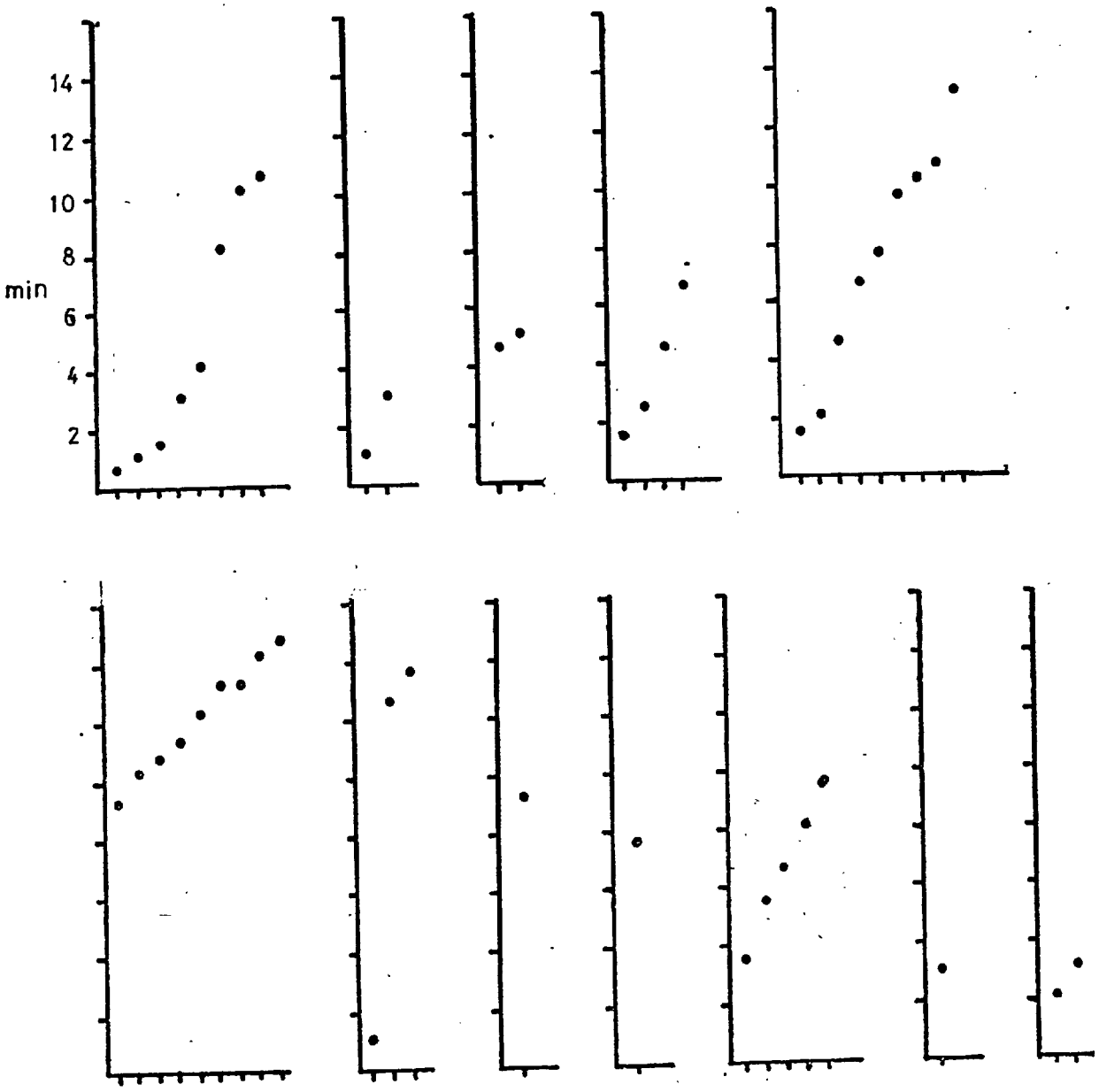
Program for patch-time simulation model of Chapter 5. This program was written with the assistance of Dr. Hugh Comins, Dept. of Zoology and Applied Entomology, Imperial College, London, and a description of the simulation is given in the text. The sub-routines employed in the program (GRAPHLIST, READLIST, PRINTLIST) were devised by Dr. Comins.

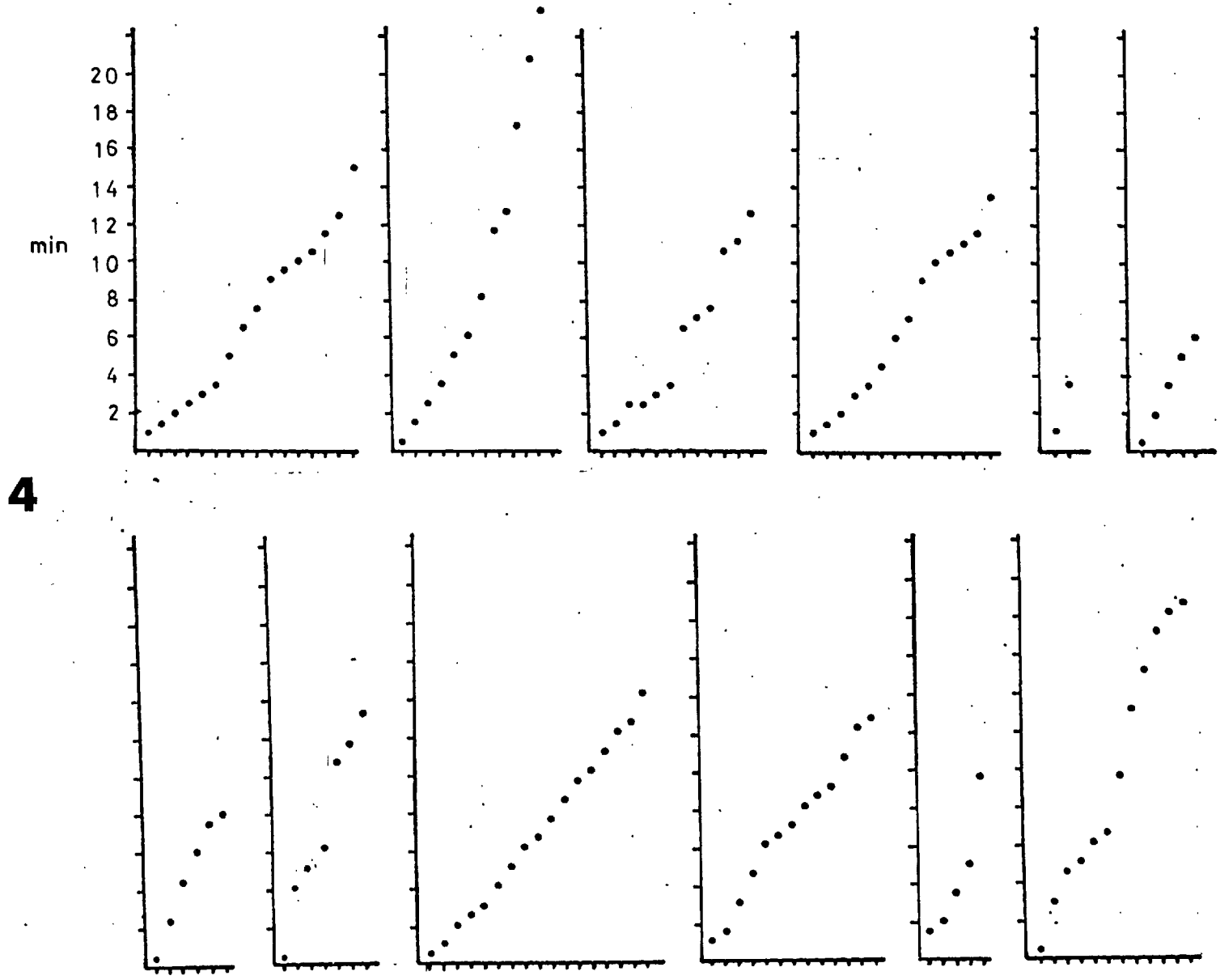
```
LNH

00100 NOTRACE
00110 PROGRAM PATCHTI(INPUT,OUTPUT,TAPE1,TAPE2)
00120 REAL INTER
00125 DATA SCALE/1./
00130 CALL BFLL(1)
00140 CALL EXEC(7HPATCHTI)
00150 20 READLIST HELP=21,GO=30,THRESH,PREY,A,TH,DECAY,INTER,OVIEFF
00155+,SCALE
00160 21 PRINT,'TIME ON PATCH FOR PRED AGGREGATION'
00170 PRINT,'THRESH=LEAVING THRESHOLD'
00180 PRINT,'A=ATTACK RATE, TH=HANDLING TIME'
00190 PRINT,'DECAY=STIMULUS DECAY'
00195 PRINT,'OVIEFF= EFFECT OF OVIPOSITION'
00200 PRINT,'INTER= INTERVAL BETWEEN FULLY EFFECTIVE OVIP STIMULI'
00210 PRINT,'THEN -- GO NSTEPS STSIZE ... NSTK STSZK'
00220 PRINT,'TO RUN PROGRAM FOR DIFFERENT INITIAL PREY NUMBERS'
00225 PRINT,'SCALE NONZERO - GRAPH OF PATCHT'
00250 GO TO 20
00260C ENTER STEPS
00270 30 PREY=0.
00275 K=0
00280 31 IF(INUM(RE).EQ.0)GOTO 20
00290 NS=RE
00300 IF(INUM(STZ).EQ.0)GOTO 20
00310 DO 40 IS=1,NS
00320 PREY=PREY+STZ
00325 K=K+1
00330C RUN
00340 TIM=0.
00350 ATTR=PREY
00360 INITP=PREY
00370 DO 45 IP=1,INITP
00380 NOP=INITP+1-IP
00400 TOD=(1.+A*TH*FLOAT(NOP))/A
00410 EFF=OVIEFF
00420 IF(IP.NE.1)EFF=OVIEFF*AMIN1(1.,TOD/INTER)
00430 ATTF=ATTR-TOD*DECAY
00446 IF(ATTF.LT.THRESH)GOTO 50
00466IF(ATTF.LT.THRESH)GOTO 50
00470 ATTR=ATTF+EFF
00480 TIM=TIM+TOD
00490 45 CONTINUE
00500 PATCHT=TIM+(ATTR-THRESH)/DECAY
00510 GOTO 60
00520 50 PATCHT=TIM+TOD*(ATTR-THRESH)/(ATTR-ATTF)
00530 60 IF(SCALE.NE.0.)GOTO 61
00533 PRINTLIST PREY,PATCHT
00535 GOTO 40
00538 61 CONTINUE
00539 GRAPHLIST K,SCALE/PATCHT
00540 40 CONTINUE
00550 GOTO 31
00560 END
READY.
```

APPENDIX B

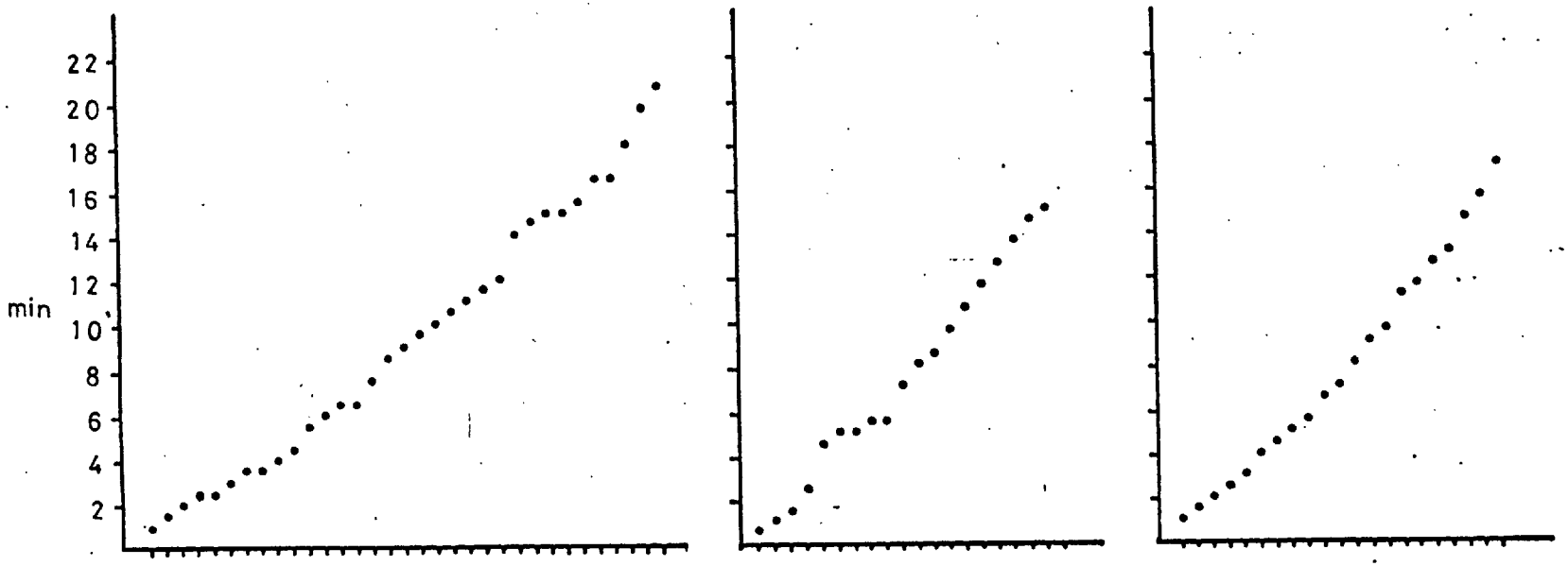
Cumulative plots from Experiment 6 of patch time versus oviposition number for each replicate at densities 1, 4, 8 and 16. The vertical distance between points represents the inter-oviposition interval, except for the last pair, where it represents the GUT. The slope of the points represents the rate of oviposition. The ordinate axis is marked at 2 min intervals, as shown in the first graph of each set of densities.

1

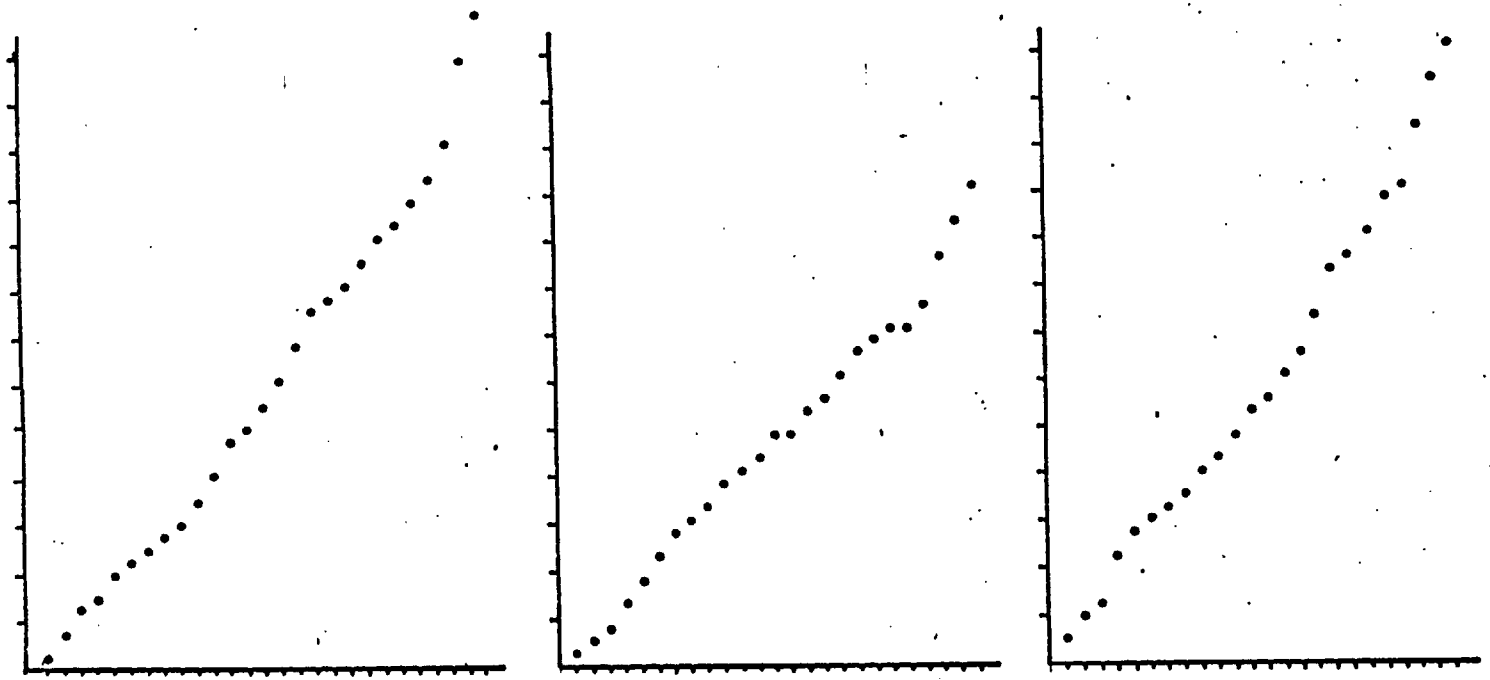


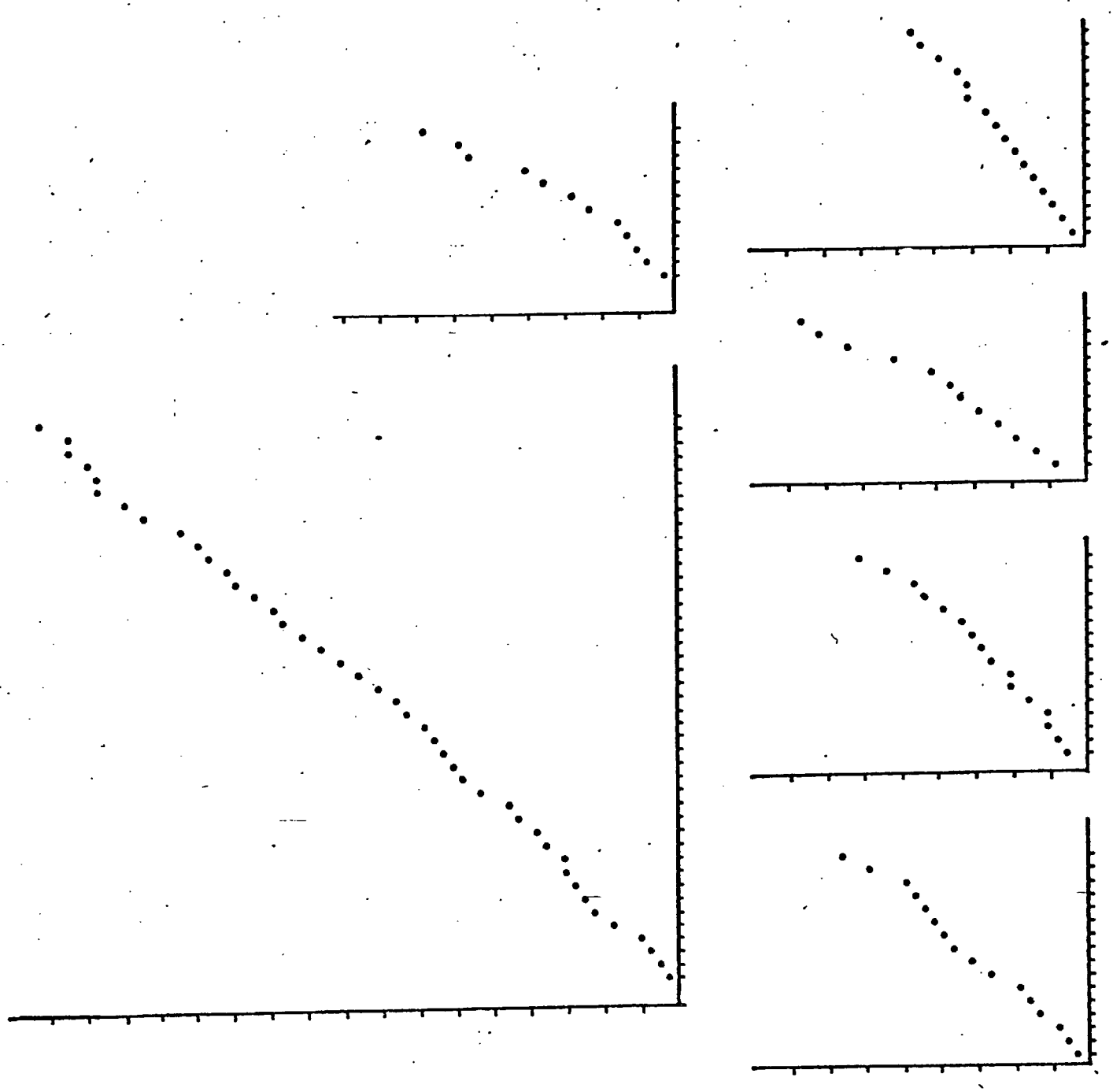


4

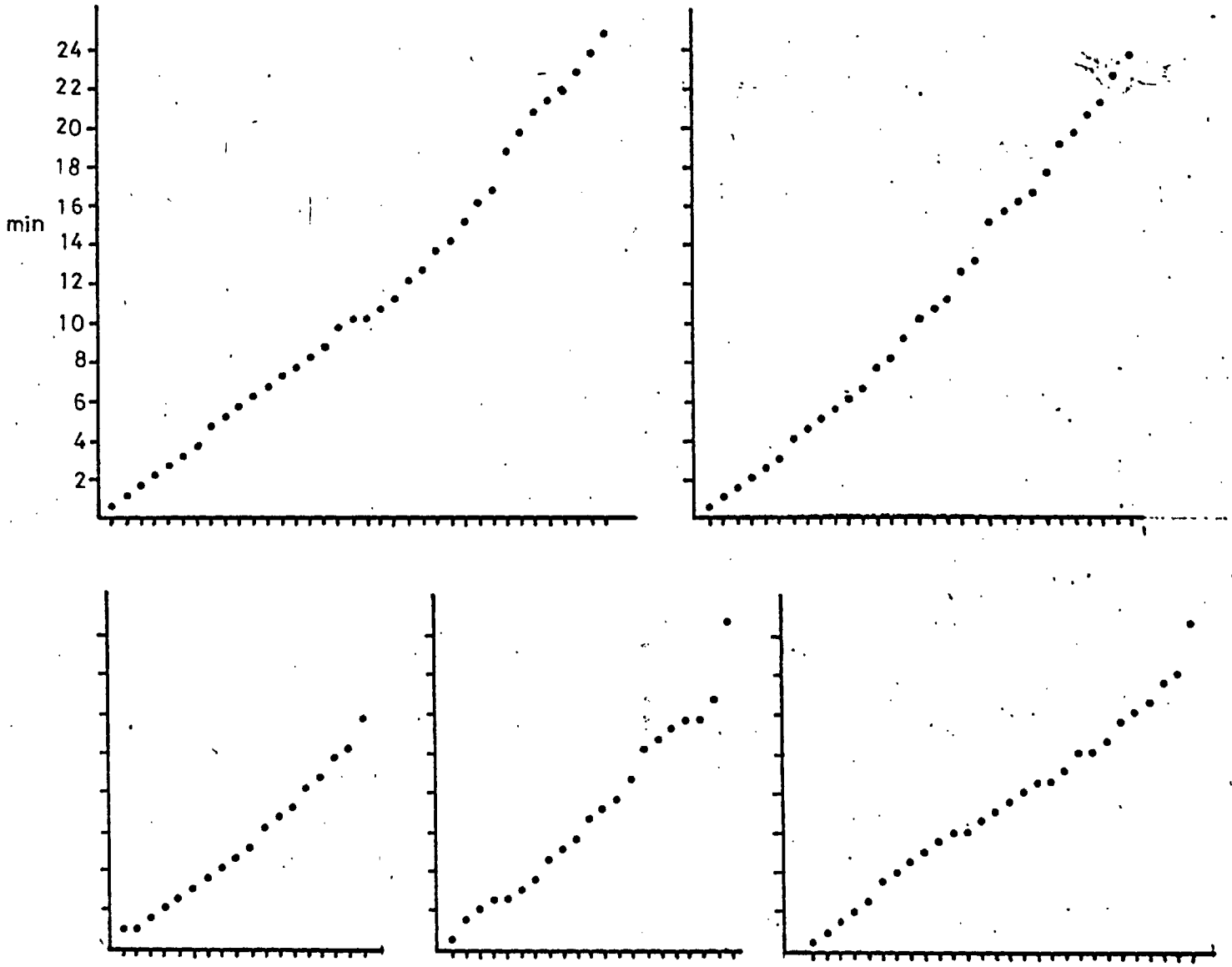


8





16



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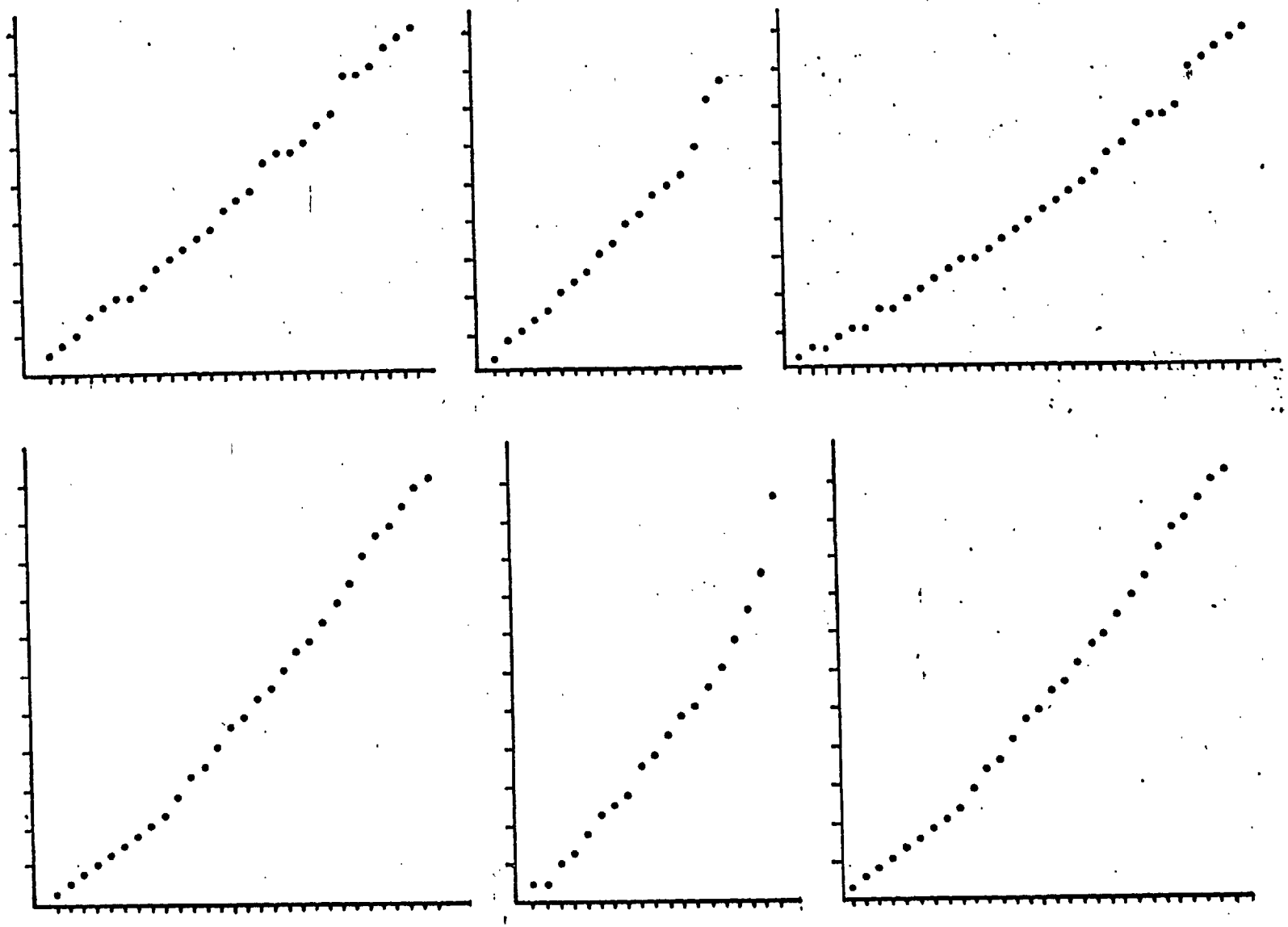
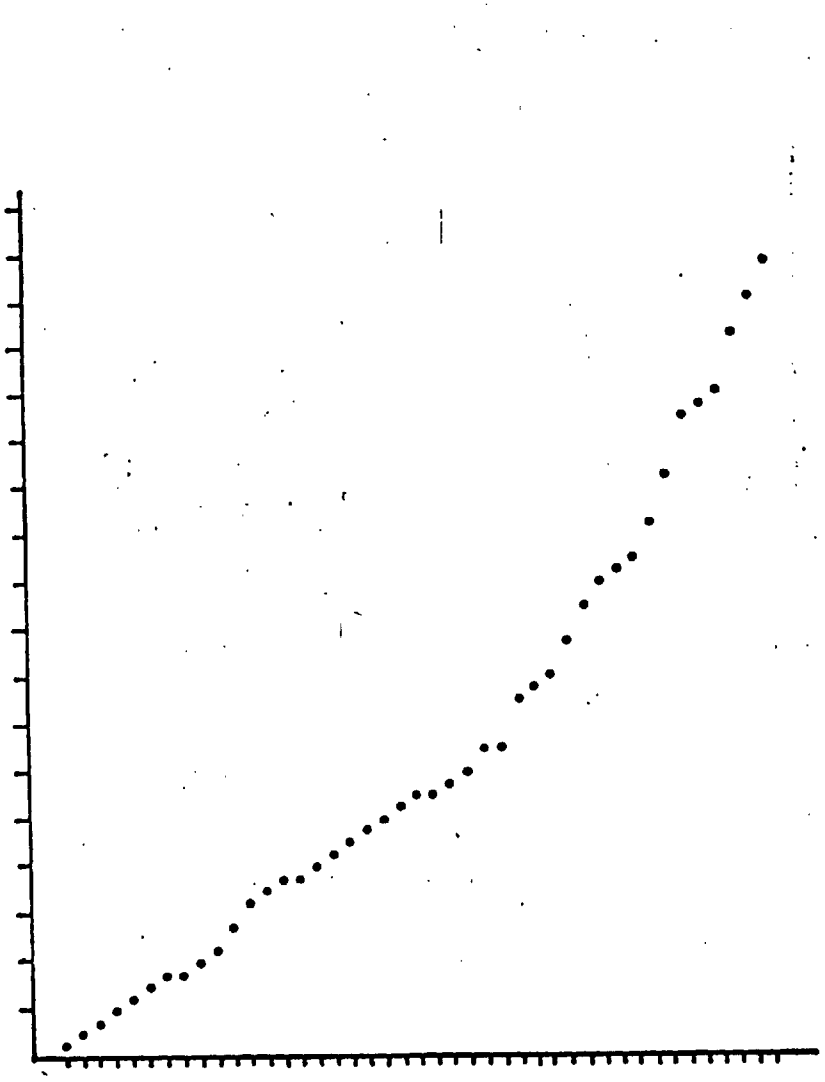
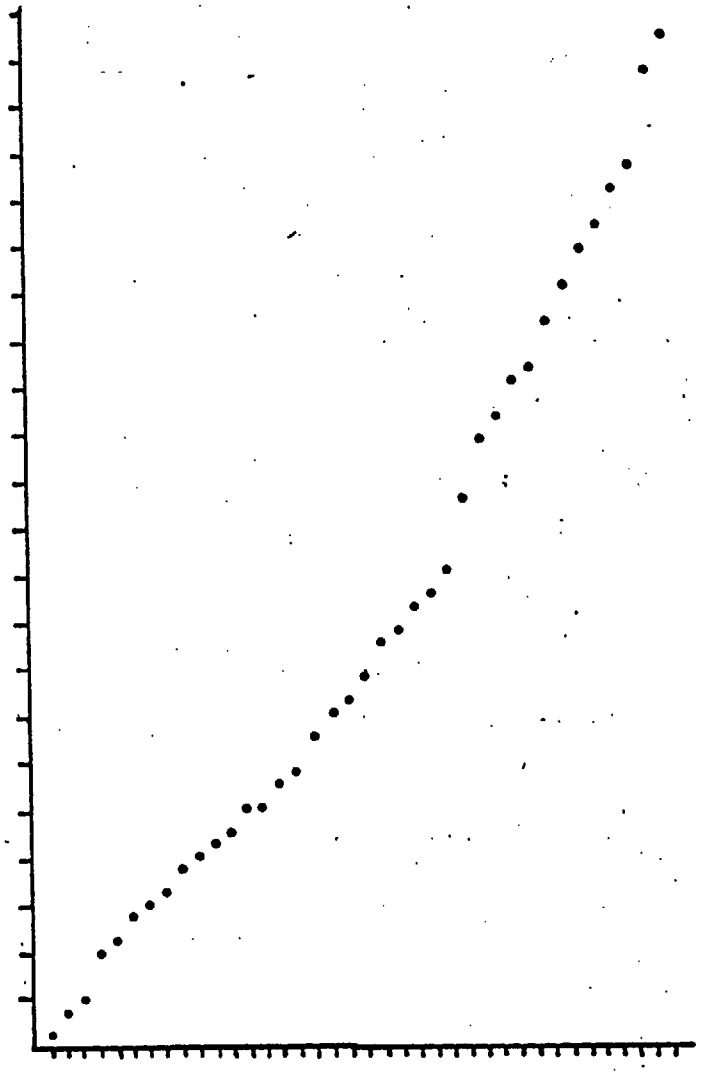


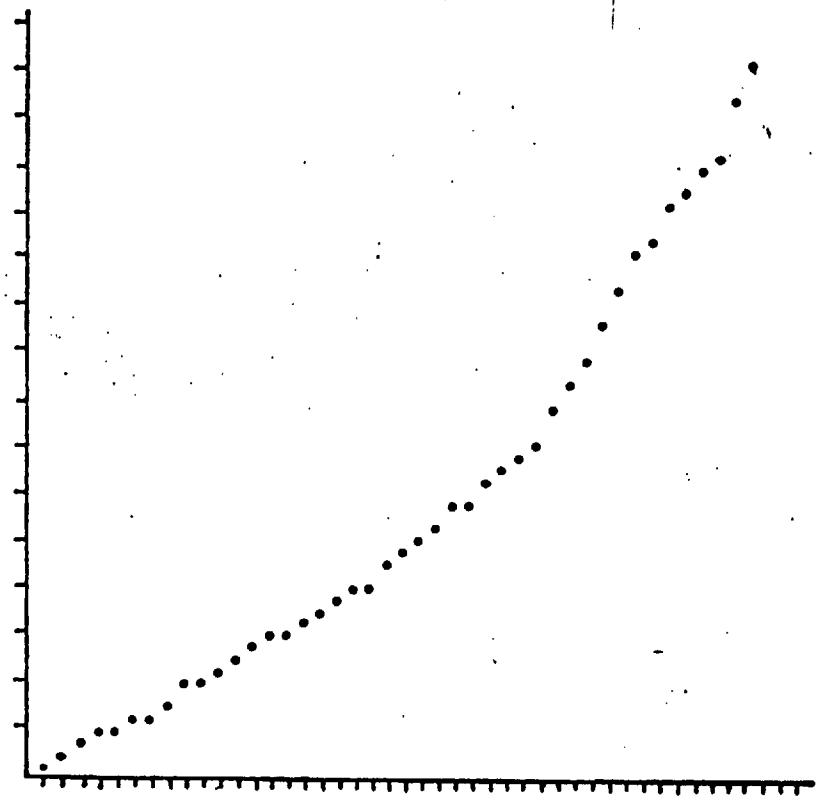
16

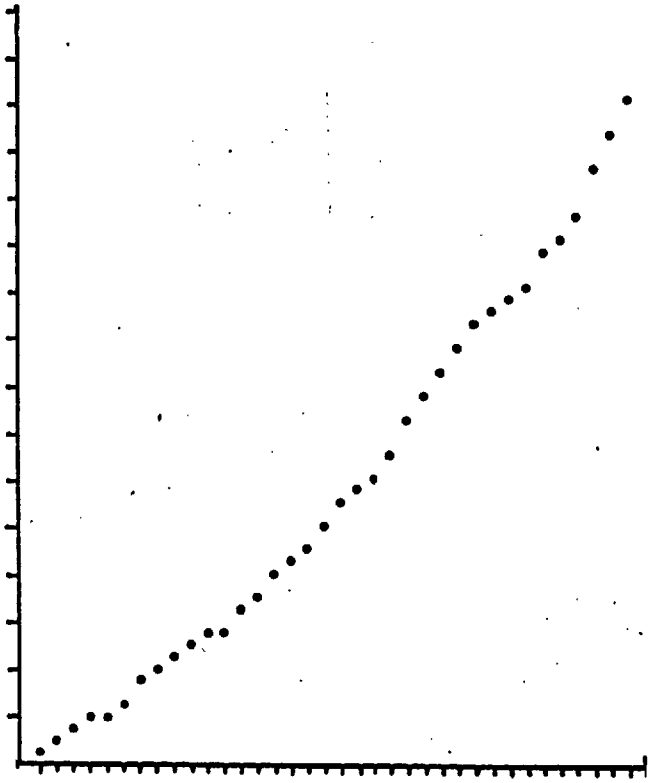


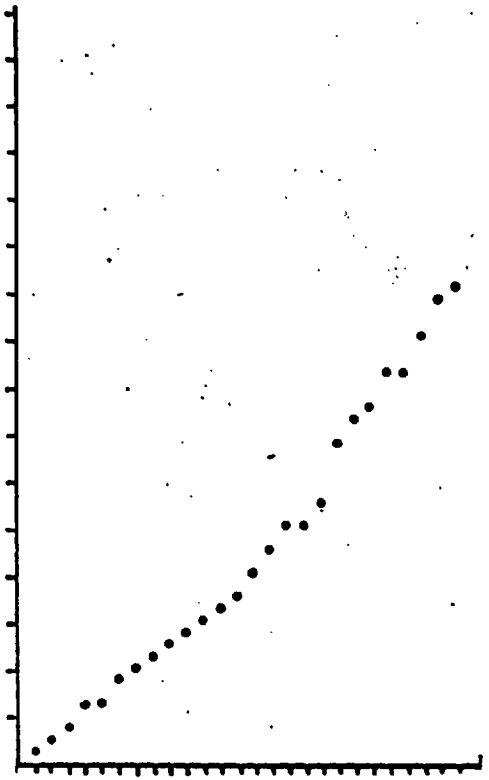


240.

16

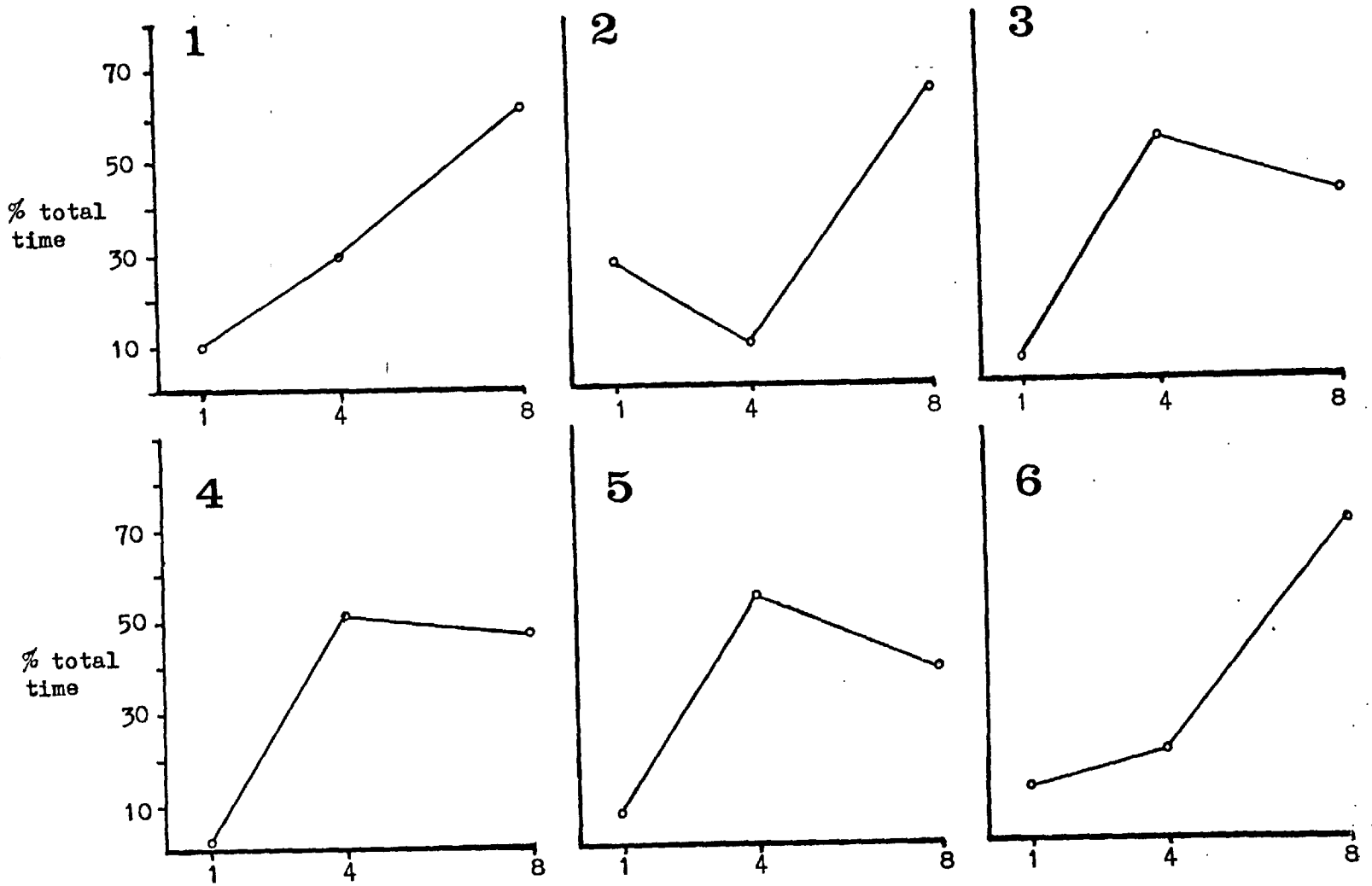


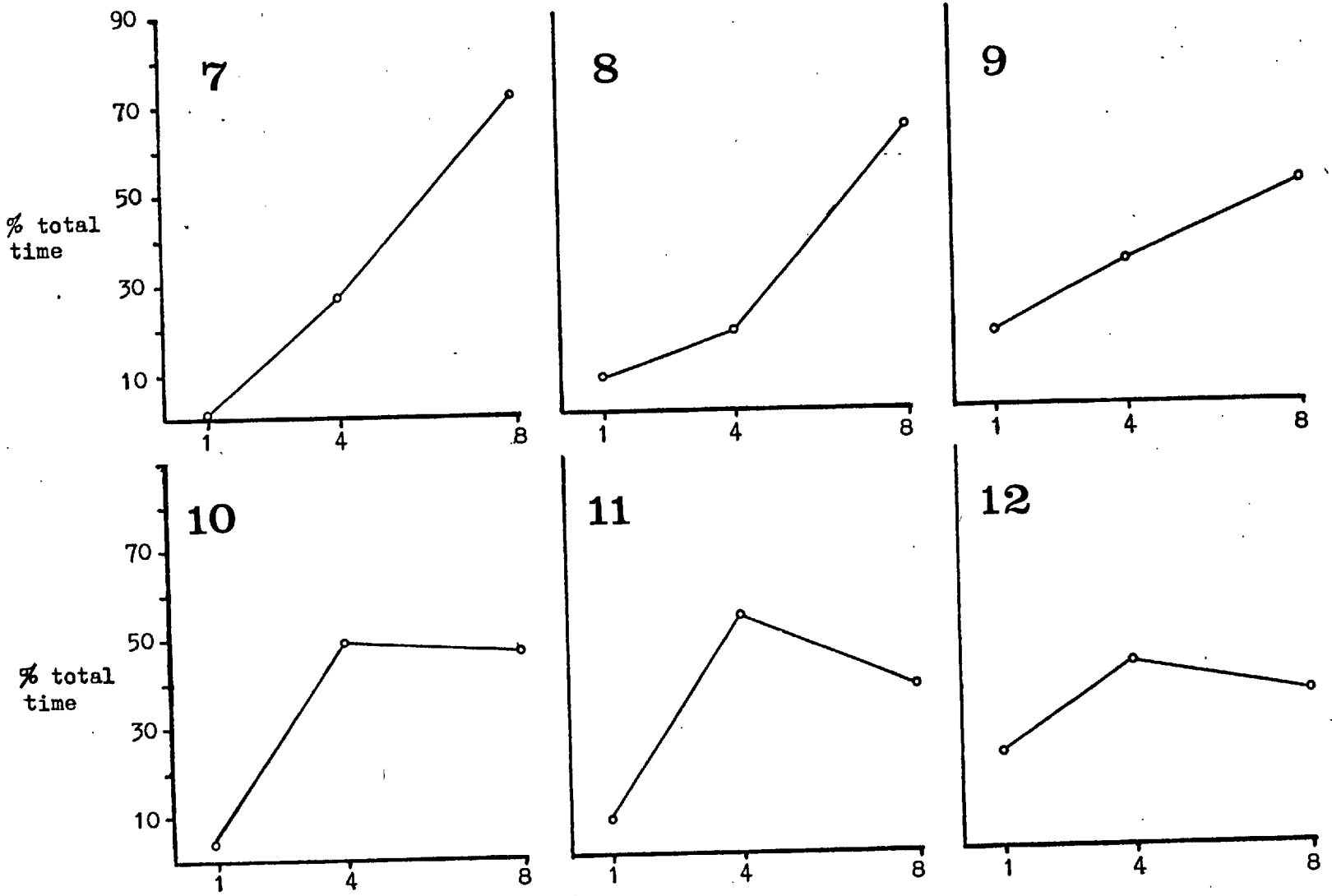


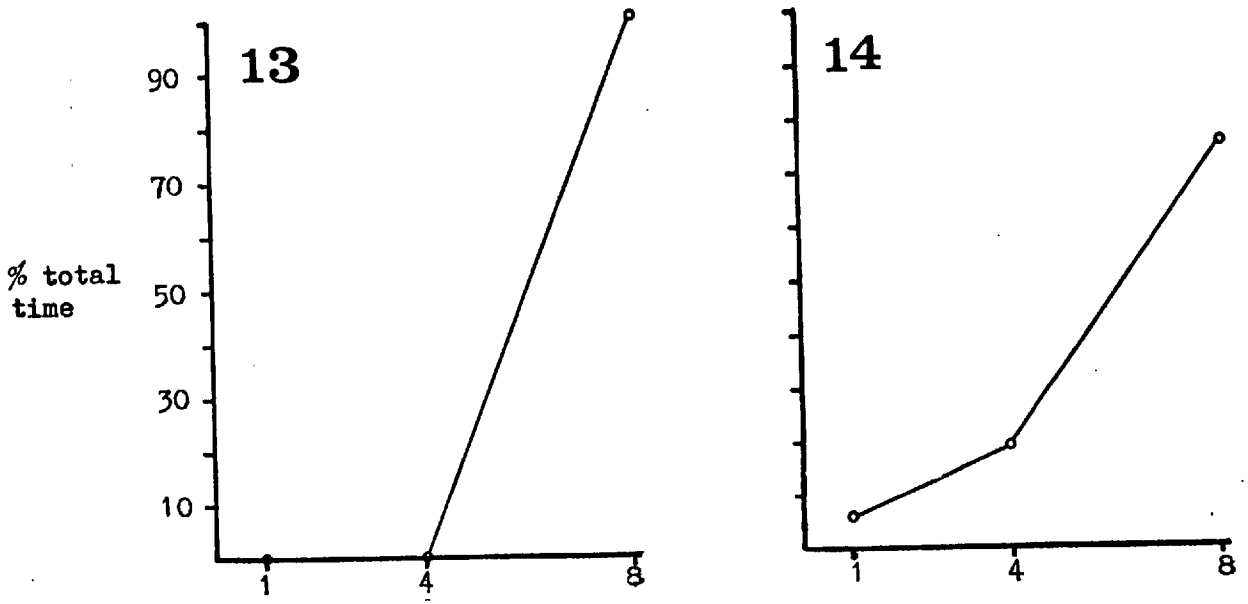


APPENDIX C

Per cent of total time spent on patches of different density in Experiment 8 for each of the 14 replicates. Abcissas - density of patch, ordinates - percent of total patch time over 120 min (100 min in #11) spent on patches of density 1, 4 and 8.


1
2
3
4
5
6
70
50
30
10
% total time
1
4
8


7
8
9
10
11
12
% total time
% total time
90
70
50
30
10
1
4
8


13
14
% total time
90
70
50
30
10
1
4
8
1
4
8