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THE FORAGING BEHAVIOR OF A PARASITOID WASP, *APHELINUS ASYCHIS*: A MODELLING APPROACH

by

Chao Li

M.Sc., Academia Sinica, Beijing, 1981

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

in the Department
of
Biological Sciences

SIMON FRASER UNIVERSITY

October 1992

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Dear Mrs. N. de Jong:

Thank you very much for your letter of September 17, 1992. I am very glad to know that the manuscript *Patch residence time and parasitism of Aphelinus asychis: a simulatin model* by Li et al. (ECOMOD 826) has in principle been found acceptable for publication. Enclosed please find a set of original figures as you required.

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Dear Dr. Enckell:

I am writing to ask your written authorization concerning the paper "The search pattern of a parasitoid wasp, *Aphelinus asychis*, for its host"(#3624) by Chao Li et al. (accepted by Oikos in February, 1992, now in press), to be used as a chapter of my Ph.D. dissertation, as required by the Simon Fraser University. I quote the relative regulations and guidelines as follows for your reference:

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The foraging behavior of a parasitoid wasp, Aphelinus asychis: A modelling approach

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ABSTRACT

Foraging by the solitary parasitoid wasp, *Aphelinus asychis* Walker (Hymenoptera: Aphidiidae, Aphelinidae) for its pea aphid host, *Acyrthosiphon pisum* Harris (Homoptera: Aphididae), on broad beans, *Vicia faba* L. cv. 'Broad Windsor', was examined in the laboratory. The process was studied within and between patches.

Within patches, the wasp searches randomly. Once a female wasp enters a patch, two kinds of behavioral "decisions" are made: host acceptance and patch leaving. The patch leaving decisions are apparently based on the identities of the last five hosts encountered which are stored in a "sliding memory window". When the proportion of parasitized, unacceptable hosts in the last five encounters exceeds 50%, or the wasp does not encounter any hosts within the initial giving-up-time, it leaves its current patch.

A female wasp can make three possible decisions upon encountering an aphid host: to lay an egg in the host; to feed on it; or to reject it. Decisions for accepting a host are optimally made with a success rate of 0.2. Host feeding can be described by a periodic function.

Wasps tended to search for patches on the same horizontal layer. The tendency to move upward was slightly greater in wasps with foraging experience than in those without experience. When a wasp is forced to search on an extended surface, its movement pattern between patches can be described by an area-restricted search or a random walk with limited time steps, with the length of each step being small relative to the surface.

A three-dimensional simulation incorporating all the information available about the system demonstrates that the model can predict the parasitism of *A. asychis* of its pea aphid hosts.

The study also showed that theory-driven simulations can be used in syntheses using information from an experimental system to demonstrate how to scale information from a lower level (within patches) to a higher level (between patches). This approach is useful for exploring possible population consequences of foraging processes.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I
GENERAL INTRODUCTION

Introduction

Studies on predation and parasitism have attracted population ecologists such as Lotka and Volterra in the 1920s and Nicholson and Bailey in the 1930s for several decades. Many mathematical models have been proposed to describe the interactions between predator and prey populations, or between parasite and host populations (Royama, 1970; Anderson & May, 1981; May & Hassell, 1988). Because of its convenience, the Lotka-Volterra model, being framed in continuous time based on differential equations that were later developed by Rosenzweig and MacArthur (1963) in graphical form, has been given much attention by mathematically oriented researchers (Croften, 1971; Anderson & May, 1978; May & Anderson, 1978). By contrast, the Nicholson-Bailey model which is based on difference equations that describe the dynamics of systems with discrete but synchronized generations of hosts and parasites, has been widely used as a basic model in studies on insect population dynamics (Hassell & May, 1973; Beddington *et al.*, 1975; Murdoch & Oaten, 1975; Hassell, 1978; Hassell & Comins, 1978).

Biologists are mostly concerned with the question: Is the model behavior consistent with reality? This concern arises because mathematical models, either analytical or numerical ones, are used to represent the dynamics of the observed interacting systems. Since populations do not normally become extinct in nature, the qualitative stability of the mathematical model has become the most important focus of exploration among researchers (Hassell & May, 1973; May, 1973, 1978; Murdoch &

Oaten, 1975; Noy-Meir, 1975; Anderson & May, 1978; May & Anderson, 1978). However, the dynamic properties of the Lotka-Volterra and Nicholson-Bailey models apparently do not help ecologists to explain the persistence of predator-prey or parasite-host interactions under natural conditions. This is for the reason of the Lotka-Volterra model's neutral trajectory in a phase plane diagram and of the Nicholson-Bailey model's expanding oscillations (*e.g.* Roughgarden, 1979). Thus, close attention has been paid to the conditions that stabilize the analytical mathematical models.

Some assumptions can tend to stabilize the models, including the following: limited prey growth in the absence of predators (Varley and Gradwell, 1963; Beddington *et al.*, 1975); a type III functional response (Holling, 1959, 1965; Hassell, 1978); mutual interference between predators (Hassell and Varley, 1969; Hassell and Rogers, 1972; Beddington *et al.*, 1975); temporal and spatial refuges for prey (Hassell and May, 1973); and aggregation of predators (Hassell and May, 1973; May, 1978; Chesson and Murdoch, 1986; Pacala *et al.*, 1990; Hassell *et al.*, 1991; Pacala & Hassell, 1991). By contrast, a type II functional response (Hassell, 1978) and time lag (Bartlett, 1957) are considered to be destabilizing factors. Aggregation has been considered as one of the strongest stabilizing factors effecting population dynamics. Because the clumping of predators or parasitoids on certain patches increases the probability that some prey or hosts will be found, while on patches with fewer predators or parasites the chances of encounter are decreased. For these reasons, the prey or host populations have a better chance of persisting, with the consequence that the predator-prey or parasite-host system will be less likely to become extinct. Generally speaking, all the behaviors of predators and parasites leading to sufficient variation in the probabilities of prey or hosts to be found, contribute to population stability (Pacala, *et al.* 1990; Pacala & Hassell, 1991). Murdoch and Stewart-Oaten (1989) suggested that results from discrete-time models overemphasized the importance of aggregation as a stabilizing mechanism, and aggregation frequently destabilizes the continuous-time, neutrally stable Lotka-Volterra predator-prey model. Recently, Ives (1992) analyzed three continuous-time models to show that the factors influencing population dynamics may be very different from those influencing discrete-time models. He demonstrated divers stability properties in different continuous-time models, a fact arguing against any generalizations derived from continuous-time models of host-parasitoid interactions. In all cases, regardless of whether or not hosts and parasitoids have either discrete, non-overlapping generations or continuous, overlapping generations, their population dynamics may be influenced by different behavioral mechanisms at the individual level. These mechanisms may be explicitly or implicitly incorporated in mathematical models of parasite-host population dynamics (Mangel and Roitberg, 1992). Therefore, it is important for population ecologists to understand the behavioral mechanisms of animals in making suitable assumptions.

Many population ecologists have studied how to incorporate individual behaviors into simple predator-prey models. For example, the functional response of predators concerns how predators react to different prey densities, and how this reaction changes the predation rate (Holling, 1959; 1965; Hassell, 1978; Abrams, 1982); and the population consequences of a predator's aggregation (Comins & Hassell, 1979; Murdoch & Stewart-

Oaten, 1989; Turchin & Kareiva, 1989; Pacala, *et al.* 1990; Pacala & Hassell, 1991; Godfray & Pacala, 1992) and antipredator behavior of prey (Hassell & May, 1985; Ives & Dobson, 1987; Parker, 1985).

Interest in the behavior of predators and parasitoids (as well as of other groups of organisms) has developed into a distinct discipline known as "behavioral ecology". Many early students of behavioral ecology were also interested in behavioral mechanisms of population regulation and species interactions (Pyke, 1984). The discipline has also attracted others who are interested in behavior itself. As a result of more people becoming interested in the field, behavioral ecology has witnessed tremendous development and growth during the last decade (Godfray & Hassell, 1987). The foraging behavior of predators and parasites is the most studied aspect in behavioral ecology, a topic often referred to as "Optimal Foraging Theory" (see review of Pyke, 1984). Optimal foraging theory focuses on an understanding of problems, such as patch selection, patch time allocation, and host choice (Stephens and Krebs, 1986). Behavioral ecologists are concerned with the ways in which parasitoids are adapted to forage efficiently, in particular, how they cope with the exploitation of patchily distributed host populations. Individuals of animal populations are commonly not distributed homogeneously throughout the environment but occur in groups. This grouping poses a problem for parasitoids. In order to exploit clumped hosts efficiently, a parasitoid must "decide" which areas or "patches" to visit and when to move from one patch to another. All these behavioral decisions may be hierarchically structured (Senft *et al.*, 1987; Kotliar & Wiens, 1990; Holling, 1992). Employing the term "behavioral decisions" does not mean cognition, but rather means that different expressions of a wasp's behavior occur under different circumstances. Each parasitoid species has its own foraging strategy, defined as a set of basic rules for scanning and movement that result in effective host encounters (Smith, 1974; Wiedenmann & O'Neil, 1992). The strategy is important for understanding the parasitism process. Practically, a foraging strategy is also important for selecting efficient biological control agents (Greathead, 1986; van Lenteren, 1986). Searching efficiency, or attack rate, results from interactions between an animal's foraging strategy and host's conditions, especially host distribution. Whether a particular foraging strategy is "good" or "bad" for a species is determined by the parasite's characteristics. It is reasonable to assume that the foraging strategies that persist are those that make the least demands on information while still permitting consistent survival and reproduction over long periods (Holling, 1992).

Many behavioral ecologists are interested in particular behaviors and often restrict themselves to single levels of decision processes, or they concentrate on one aspect of the whole process. In fact, only a few papers in behavioral ecology have considered the implications of a variety of behaviors in a whole population. Thus, it would be more valuable if we observed the whole foraging process within a particular experimental system, and took the system modelling approach to combine separate observations in the same system, into a model to show the mechanisms used by an animal. In this way, a more profound understanding of the foraging process within a specific experimental system could be obtained, a result contributing to the understanding of population dynamics.

The disciplines of behavioral ecology and population dynamics have separate goals and problems to deal with (Hassell and May, 1985).

Behavioral ecology is concerned with the way that animals behave and the adaptive significance of behavior patterns. It generally focuses on phenomena within generations. In doing so, it often ignores the consequences of behavior for population dynamics. Usually, its goal is to show how behaviors affect inclusive fitness. By contrast, population dynamics focuses on the demographic processes of births, deaths, immigration and emigration, and factors that affect all of these. It is concerned with phenomena between generations, and it often ignores the behavioral mechanisms that may underlie those processes. Sometimes it considers the individual hosts and parasitoids as static and applies rules of chemical kinetics to their encounters (Godfray & Hassell, 1987); its goal in general is to show demographic consequences. Both disciplines have limits: behavioral ecology sacrifices breadth for depth and population dynamics does the reverse. The relationship between the two disciplines is lop-sided: population dynamics cannot completely ignore behavior, but behavioral ecology need not be concerned with the dynamic consequences of behavior.

Recently, many ecologists have emphasized the need to establish connections between specific behaviors and its population consequences (Real 1983; Sibley and Smith 1985; Lomnicki 1988; Koehl 1989). Mooney and Lubchenco (1990) even suggested that the link between specific actions and population phenomena should be a major ecological research objective for the next decade. To bridge the gap that exists between traditional population dynamics and behavioral ecology is to study the population consequences of adaptive behavior, *i.e.*, to identify which kinds of behaviors are most likely to influence host population dynamics and how these behavioral "decisions" will influence host population dynamics? Foraging behavior is one such kind of behavior. The first step in linking foraging behavior of a parasitoid to its host population dynamics is to develop a research tool, a detailed simulation model, that can describe the foraging behavior process. My thesis is an attempt toward this first step. Here, I employ a mechanistic modelling approach and an experimental system consisting of a species of solitary parasitoid wasp, *Aphelinus asychis* Walker (Hymenoptera: Aphelinidae), searching for its host, the pea aphid, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae), on broad bean, *Vicia fabae* L. (cv. 'Broad Windsor').

Normally, three basic processes can be identified when a parasitoid forages for its hosts: The first is patch selection, *i.e.*, how a wasp finds a suitable patch for foraging. The second is patch time allocation, *i.e.*, the questions of how a wasp allocates its time to searching, resting, handling, etc., and how a wasp decides whether or not to leave the patch. The third is the decision that is required when a wasp encounters a host. Here, the question addresses how a wasp decides whether to lay an egg in, or to reject, or to feed on a host that it has encountered. These three basic processes correspond to different levels of a host-parasitoid interaction system, *i.e.*, between patches, within patches, and event decisions. I shall use a patch as a basic unit throughout my thesis because of its important role in studies of foraging behavior. Thus, event decisions are included in parasitism dynamics within patches.

The objectives of this study are (1) to give a detailed description of the female parasitoid's foraging behavior for its pea aphid hosts on broad bean plants; and (2) to show that theory-driven simulation models can be used in syntheses from the information available about an experimental system to demonstrate how one can scale information at a lower level (within patches) up to a higher level (between patches), and thus to provide a useful tool for exploring the possible population consequences of foraging processes involved in the system.

Outline of the thesis

If we divide a habitat within which a parasitoid wasp forages for its aphid hosts into a number of patches, then the foraging processes that occured in my experimental system can be divided into two levels: within and between patches. The major components at the level of between patches are the foraging dynamics within patches and the movement pattern of the wasp between patches. Important factors that effect foraging dynamics within patches are the search pattern and the rules for host acceptance and patch leaving. The foraging dynamics can be evaluated based on the number of hosts parasitized and the time budget of the wasp for different behaviors.

The thesis consists of seven chapters. Since the foraging dynamics of a parasitoid species within patches (including host acceptance decisions) are critical for an understanding of the foraging process, I have paid most attention to them, the foraging dynamics within patches are presented in chapters II to V. Chapter II examines the within-patch search patterns of a wasp and uses a simulation model to find the general conditions under which a random or a systematic search pattern would be favored by natural selection. Chapter III extends the concept of initial giving up time (IGUT) to include non-host-containing patches and addresses questions related to the duration of parasitoid search in non-host-containing patches, and which cues are used to determine search time allocation. Chapter IV deals with the rules used by a wasp for making patch-leaving decisions when searching for pea aphids as hosts and as sources of nutrients on broad bean-leaflet patches. Chapter V develops a simulation model to predict the patch residence time and rate of parasitism of the wasp. A host acceptance decision matrix is used in the model. The matrix which is calculated by a dynamic programming technique contains the optimal responses of the wasp after encountering a host and examining it. The model is then used for testing the hypothesis that a wasp's decision to leave a patch, or to accept or to reject a host is based on information about previously encountered hosts stored in a "sliding memory window". The simulation results suggest that searching females of *A. asychis* store information about a changing environment in five units of a sliding memory window. In Chapter VI, I first present the observations of the movements of the wasp between patches. Then a three-dimensional simulation model is developed based on the information available to determine the foraging consequences of the wasp's movement patterns between patches. I demonstrate that the model can predict the parasitism of *A. asychis* to its pea aphid hosts as shown by the comparison of the results from simulations with those from experiments. The last Chapter covers the general conclusions and discussion.

Parasitoid biology and behavior

Aphelinus asychis was introduced into North America from Iran for the biological control of the greenbug, *Schizaphis graminum* (Rondani) (Raney, *et al.*, 1971; Jackson and Eikenbary, 1971). The wasp is a solitary parasitoid with a wide range of host species, including the pea aphid (Jackson and Eikenbary, 1971; Cate *et al.* 1973; Bai and Mackauer, 1990). The adult wasp is about 1 mm in length, has 17-21 days in mean longevity, and prefers temperatures from 26-29 ^{o}C (Hartley, 1922; Force and Messenger, 1964; Jackson & Eikenbary, 1971; Raney *et al.*, 1971).

A. asychis females may behave either as parasitoids by depositing an egg into an attacked aphid, or as predators by host-feeding. The wasps can discriminate between unparasitized and previously parasitized aphids and normally reject the latter for oviposition (Bai & Mackauer, 1990). Usually females lay a single egg per attack. The developing larva eventually kills its host and pupates inside the dried body of the dead aphid, which is called a mummy.

Nutrients obtained by host feeding are probably necessary for oogenesis in *Aphelinus* (DeBach, 1943; Askew, 1971). Oogenesis occurs throughout the adult life of the wasp (Schlinger & Hall, 1959). Therefore, periodic host feeding is necessary to obtain nutrients for continuous oogenesis. However, *A. asychis* usually does not feed on parasitized aphids (Bai and Mackauer 1990), a behavior described as non-concurrent and destructive host-feeding (Jervis and Kidd, 1986).

The attack process of *A. asychis* was described by Boyle and Barrows (1978) and Gerling *et al.* (1990). When encountering a host, the wasp begins to sway its body from side-to-side during "external examination". Then it rapidly turns about 180° and everts its ovipositor and stabs at the aphid. When its ovipositor pierces the aphid, "internal examination" begins. During this step, the wasp stands motionless and injects a paralyzing venom into the host. Usually, it is difficult to distinguish between the period of internal host examination and oviposition. Experimental results show that oviposition has occurred when the ovipositor was inserted in an aphid for at least 60 - 80 sec (Boyle & Barrows, 1978; Bai & Mackauer, 1990). Successful parasitism by *A. asychis* on pea aphids is dependent on the behavioral interactions between the two species (Gerling *et al.*, 1990).

References

Abrams, P. A. 1982. Functional responses of optimal foragers. - *The American Naturalist*, 120: 382-390.

Anderson, R. M., and May, R. M. 1978. Regulation and stability of host-parasite population interactions: I. Regulatory processes. - *Journal of Animal Ecology* , 47:219-247.

Anderson, R. M., and May, R. M. 1981. The population dynamics of microparasites and their invertebrate hosts. - *Philosophical Transactions of the Royal Society, London. B*, 291, 451-524.

Askew, R. R. 1971. *Parasitic Insects*. New York: American Elsevier. 820 pp.

Bai B. and Mackauer, M. 1990. Oviposition and host feeding patterns in *Aphelinus asychis* at different aphid densities. - *Ecological Entomology* , 15: 9-16.

Bartlett, M. S. 1957. On theoretical models for competitive and predatory biological systems. - *Biometrika*, 44: 27-42.

Beddington, J. R., Free, C. A., and Lawton, J. H. 1975. Dynamic complexity in predator-prey models framed in difference equations. - *Nature*, 255: 58-60.

Boyle, H. and Barrows, E. M. 1978. Oviposition and host feeding behavior of *Aphelinus asychis* (Hymenoptera: Chalcidoidea: Aphelinidae) on *Schizaphis graminum* (Homoptera: Aphididae) and some reactions of aphids to this parasite. - *Proceedings of the Entomological Society of Washington*, 80(3): 441-455.

Cate, R.H., Archer, T.L., Eikenbary, R.D., Starks, K.J., and Morrison, R.D., 1973. Parasitization of greenbug by *Aphelinus asychis* and the effect of feeding by the parasitoid on aphid mortality. - *Environmental Entomology*, 2(4): 545-553.

Chesson, J. and Murdoch, W. W. 1986. Aggregation of risk: relationships among host-parasitoid models. - *The American Naturalist*, 127: 696-715.

Comins, H. N. and Hassell, M. P. 1979. The dynamics of optimally foraging predators and parasitoids. - *Journal of Animal Ecology*, 48: 335-351.

Croften, H. D. 1971. A model of host-parasite relationships. - *Parasitology*, 63: 343-364.

DeBach, P. 1943. The importance of host-feeding by adult parasites in the reduction of host populations. - *Journal of Economic Entomoloty*, 36: 647-658.

Force, D. C., and Messenger, P. S. 1964. Duration of development, generation time, and longevity of three hymenopterous parasites of *Therioaphis maculata*, reared at various constant temperatures. - *Annals of the Entomological Society of America*, 57: 405-413.

Gerling, D., Roitberg, B. D. and Mackauer, M. 1990. Instar-specific defense of the pea aphid, *Acyrthosiphon pisum*: influence on oviposition success of the parasite *Aphelinus asychis* (Hymenoptera: Aphelinidae).- *Journal of Insect Behavior*, 3(4): 501-514.

Godfray, H. C. J. and Hassell, M. P. 1987. Natural enemies may be a cause of discrete generations in tropical insects. - *Nature*, 327: 144-147.

Godfray, H. C. J. and Pacala, S. W. 1992. Aggregation and the poulation dynamics of parasitoids and predators. - *The American Naturalist*, 140: 30-40.

Greathead, D. J. 1986. Parasitoids in classical biological control. In *Insect Parasitoids*. Eds. Waage, J. and Greathead, D. page 290-318.

Hartley, E. A. 1922. some bionomics of *Aphelinus semiflavus* (Howard). - *Ohio Journal of Sciences*, 22(8): 209-237.

Hassell, M. P. 1978. *The Dynamics of Arthropod Predator-Prey Systems*. Princeton University Press. Princeton, New Jersey.

Hassell, M. P. & Comins, H. N. 1978. Sigmoid functional responses and population stability. - *Theoretical Population Biology,* 14: 62-67.

Hassell, M. P. and Rogers, D. J. 1972. Insect parasite responses in the development of population models. - *Journal of Animal Ecology*, 41: 661-676.

Hassell, M. P. and May, R. M. 1985. From individual behavior to population dynamics. - In *Behavioral Ecology: Ecological Consequences of Adaptive Behaviour*, Eds. Sibly, R. M. and Smith, R. H., Page 3-32.

Hassell, M. P. and May, R. M. 1973. Stability in insect host-parasite models. - *Journal of Animal Ecology*, 42: 693-736.

Hassell, M. P. and May, R. M. 1985. From individual behaviour to population dynamics. In *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour*. Eds. Sibly, R. M. and Smith, R. H. Blackwell, Oxford. Pages 3-23.

Hassell, M. P. and Varley, G. C. 1969. New inductive population model for insect parasites and its bearing on biological control. - *Nature*, 223: 1133-1136.

Hassell, M. P., May, R. M., Pacala, S. W., and Chesson, P. L. 1991. The persistence of host-parasitoid associations in patchy environments. I. A general criterion. - *The American Naturalist*, 138: 568-583.

Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. - *The Canadian Entomologist,* 91: 385-398.

Holling, C. S. 1965. The analysis of complex population processes. - *The Canadian Entomologist,* 96: 335-347.

Holling, C. S. 1992. Cross-scale morphology, geometry and dynamics of ecosystems. - *Ecological Monographs*, In Press.

Ives, A. T. 1987 Antipredator behavior and the population dynamics of simple predator-prey systems. - *The American Naturalist*, 130: 431-447.

Ives, A. T. 1992. Continuous-time models of host-parasitoid interactions - *The American Naturalist,* 140: 1-29.

Jackson, H. B., and Eikenbary, R. D. 1971. Bionomics of *Aphelinus asychis* (Hymenoptera: Eulophidae), an introduced parasite of the sorghum greenbug. - *Annals of the Entomological Society of America,* 64: 81-85.

Jervis, M. A., and Kidd, N. A. C. 1986. Host-feeding strategies in hymenopteran parasitoids. - Biological Review, 61: 395-434.

Koehl, M. A. R. 1989. Discussion: from individuals to populations. - Pages 39-53 in J. Roughgarden, R. M. May, and S. A. Levin, eds. *Perspectives in ecological theory*. Princeton University Press, Princeton, N.J.

Kotliar, N. B. and Wiens, J. A. 1990. Multiple scales of patchiness and patch structure: a hierarchican framework for the study of heterogeneity. - *Oikos*, 59: 253-260.

Lomnicki, A. 1988. *Population Ecology of Individuals*. Princeton University Press, Princeton, New Jersey.

Mangel, M. and Roitberg, B. D. 1992. Behavioural stabilization of host-parasite population dynamics. - *Theoretical Population Biology*, (In press).

May, R. M. 1973. *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton.

May, R. M. 1978. Host-parasitoid systems in patchy environments: a phenomenological model. - *Journal of Animal Ecology*, 47: 833-843.

May, R. M. & Anderson, R. M. 1978. Regulation and stability of host-parasite population interactions. II. Destabilizing processes. - *Journal of Animal Ecology*, 47: 249-268.

May, R. M., and Hassell, M. P. 1988. Population dynamics and biological control. - *Philosophical Transactions of the Royal Society, London B,* 318,129-169.

Mooney, H., and Lubchenco, J. 1990. Looking ahead. - *Bulletin of the Ecological Society of America*, 71: 4-5.

Murdoch, W. W. and Oaten, A. 1975. Predation and population stability. - *Advances in Ecological Researches,* 9: 2-131.

Murdoch, W. W. and Stewart-Oaten, A. 1989. Aggregation by parasitoids and predators: effects on equilibrium and stability. - *The American Naturalist*, 134: 288-310.

Noy-Meir, I. 1975. Stability of grazing systems: An application of predator-prey graphs. - *Journal of Ecology*,, 63: 459-481.

Pacala, S. W., and Hassell, M. P. 1991. The persistence of host-parasitoid associations in patchy environments. II. Evaluation of field data. - *The American Naturalist*, 138(3): 584-605.

Pacala, S. W., Hassell, M. P., and May, R. M. 1990. Host-parasitoid associations in patchy environments. - *Nature*, (Lond.), 344: 150-153.

Parker, G. A. 1985. Population consequences of evolutionarily stable strategies. In *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour*. Eds. Sibly, R. M. and Smith, R. H. Blackwell, Oxford. Pages 33-58.

Pyke, G. H. 1984. Optimal foraging theory: a critical review. - *Annual Reviews of Ecology and Systematics*, 15: 523-575.

Raney, H. G., Coles, L. W., Eikenbary, R. D., Morrison, R. D., and Starks, K. J. 1971. Host preference longevity, developmental period, and sex ratio of *Aphelinus asychis* with three sorghum-fed species of aphids held at controlled temperatures. - *Annals of the Entomological Society of America*, 64: 169-176.

Real, L. A. 1983. Microbehavior and macrostructure in pollinator-plant interactions. - Page 287-304 in *Pollination Biology*. (L. A. Real, ed.) Academic Press, New York.

Royama, T. 1970. A comparative study of models of predation and parasitism. - *Researches on Population Ecology,* 1: 1-91.

Rosenzweig, M. L., and MacArthur, R. H. 1963.Graphical representation and stability conditions of predator-prey interactions. - *The American Naturalist*, 97: 209-223.

Roughgarden, J. 1979. *Theory of Population Genetics and Evolutionary Ecology: An Introduction*. New York, Macmillan.

Schlinger, E. I., and Hall, J. C. 1959. A synopsis of the biologies of three imported parasites of the spotted alfalfa aphid. - *Journal of Economic Entomology*, 52: 154-157.

Senft, R. L., Coughenour, M. B., Bailey, D. W., Rittenhouse, L. R., Sala, O. E., and Swift, D. M. 1987. Large herbivore foraging and ecological hierarchies. - *BioScience*, 37: 789-799.

Sibley, R. M. and Smith, R. H. (Eds.) 1985. *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour*. Blackwell Scientific Publications, Oxford.

Smith, J. N. M. 1974. The food searching behavior of two European thrushes. II. The adaptiveness of the search patterns. - *Behaviour*, 49: 1-61.

Stephens, D. W. and Krebs, J. R. 1986. *Foraging Theory*. Princeton University Press, Princeton, New Jersey.

Turchin, P. and Kareiva, P. 1989. Aggregation in Aphis varians: an effective strategy for reducing predation risk. - *Ecology*, 70: 1008-1016.

van Lenteren, J. C. 1986. Parasitoids in the greenhouse: successes with seasonal inoculative release systems. In *Insect Parasitoids*. Eds. Waage, J. and Greathead, D. page 342-374.

Varley, G. C., and Gradwell, G. R. 1963. The interpretation of insect population changes. - *Proceedings of the Ceylon Association for the Advancement of Science,* 18: 142-156.

Wiedenmann, R. N., and O'Neil, R. J. 1992. Searching strategy of the predator *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae). - *Environmental Entomology*, 21(1): 1-9.

CHAPTER II

SEARCH PATTERN WITHIN PATCHES*

Abstract

I examined the within-patch foraging behavior of a parasitoid wasp, using an experimental system that consisted of *Aphelinus asychis* females searching for pea aphids in a petri dish. The wasps' encounter rate with aphids agreed with an expected random distribution in 18 of 22 cases examined. I used a simulation model to find the general conditions under which a random or a systematic search pattern would be favoured by natural selection. I compared the influence of four combinations of searching behavior (random *vs.* systematic) and target movement (moving *vs.* non-moving) on the numbers of targets encountered, of (hosts) accepted for oviposition, and of (prey) consumed by a forager. Systematic searching was the best strategy if hosts did not move within the patch, whereas random searching was the best strategy for a forager searching for random-moving targets. The dispersion (near-random *vs.* clumped) of the target population on the forager's payoff was of relatively greater importance at low than at high density. I discuss my findings with regard to the definition of patch and the assumptions of random and systematic searching by foragers in mathematical models.

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Introduction

Foraging behavior represents one of the central problems in the study of animal behavior. We can conveniently distinguish between two levels of foraging behavior: between and within patches, with a patch being defined as a spatial subunit of the environment in which resource items are aggregated (Hassell and Southwood 1978; Bell 1990). Foraging behavior between patches generally deals with the movement patterns of animals, including the direction, distance and speed of searching (Waddington and Heinrich 1981; Stillman and Sutherland 1991). By comparison, foraging behavior within patches is concerned mainly with resource utilization within a given patch.

Mathematical models assume that foragers search either randomly or systematically for hosts or prey within a patch. For example, several models (Hassell and May 1974; Murdoch and Oaten 1975; Iwasa *et al.* 1981) are based on the assumption that parasitoid wasps search randomly, and independent of each other, for hosts in a homogeneous environment. A random-search strategy implies that each site within a patch has an equal probability of being searched, regardless of whether or not it was searched previously. Under this assumption, the approximately uniform distribution of prey remains unchanged as the density declines. Evidence of random searching was reported, *e.g.*, for small bluegill sunfishes, *Lepomis macrochirus*, searching for chironomid larvae within a single patch (DeVries *et al.* 1989; Marschall *et al.* 1989).

By contrast, Green's (1980; 1984; 1987) models are based on the assumption that foragers search systematically for prey or hosts.

Specifically, the forager is assumed to start searching from a particular point and to continue by moving over the patch until the entire area has been covered without retracing its path. In this process, all encountered prey are consumed in a manner analogous to the action of a vacuum cleaner. Under this assumption, the probability of the forager finding a host or prey is invariant and identical for all sites within the patch (Baum 1987; Green 1987). The observed pattern of flower visits by Hawaiian honeycreepers, *Loxops virens* (Kamil 1978), and of ants foraging for honeydew excreted by aphids on racemose inflorescences (Veena and Ganeshaiah 1991) are consistent with an assumed systematic search strategy.

In this Chapter, I focus mainly on the within-patch foraging strategies of parasitoid wasps. First, I present data from an experimental host-parasitoid system to characterize the foraging strategy of the parasitoid *A. asychis* searching for hosts, the pea aphid. Next, I address the question of why some parasitoids may use a random-searching pattern to find hosts, while others may search systematically. I identify the general conditions under which natural selection is expected to favour a random- or a systematic-search strategy. Using a simulation model, I show that a wasp's searching efficiency is dependent on host behavior. If the target hosts move within the patch, a wasp realizes a higher payoff by adopting random-search. However, a wasp searching for non-moving hosts within a patchy environment is expected to gain by searching systematically.

Experimental analysis

Materials and methods

My experimental system consisted of a species of solitary parasitoid wasp, *A. asychis* Walker (Hymenoptera: Aphelinidae), and its host, the pea aphid, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae). Parasitoids were reared in the laboratory on a mixed-age colony of apterous virginoparae feeding on broad bean, *Vicia fabae* L. cv. 'Broad Windsor'. The colony of pea aphids was maintained at 21 ± 2°C, 55 ± 10% RH, and continuous light. The broad beans were potted in standard garden mix soil in a greenhouse. *A. asychis* females may behave either as parasitoids by depositing an egg into an attacked aphid, or as predators by host-feeding. Usually females lay a single egg per attack. The developing larva eventually kills its host and pupates inside the body of the dead aphid, which is called a mummy. In all trials, I used 3-to 4-day-old wasps which had been kept with aphids on the first day after eclosion to gain experience: wasps were provided with water-diluted honey as supplementary food. As hosts, I used second nymphal instars of the pea aphid which are the "preferred" age class for oviposition (Gerling *et al.* 1990).

The attack process of *A. asychis* was described by Boyle and Barrows (1978) and Gerling *et al.* (1990). The latter defined host recognition as a change in the direction of walking or stopping when approaching an aphid, usually at a distance of 1.4 - 1.8 mm. On encountering a host, a wasp examines it first by antennation, moving its head from one side to the other. External host examination is followed by internal examination with the ovipositor, a behavior which is often accompanied by the injection of a paralyzing venom. *A. asychis* wasps discriminate between unparasitized and previously parasitized aphids and normally reject the latter for oviposition; they usually do not feed on parasitized aphids (Bai and Mackauer 1990).

I tested the hypothesis that *A. asychis* females use random searching to locate hosts in a patch. Because these wasps tend to walk rather than fly when searching on a plant, I used an open petri dish (14 cm in diam) as the experimental habitat. Each petri dish contained five bean leaflets, one in the centre and four spaced around it, defined as a patch. I placed eight second nymphal instars of the pea aphid on the central leaflet; the aphids were lightly anaesthetized with carbon dioxide so as to limit their movements; anaesthesis does not affect the probability of an aphids being attacked by *A. asychis* (Gerling *et al.* 1990). Aphids were marked with a water-coloring pen, each with a different color, to enable their identification. After introducing a female of *A. asychis* into the petri dish, I recorded its behavior with a video camera until the wasp either reached the habitat boundary (*i.e.*, petri dish) or left it. For each wasp, I compiled the numbers of encounters with each aphid in a trial into a frequency distribution. I calculated for each observed distribution the variance/mean ratio, with a ratio of unity indicating a random distribution. I tested this ratio for statistical significance by the index of dispersion, I_D (Southwood 1978, p. 39):

$$I_D = \frac{S^2(n-1)}{\bar{x}}$$

where n is the number of samples and $\bar{x}$ and S^2 are the mean and the variance of the observed distribution; I_D is approximately distributed as χ^2 with (n - 1) degrees of freedom.

Experimental results

The average number of host/parasitoid encounters recorded in each trial was 34.0 (SEM = 5.1; n = 22). The index of dispersion showed a significant departure from unity in four of the 22 observed distributions. (This result was confirmed when I compared the observed distributions with expected Poisson distributions with equal means). However, in none of the cases was the distribution underdispersed ($S^2/\bar{x} < 1$), a result that would be expected if *A. asychis* females searched systematically for hosts.

Simulation model

Description of model

I used a stochastic simulation model to evaluate the influence of dispersion and within-patch movement of the targets (*i.e.*, aphids) on the encounter rate and payoff of a forager (*i.e.*, wasps), employing different searching strategies. I defined as an encounter the assignment by the computer of a forager into a cell that was occupied by a target. I defined payoff in two ways. A foraging wasp could either deposit an egg in an encountered host or kill its prey by consuming it. If the wasp oviposited in a host, its payoff was determined by the probability of the egg surviving to the next generation. In competition between conspecific offspring of solitary parasitoids, the first-laid egg has a significantly higher probability of surviving as a larva than any eggs laid later, except in cases where age-differences between the immatures are small (Mackauer 1990). Thus, any first encounter between a wasp and an unparasitized host was assigned a payoff value of 1, while any subsequent encounters with an (already parasitized) host was assigned a payoff value of 0.1. Alternatively, a forager (*i.e.*, predator) could gain 1 payoff unit if it killed and consumed an encountered prey. Because these targets could not be re-encountered, they were deleted from subsequent simulations.

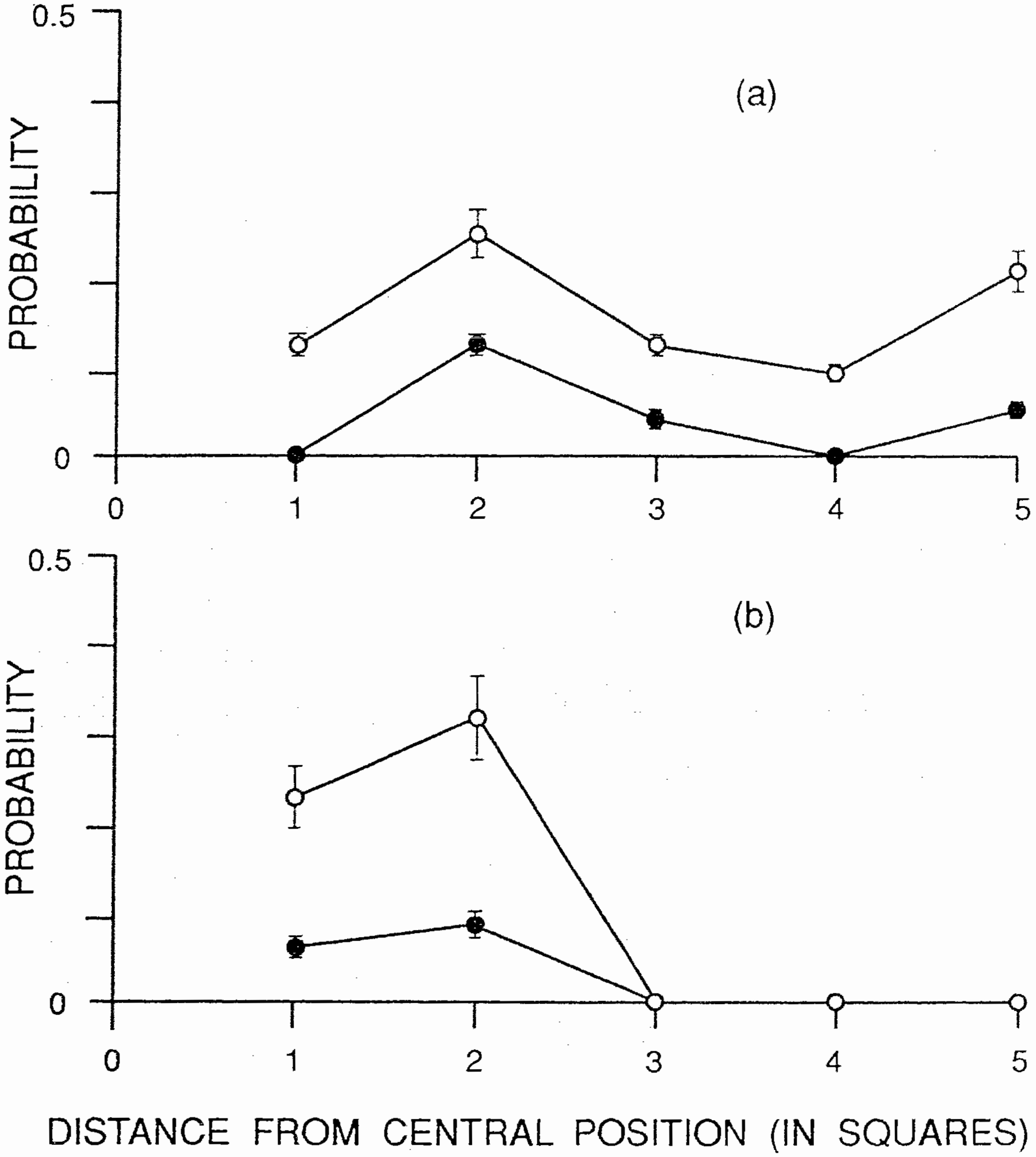
I compared the numbers of encounters, of offspring produced, and of prey eaten under four different assumptions: (1) the forager searches systematically for moving targets; (2) the forager searches randomly for moving targets; (3) the forager searches systematically for non-moving targets; and (4) the forager searches randomly for non-moving targets. The model targets were distributed in a two-dimensional grid consisting of 100 cells (10 rows by 10 columns); the first cell in the first row was numbered [1,1] and the last cell in the last row was numbered [10,10]. A particular cell could be either empty or occupied by one "aphid". I used the following procedure to assign targets to cells. The first target was assigned to the central cell [5,5]. Next, I assigned either 0 or 1 target to each of the eight adjoining cells, using a Monte Carlo technique. The computer drew a random number between 0 and 1 from a uniform distribution ($S^2 < m$). If the number was larger than the zero term of a negative binomial distribution, the cell was classified as occupied. For generating a near-random distribution, I set $k = 0.7$ and target density as either 5/100 (low) or 20/100 (high). By contrast, for generating a clumped target distribution, I set again $k = 0.7$ but density as 120/100 (both low and high). After all the cells adjacent to [5, 5] were classified, the cells that were two cells distant from the central one were evaluated in the same manner. This procedure was continued until all the available computer targets (5 or 16) were assigned to cells. The probability of a cell being occupied in relation to its distance from the central position [5,5] is shown in Fig. 2.1.

For testing the influence of assumptions 3 and 4 (non-moving targets) on encounter rates, I set the initial position of each target by the above Monte Carlo technique; targets remained in these positions throughout a single run. By contrast, for assumptions 1 and 2 (moving targets), "surviving aphids" moved from their initial position by random walk (Berg 1983) to one of the eight adjoining cells, until they had completed 100 steps.

Wasps that systematically searched for hosts were "released" in cell [1,1]. From there they moved to cell [1,2], [1,3], etc. until they reached the last cell [10,10] so that each cell was visited once only. Random-searching wasps were "released' onto the grid by random selection at varying distances (1, 2, 3, etc. cells) from the centre. They moved from one cell to the next by random walk, as above. Both the foragers and the targets were equally probable either to remain in a current cell or to move to an adjoining cell.

For each set of assumptions, the model was run 100 times. The program accumulated the total number of encounters and the expected payoff value for the forager in terms of the numbers of hosts parasitized and prey consumed. I predicted that the efficiency of a forager in finding hosts or prey would vary with target behavior. For moving targets, a forager adopting random searching was expected to have a greater encounter rate than one searching systematically. By contrast, systematic searching was expected to provide a greater payoff if the targets did not move.

Fig. 2.1. Probability of a cell being occupied by a target in relation to cell distance from the centre [5,5] of a 10 × 10 cell grid: (a) near-random distribution; (b) clumped distribution. Values shown are means ± 1 *s* (o, high host density; black o, low host density; see text for details).


0.5
(a)
PROBABILITY
0
0
1
2
3
4
5
0.5
(b)
PROBABILITY
0
0
1
2
3
4
5
DISTANCE FROM CENTRAL POSITION (IN SQUARES)

Simulation results

Random-searching foragers encountered significantly more targets than their systematically searching counterparts, regardless of target behavior (Fig. 2.2 a, b). However, higher encounter rates did not necessarily result in increased fitness (Fig. 2.2 c, d) or consumption rates (Fig. 2.2 e, f). Random search was the best strategy for foragers searching for targets that moved randomly within a patch, while systematic search was the best strategy if targets did not move, especially with regard to the numbers of prey consumed. Also, the combination of search strategy and target behavior had a relatively greater influence on foraging efficiency at low than high target density (Table 2.1).

For random-searching wasps, the distance between the centre of the target population [cell 5,5] and the cell in which the search was initiated was inversely proportional to the estimated encounter rate and payoff value (Fig. 2.3). This was to be expected because, under my model of a random-searching forager, an encounter with a target was independent of the success or failure of the next selection rather than, as in nature, a function of clumping among targets.

Discussion

The simulation of foraging behavior under different assumptions indicates that systematic searching is the optimal strategy when targets do not move, whereas random searching is optimal when targets move within the model universe (Fig. 2.2, 2.3). As expected, a "random forager"

Fig. 2.2. Efficiency of a forager searching either systematically or randomly for targets in relation to target behavior (moving and non-moving) and density (5 and 16). Values shown are means ± 1 *s* ($n = 100$). Solid columns = forager searches systematically for moving targets (assumption 1); Stippled columns = forager searches randomly for moving targets (assumption 2); cross-hatched columns = forager searches systematically for non-moving targets (assumption 3); open columns = forager searches randomly for non-moving targets (assumption 4).

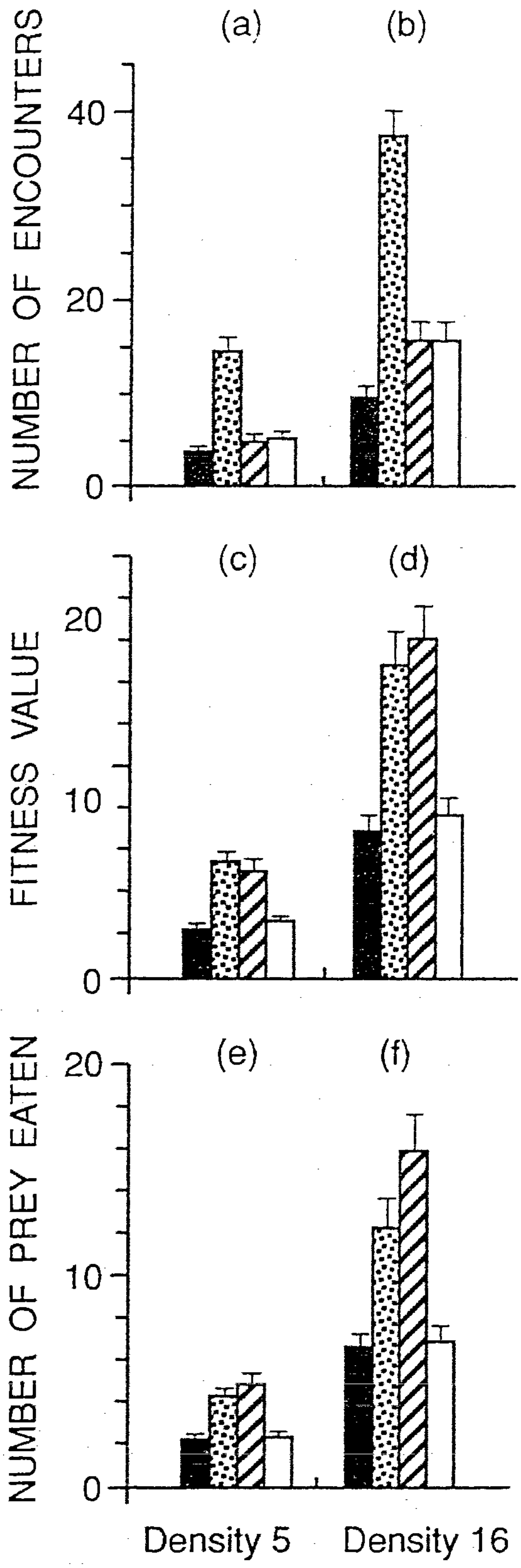
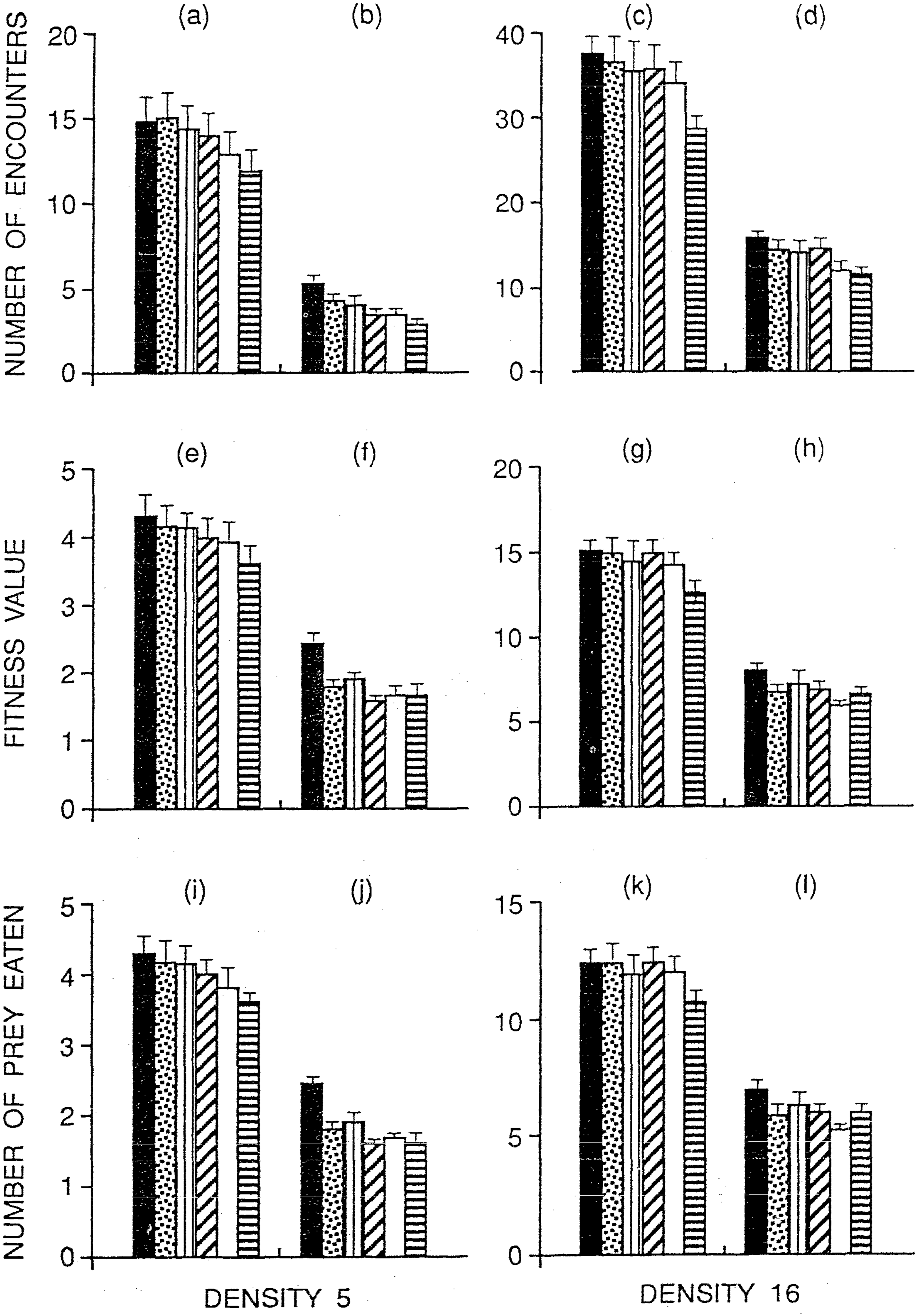

(a)
(b)
NUMBER OF ENCOUNTERS
0
20
40
(c)
(d)
FITNESS VALUE
0
10
20
(e)
(f)
NUMBER OF PREY EATEN
0
10
20
Density 5
Density 16

Table 2.1. Influence of target density on the efficiency of a forager searching randomly for non-moving targets that are dispersed in a random or clumped pattern over a 10 × 10 cell grid.

Foraging index	Host density	*F*-value*	*p*
No. encounters	5	64.798	0.0001
	16	48.656	0.0001
Fitness value	5	70.356	0.0001
	16	0.797	0.3722
No. eaten	5	65.012	0.0001
	16	10.144	0.0015

* Differences between means compared by 1-way ANOVA with 1 and 1198 degrees of freedom.

Fig. 2.3. Influence of target behavior (moving and non-moving) and density (5 and 16) on the efficiency of a forager. Foragers searched randomly for moving (a, c, e, g, i, k) and non-moving targets (b, d, f, h, j, l). Searching was initiated at various distances (0 - 5 cells) from the centre [cell 5,5] of the target population; differently shaded columns correspond to distance from the centre, from left column (solid; 0 distance) to right column (cross-hatched; 5 cells distance). Values shown are means ± 1 *s* (*n* = 100).


(a)
(b)
(c)
(d)
NUMBER OF ENCOUNTERS
20
15
10
5
0
40
30
20
10
0
(e)
(f)
(g)
(h)
FITNESS VALUE
5
4
3
2
1
0
20
15
10
5
0
(i)
(j)
(k)
(l)
NUMBER OF PREY EATEN
5
4
3
2
1
0
15
10
5
0
DENSITY 5
DENSITY 16

initiating search at, or close to, the centre of the target population will realize greater benefits than one initiating search at a distance (Fig. 2.3). The relative influence of the searching strategy on payoff values varied with the host density. Excepting the encounter rate, a wasp's searching strategy was most important when the host density was low but had less influence on the estimated payoff values at a high density (Table 2.1).

A wasp that searched systematically for non-moving targets achieved a higher consumption rate than one searching randomly, although the latter encountered more targets. The reason for this difference is that a random-searching forager will not search all the cells in the environment and that, consequently, some targets may escape. By contrast, a forager searching systematically will visit all the cells once. While such a strategy is more efficient at finding non-moving targets, it is less efficient for mobile targets which may escape by moving to an already searched cell.

Most of the evidence of systematic searching by foragers comes from nectar-feeding birds (Gill and Wolf 1977; Kamil 1978; Lima 1984). Because flowers do not move, this finding is consistent with my model predictions. By contrast, a wasp foraging for hosts which can move within the patch, such as *A. asychis* searching for (un-anaesthetized) pea aphids, can be expected to use random searching.

I defined a patch in accordance with Hassell and Southwood (1978) and Bell (1990) as a spatial subunit of the foraging area in which targets are aggregated. However, other definitions are possible and, I suspect, will determine which search strategy (random *vs.* systematic) is in fact optimal. For example, a patch may be defined as the territory of an animal (amakihi territory, Kamil 1978), or as a whole plant (elementary unit of foraging, Ayal 1987), or as a part of a plant (bean leaflet, present study), or as a single prey item (Cook and Cockrell 1978; Yamamura and Tsuji 1987).

Searching between patches may indicate either a random pattern (Varley 1941; Burnett 1958; Tripp 1962), or a non-random pattern (Hassell and May 1974; Hassell 1978), or a systematic pattern (Reeve 1987). By contrast, within-patch searching is either random or systematic; non-random searching is unlikely to occur under my definition of patch. Foragers may not always employ a pure searching strategy but rather a mixed strategy which includes elements of both random and systematic searching, considered by Baum (1987) the extremes of a continuum. For example, 12 of 17 observed distributions of flower visits by amakihi differed significantly from Poisson, a result indicating that these birds forage systematically for flowers on most, and randomly, on some occasions (Kamil 1978). Similarly, Gill and Wolf (1977) found that nectar-feeding sunbirds, *Nectarina reichenowi*, searched systematically for flowers; however, 10 of 21 observed frequency distributions were not significantly different from Poisson. Studying the small bluegill sunfish in the laboratory, Marschall *et al.* (1989) compared the observed distributions of time intervals between the captures of (sessile) chironomid larvae with those expected according to standard models of within-patch random searching (Murdoch and Oaten 1975; McNair 1982; McNamara 1982; Stephens and Charnov 1982; Chesson 1983). Only one of seven distributions (*i.e.*, fishes) differed significantly from an expected random distribution. Because bluegills forage in nature for a broad range of prey, including free-swimming insect larvae, Marschall *et al.* (1989) concluded that an animal's searching strategy should be adapted to its natural host/prey species rather than to the experimental species provided in the laboratory.

As I have shown, the relative efficiency of a particular search strategy is dependent on the targets' behavior, especially movement. Systematic searching would appear more efficient than random searching, because paths are not retraced. The available energy will be allocated mainly to situations that are likely to provide a payoff (Baum, 1987). However, systematic searchers may miss any hosts that have moved to an already visited area during the search period. Thus, random searchers may, under some conditions,achieve higher encounter rates with hosts by revisiting some areas. Also, systematic searching requires that the forager is able to distinguish between different locations and to store in memory any distinguishing features of the habitat. If the cost of such a system is higher than the expected benefits in terms of time and energy saved, random searching will be the better strategy.

References

Ayal, Y. 1987. The foraging strategy of *Diaeretiella rapae*. I. The concept of the elementary unit of foraging. - *Journal of Animal Ecology* 56: 1057-1068.

Bai B. and Mackauer, M. 1990. Oviposition and host feeding patterns in *Aphelinus asychis* at different aphid densities. - *Ecological Entomology*, 15: 9-16.

Baum, W. M. 1987. Random and systematic foraging, experimental studies of depletion, and schedules of reinforcement. - In: Kamil, A.C., Krebs, J.R. and Pulliam, H.R. (Eds), *Foraging Behavior*, Plenum Press, New York, pp. 587-607.

Bell, W.J. 1990. Searching behavior patterns in insects. - *Annual Review of Entomology*, 35: 447-467.

Berg, H. C. 1983. *Random Walks in Biology*. - Princeton University Press, Princeton, New Jersey.

Boyle, H. and Barrows, E. M. 1978. Oviposition and host feeding behavior of *Aphelinus asychis* (Hymenoptera: Chalcidoidea: Aphelinidae) on *Schizaphis graminum* (Homoptera: Aphididae) and some reactions of aphids to this parasite. - *Proceedings of the Entomological Society of Washington*, 80(3): 441-455.

Burnett, T. 1958. A model of host-parasite interaction. - *Proceedings of the Xth International Congress of Entomology*. (1956), 2: 679-686.

Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. - *Ecology*, 64: 1297-1304.

Cook, R.M. and Cockrell, B.J. 1978. Predator ingestion rate and its bearing on feeding time and the theory of optimal diets. - *Journal of Animal Ecology*. 47: 529-547.

DeVries, D.R., Stein, R.A. and Chesson, P. L. 1989. Sunfish foraging among patches: the patch-departure decision. - *Animal Behaviour*, 37: 455-464.

Gerling, D., Roitberg, B. D. and Mackauer, M. 1990. Instar-specific defense of the pea aphid, *Acyrthosiphon pisum*: influence on oviposition success of the parasite *Aphelinus asychis* (Hymenoptera: Aphelinidae). - *Journal of Insect Behavior*, 3(4): 501-514.

Gill, F. B. and Wolf, L. L. 1977. Nonrandom foraging by sunbirds in a patchy environment. - *Ecology*, 58: 1284-1296.

Green, R. F. 1980. Bayesian birds: a simple example of Oaten's stochastic model of optimal foraging. - *Theoretical Population Biology*, 18: 244-256.

Green, R. F. 1984. Stopping rules for optimal foragers. - *The American Naturalist*, 123: 30-43.

Green, R. F. 1987. Stochastic models of optimal foraging. - In: Kamil, A.C., Krebs, J.R. and Pulliam, H.R. (Eds), *Foraging Behavior*, Plenum Press, New York, pp. 273-302.

Hassell, M. P. 1978. *The Dynamics of Arthropod Predator-Prey Systems.* - Princeton University Press. Princeton, New Jersey.

Hassell, M. P. and May, R. M. 1974. Aggregation in predators and insect parasites and its effects on stability. - *Journal of Animal Ecology*, 43: 567-594.

Hassell, M. P. and Southwood, T. R. E. 1978. Foraging strategies of insects. - *Annual Review of Ecology & Systematics*, 9: 75-98.

Iwasa, Y., Higashi, M. and Yamamura, N. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. - *The American Naturalist*, 117: 710-723.

Kamil, A. C. 1978. Systematic foraging by a nectar-feeding bird. - *Journal of Comparative and Physiological Psychology*, 92: 388-396.

Lima, S. L. 1984. Downy woodpecker foraging behavior: efficient sampling in simple stochastic environments. - *Ecology*, 65: 166-174.

Mackauer, M. 1990. Host discrimination and larval competition in solitary endoparasitoids. In: Mackauer, M., Ehler, L. E., and Roland, J. (Eds), *Critical Issues in Biological Control*, Intercept Ltd. Andover, Hants, UK, pp. 41-62.

McNamare, J. 1982. Optimal patch use in a stochastic envoronment.- *Theoretical Population Biology*, 21: 269-288.

McNair, J.N. 1982. Optimal giving-up times and the marginal value theorem. - *The American Naturalist*, 119: 511-529.

Marschall, E.A., Chesson, P.L. and Stein, R.A. 1989. Foraging in a patchy environment: prey-encounter rate and residence time distributions. - *Animal Behaviour*, 37: 444-454.

Murdoch, W. W. and Oaten, A. 1975. Predation and population stability. - *Advances in Ecological Research*, 9: 2-131.

Reeve, J.D. 1987. Foraging behavior of *Aphytis melinus*: effects of patch density and host size. - *Ecology*, 68: 530-538.

Southwood, T. R. E. 1978. *Ecological Methods - with particular reference to the study of insect populations*. - Chapman and Hall. 2nd Ed..

Stephens, D. W. and Charnov, E. L. 1982. Optimal foraging: some simple stochastic models. - *Behavioral Ecology and Sociobiology*, 10: 251-263.

Stillman, R. A. and Sutherland, W. J. 1991. The optimal search path in a patchy environment. - *Journal of Theoretical Biology*, 145: 177-182.

Tripp, H.A. 1962. The relationship of *Spathimeigenia spinigera* Townsend (Diptera: Tachinidae) to its host, *Neodiprion swainei* Midd. (Hymenoptera: Diprionidae). - *The Canadian Entomologist*, 94: 809-918.

Varley, G.G. 1941. On the search for hosts and the egg distribution of some chalcid parasites of the knapweed gall-fly. - *Parasitology*, 33: 47-66.

Veena, T. and Ganeshaiah, K. N. 1991. Non-random search pattern of ants foraging on honeydew of aphids on cashew inflorescences. - *Animal Behaviour*, 41: 7-15.

Waddington, K. D., and Heinrich, B. 1981. Patterns of movement and floral choice by foraging bees. - In: Kamil, A. C., and Sargent, T. D. (Eds), *Foraging Behavior*, Garland, New York, pp. 215-230.

Yamamura, N. and Tsuji, N. 1987. Optimal patch time under exploitative competition. - *The American Naturalist*, 129(4): 553-567.

CHAPTER III

INITIAL GIVING UP TIME (IGUT): EFFECTS OF CONTACT KAIROMONEAND EXPERIENCE

Abstract

I extend the concept of initial giving up time (IGUT) to include non-host-containing patches, and address questions related to the duration of parasitoid search in non-host-containing patches and which cues are used to determine search time allocation. I test the hypothesis that, for the aphid parasitoid *Aphelinus asychis*, the contact kairomone (which is present in aphid honeydew) is the first cue used by inexperienced or naive wasps to locate their hosts, but that honeydew is used less as the wasps gain foraging experience. My experimental results support this hypothesis. The inexperienced wasps spent a significantly longer time searching in patches with honeydew than in clean patches. The experienced wasps remained in patches with honeydew, or in clean patches, for similar periods. Wasps with intermediate levels of experience searched significantly longer in patches with honeydew than in clean patches, but these times were shorter than those of inexperienced wasps. I consider explanations for this phenomenon.

Introduction

The foraging efficiency of a parasitoid species is defined as the number of hosts parasitized per unit of time. Thus, the search time allocation of the species is important in measuring its foraging efficiency. Such efficiencies are generally measured within host-containing patches where a patch is defined as a spatial subunit of the foraging area in which aggregations of resource items may occur (Hassell and Southwood; 1978; Chapter II of this thesis). But non-host-containing patches can also (negatively) influence total parasitism, because parasitism cannot occur in such patches and foraging time is wasted. If a parasitic wasp spends more time in non-host-containing patchs, then less time is available for it to search other host-containing patches, which decreases the total number of hosts parasitized. In this way, the time spent in non-host-containing patches is important to rates of parasitism at the level of between patches. This fact has been largely ignored in the past, because the goal in most studies has been to evaluate patch residence time as a function of host density.

The question of "how long a parasitoid should spend searching a non-host-containing patch?" is of great interest here. However, I do not discuss it at length, but rather concentrate on what cues parasitoids use to determine how long to search in such patches (*viz.*, patch residence time and the implications of such use). To do this, I employed the useful concept of "initial giving up time" (IGUT) which was proposed by Morrison and Lewis (1981). They defined IGUT as the amount of time which a parasitoid allocates to any kairomone-contaminated patch before abandoning it if no hosts were encountered. This concept was derived from results, wherein the parasitoid, *Trichogramma pretiosum*, frequently abandoned host-containing patches before encountering and parasitizing individual hosts. Here, I extend the concept of IGUT to include non-host-containing patches. The time investment for a patch, in which no encounters with hosts occur, should be the same or similar, whether the patch contains hosts or not. Apparently no studies have been devoted to this problem; a literature review failed to find any research papers on empty patch exploration. My goal in this chapter is to examine how the existence of host cues and past experience with patch quality may influence the IGUT. I shall use my experimental system to test an hypothesis that a contact kairomone, which is present in aphid honeydew, is the first cue used by inexperienced or naive wasps (those that have never had the chance to assess any hosts) to locate their hosts, and that with increasing foraging experience, the wasps no longer use this cue to locate hosts. Experienced wasps may use other factors such as visual image of the host.

This hypothesis arises from a general consideration about the functions of honeydew cues. The honeydew can serve as a general cue as to the possible presence of aphids. As shown by Bouchard and Cloutier (1985) the aphid parasitoid, *Aphidius nigripes*, not only responds to honeydew odors from a preferred host, *Macrosiphum euphorbiae*, but also to honeydew of the much less preferred host *Myzus persicae* and *Aphis nasturtii*, and even to that of a nonhost aphid, *Rhopalosiphum maidis*. When a wasp is a generalist (*i.e.*, one which attacks more than a single species of aphid) and the potential hosts cannot be predicted in advance, then experience must be used to evaluate other criteria (*e.g.*, visual cues).

These other cues are more accurate, but the nature of them cannot be predicted in advance. Thus, a good rule would be to orient to the honeydew until local experience can be used to assess the presence of other species with specific cues.

If this hypothesis is correct, then inexperienced *A. asychis* wasps will search longer in patches with pea aphid honeydew than in clean patches without honeydew. For experienced wasps, the time spent in both kinds of patches should be equal or similar, as long as other conditions are similar. Patch residence time will be determined by cues other than a contact kairomone. For wasps with an intermediate level of experience in handling hosts, I would expect the time spent in patches with honeydew, compared to clean patches, to be intermediate between that of inexperienced and highly experienced wasps.

Materials and Methods

A large petri dish (14 cm diam) with 5 broad bean leaflets was used as a habitat for the wasp. I put one broad bean leaflet (with or without honeydew) in the center of the petri dish, and surrounded it with 4 other clean broad bean leaflets. Each leaflet was defined as a patch. The broad bean leaflets with honeydew were obtained by introducing adult pea aphids onto a clean broad bean plant for several days, and then visually choosing leaflets with similar amounts of honeydew, and removing all aphids from theses leaflets with a fine camel's hair brush. A group of inexperienced wasps consisted of one-day-old wasps, fed with honey water, which had never encountered any pea aphids. The wasps in the experienced group had

had three to four-days experience in handling hosts on bean leaflet patches. The intermediate group had limited (*i.e.* one day) experience with hosts.

Following treatments, the wasps were individually released on one of two patch types, clean or honeydew, and their patch residence times measured. Patch residence time is defined as the time from a wasp's entry into a patch until it leaves the patch. Six treatment groups resulted from this design: EH, experienced wasps foraging on leaflets with honeydew, sample size n = 37; IEH, inexperienced wasps foraging on leaflets with honeydew, n = 38; EC, experienced wasps foraging on leaflets without honeydew, n = 37; IEC, inexperienced wasps foraging on leaflets without honeydew, n = 52; LEH, wasps with limited experience foraging on leaflets with honeydew, n = 36; LEC, wasps with limited experience foraging on leaflets without honeydew, n = 36.

Age effect can be a concern with this experimental design. In my experiments, the parasitoids in groups of inexperienced and limited experience were 1 day old, whereas the wasps in the experienced group were 3-4 days old. Thus, there might be a possibility of age effect, in addition to experience, on the determination of patch residence time. However, this age effect should be small in *A. asychis*, since the variance is small in physiological status in terms of egg load, *i.e.*, the maximum number of eggs a parasitoid could hold, between wasps of ages from 1 to 10 days (Bai, 1991, Fig. 8.1). Therefore, I assumed that any differences in patch residence times for the different treatment groups resulted from experience with hosts.

Results

Fig. 3.1 shows the average patch residence time and the standard error for each treatment. For parasitoids released on patches with honeydew, the inexperienced wasps spent the longest time, the experienced wasps spent the shortest time, and the wasps with limited experience spent intermediate time. For wasps in patches without honeydew, inexperienced wasps also spent the longest time, but the experienced wasps and the wasps with limited experience spent almost same length of time in the patches.

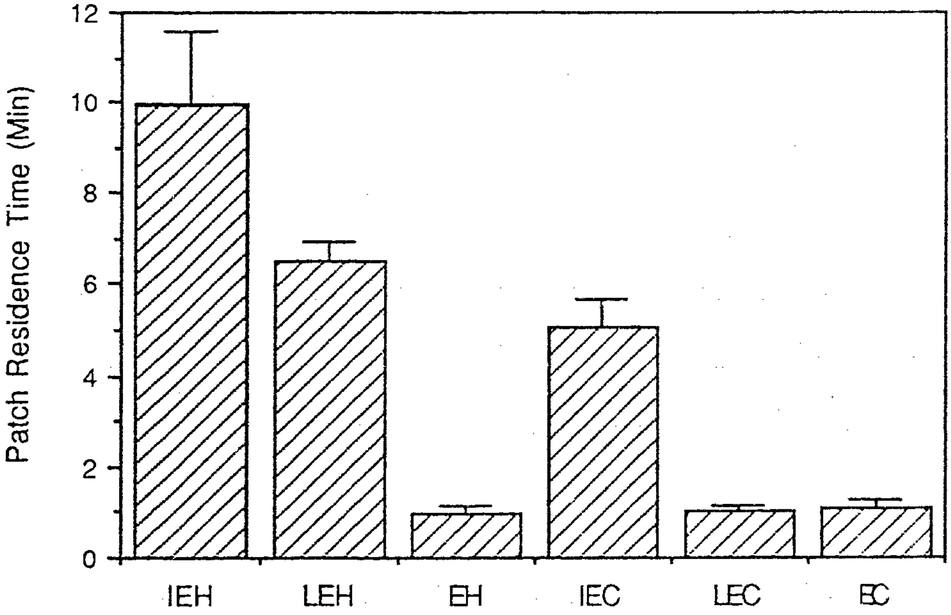
The results of a one-way ANOVA analysis indicate that significant differences existed among the treatments ($F_{5,230} = 24.942$, $p = 0.0001$). Further tests with the Fisher PLSD and Scheffe F-test show that: inexperienced wasps remained significantly longer (at the 95% level) in the patches with honeydew (9.97 min) than those in the patches without honeydew (5.07 min); experienced wasps remained in the patches with honeydew (0.97 min) for periods similar to those in the patches without honeydew (1.09 min); wasps with limited experience remained significantly longer in patches with honeydew (6.54 min) than those in the patches without honeydew (1.06 min), but shorter than inexperienced wasps in patches with honeydew (9.97 min).

These results are consistent with my hypothesis.

Discussion

The mechanisms by which parasitoids locate suitable hosts for their offsping are important in studies of parasitoid-host relationships. Many

Fig. 3.1: The average patch residence time and the standard error for each treatment: EH = **E**xperienced wasps foraging on leaflets with **h**oneydew; IEH = **Ine**xperienced wasps foraging on leaflets with **h**oneydew; EC = **E**xperienced wasps foraging on **c**lean leaflets without honeydew; IEC = **Ine**xperienced wasps foraging on **c**lean leaflets without honeydew; LEH = wasps with **l**imited **e**xperience foraging on leaflets with **h**oneydew; LEC = wasps with **l**imited **e**xperience foraging on **c**lean leaflets (without honeydew).


Patch Residence Time (Min)
0
2
4
6
8
10
12
IEH
LEH
EH
IEC
LEC
EC

insect parasitoids use kairomones secreted or excreted by their hosts, as cues for host location (Vinson, 1981; Weseloh, 1981). Several aphid parasitoids in the family Aphidiidae (Hymenoptera) have been shown to use honeydew as a contact kairomone to locate hosts (Bouchard and Cloutier, 1984; Hågvar and Tofsvang, 1989; Budenberg, 1990; Cloutier and Bauduin, 1990). McGregor and Mackauer (1989) showed that adults of *Aphidius smithi* spent significantly less time searching on clean broad bean leaflets than on leaflets covered with droplets of pea-aphid honeydew.

Since evidence that aphid parasitoids respond to honeydew is widely reported, it is reasonable to assume that such parasitoid species recognize that patches with honeydew probably do harbour aphids, and that this recognition is most likely inherited, rather than learned. If this is true, then inexperienced parasitoids should tend to stay longer in patches with honeydew when searching for hosts than those in patches without honeydew, whether the hosts are actually present or not. The data presented here indicate that this was the case in my experimental system.

The response of inexperienced *A. asychis* to honeydew is apparently innate. This is consistent with several results reported in the literature, such as those for inexperienced *Aphidius smithi* (McGregor and Mackauer, 1989), and for 3-day old inexperienced females of *Aphidius rhopalosiphi* (Budenberg, 1990). Hågvar and Hofsvang (1989) used 0-3 day-old *Ephedrus cerasicola* in their experiments, but did not mention in their paper whether these wasps had experience with hosts before being released into the glasshouse or cages. If the wasps had never made contact with hosts before testing, which would be most likely, the results would also support my argument here. It is important to recall that honeydew may not be a reliable indicator of a host's presence, particularly when the hosts are mobile. The assessment of patch quality through actual encounters can provide more reliable estimates for parasitoids than would honeydew cue. Morrison and Lewis (1981) found that plotting patch residence time against the number of hosts attacked produces a much higher correlation than plotting patch residence time against actual host density. This suggests that the parasitoid's "perception" of host density per patch is indexed by the number of hosts attacked, rather than actual host density. If this is so in my experimental system, then the experienced wasps would spend the same time on non-host-containing patches with or without honeydew. My data agreed with this prediction. A lower probability of host encounter resulting from the combination of large patch surface area and a low number of hosts on that patch, would probably cause the parasitoid to abandon the patch before encountering any hosts, because IGUT would frequently be exceeded. Thus, the concept of initial giving up time can be extended to include non-host-containing patches.

The difference in patch residence times for inexperienced versus experienced wasps, when foraging in patches with or without honeydew, indicates the importance of experience with patches. With increasing experience with patches, the wasps can apparently modify their original patch quality estimate using other cues such as host encounters and then modify their patch residence time. The demonstrated effects on patch residence time may be referred to as "learning". The performance of the wasps in the group with limited experience was intermediate to those in inexperienced and experienced groups. My data suggest that the parasitoid probably learned to modify patch residence time on patches without honeydew first, then patches with honeydew. I conclude this because the wasps with one-day experience had patch residence times similar to those of experienced wasps on patches without honeydew, but still spent much more time than experienced wasps on patches with honeydew.

Bouchard and Cloutier (1984) showed that when *Aphidius nigripes* wasps, both inexperienced and experienced, were given access to plants infested with aphids for the first two days, and the infested plants were removed for one day before the experiments, they searched significantly longer on previously infested than on fresh plants. They also demonstrated that experienced *A. nigripes* females were attracted by honeydew odors carried by an airstream in a olfactometer (Bouchard and Cloutier, 1985). However, their Table 7 in the first paper showed that the time spent by individual parasitoids within the honeydew-contaminated area decreased sharply on their second, third and fourth visits to the same test filter paper discs, but retention reappeared after a 1-h rest. They stated that: "responsiveness to honeydew is restored relatively rapidly". Since their experienced wasps started to search after one day's "rest", and the wasps were tested only once, their results might somehow be biased by highly experienced wasps, *i.e.*, the wasps stayed longer on the filter paper dics than those highly experienced wasps would be.

Differences between results from Bouchard and Cloutier (1984, 1985) and mine suggest that conclusions about honeydew effects should be drawn with caution, because they may depend upon species identity and experimental design.

References

Bai, B. 1991. Conspecific and heterospecific interactions in two species of aphid parasitoids, *Aphidius ervi* and *Aphelinus asychis* (Hymenoptera: Aphidiidae, Aphelinidae). - Ph. D. Thesis, Simon Fraser University, British Columbia, Canada. 121 pages.

Bouchard, Y., and Cloutier, C. 1984. Honeydew as a source of host-searching kairomones for the aphid parasitoid *Aphidius nigripes* (Hymenoptera: Aphidiidae). - *The Canadian Journal of Zoology*, 62: 1513-1529.

Bouchard, Y., and Cloutier, C. 1985. Role of olfaction in host finding by aphid parasitoid *Aphidius nigripes* (Hymenoptera: Aphidiidae). - *Journal of Chemical Ecology*, 11(6): 801-808.

Budenberg, W. J. 1990. Honeydew as a contact kairomone for aphid parasitoids. - *Entomologia experimentalis et applicata,* 55: 139-148.

Cloutier, C. and Bauduin, F. 1990. Searching behavior of the aphid parasitoid *Aphidius nigripes* (Hymenoptera: Aphidiidae) foraging on potato plants. - *Environmental Entomology*, 19(2): 222-228.

Hågvar, E. B., and Hofsvang, T. 1989. Effect of honeydew and hosts on plant colonization by the aphid parasitoid *Ephedrus cerasicola*. - *Entomophaga*, 34(4): 495-501.

Hassell, M. P. and Southwood, T. R. E. 1978. Foraging strategies of insects. - *Annual Review of Ecology and Systematics*, 9: 75-98.

McGregor, R., and Mackauer, M. 1989. Toxicity of carbaryl to the pea-aphid parasite *Aphidus smithi*: influence of behaviour on pesticide uptake. - *Crop Protection*, 8: 193-196.

Morrison, G. R., and Lewis, W. J. 1981. The allocation of searching time by *Trichogramma pretiosum* in host-containing patches. - *Entomologia experimentalis et applicata*,30: 31-39.

Vinson, S. B. 1981. Habitat location. - In *Semiochemicals, Their Role in Pest Control*. Eds. Nordlund, D.A., Jones, R. L. & Lewis, W. J. pp. 51-77. Wiley, New York.

Weseloh, R. M. 1981. Host location by parasitoids. - In *Semiochemicals, Their Role in Pest Control*. Eds. Nordlund, D.A., Jones, R. L. & Lewis, W. J. pp. 79-95. Wiley, New York.

CHAPTER IV

PATCH LEAVING RULES

Abstract

I address the question of decision rules that the solitary parasitoid wasp, *Aphelinus asychis*, may use for making patch leaving decisions when searching for pea aphid hosts on broad bean leaf patches. I compared my data with several decision rules and mechanisms reported in the literature. I found that the rules for fixed-time, fixed-number, and fixed-GUT (giving-up-time) did not fit the wasp's situation; but there were two possible patch leaving rules: (1) the wasp should leave the current patch when the GUT has elapsed, and the GUT should increase with host density by 5.7162 + 0.5991 × host density per leaflet; (2) a sliding memory window with a length of at least 3 units, and when the percentage of parasitized hosts in the memory window is more than half, the wasp should leave the current patch.

Introduction

The way in which an animal perceives its surroundings is important for answering the question of why an animal performs a particular behavior. Hassell and Southwood (1978) classified hierarchical levels of how animals perceive their environment, recognizing that "any framework is bound to be plagued with exceptions and examples of blurred boundaries". Their classification includes (1) resource items, which are the individual prey or hosts; (2) patches, which are aggregations of resource items or spatial subunits of the foraging area in which aggregations of resource items occur; and (3) habitats, which are clusters of patches. These spatial units provide a framework for searching behavior so that we can usually distinguish the movements of animals between habitats, patches, and resources from their movements within habitats and patches.

I concentrated on two different levels, within and between patches in Chapter II where a patch was defined as a broad bean leaflet. Thus, once on a plant the parasitoid wasp faces many broad bean leaflets among which its hosts are distributed. When foraging within this particular habitat, there are four different kinds of "decisions" that an *A. asychis* female must make: (1) patch selection: where to locate a patch, and how to move between patches; (2) patch time allocation: the questions of how long it should stay in a particular patch or when it should leave that patch; (3) host acceptance: when to accept an encountered host, including superparasitism that comprises a wasp laying an egg in a previously parasitized host, from which only one offspring will emerge (van Alphen and Visser, 1990; Visser *et al.*, 1990; Mangel, 1992); (4) search pattern: movement within patches. This Chapter deals with (2) the question of patch time allocation.

Patch time allocation addresses the question of how a parasitoid allocates its searching time within patches under different conditions such as varying host density and quality. Thus, the problem of patch time allocation can be elucidated by studying patch residence time, which is defined as the time from which a parasitoid individual enters a patch until that wasp leaves the patch, under different conditions (see Chapter II and III).

Patch residence time can be viewed from two directions. The first is to ask how long a parasitoid should remain in a particular patch. The possible solutions are either to identify directly the relationships between the patch residence time and host density, or to identify the major components which determine the patch residence time, and thus the relationship between the patch residence time and these components. In a section of the next Chapter, by using a stepwise regression analysis, I shall show that the patch residence time of *A. asychis* was a function of several foraging activities such as the number of ovipositions, the number of host feedings, and the number of rejections. This result may provide a picture of the components of patch residence time, and help us to understand how the wasp allocates its time. However, this approach may not be the best way to understand the population consequences, because of a precondition: we must be able to predict the frequencies of different behavioral activities under different circumstances.

The second way to address the problem of patch residence time, which is emphasized in this Chapter, is to ask when a parasitoid should leave a particular patch. A common practical method is to compare experimental data with "rules of thumb". Several simple rules of thumb for patch leaving have been postulated, *e.g.*, fixed number expectation (Gibb, 1962), where the parasitoid leaves each patch after a certain number of hosts has been found; fixed time expectation (Krebs, 1973), where the parasitoid leaves the patch after a certain amount of time has been spent there; fixed giving up time, GUT, defined as the interval from the time of last oviposition to the time of leaving the patch, and if no parasitization occurs, the total time spent on the patch (Krebs *et al.*, 1974), where the GUT is nearly constant for all patches; and dynamic GUT (Waage, 1979), where the GUT is an increasing function of host density. Of course some of these rules require the animal to assess and learn something about its current patch. To facilitate this learning in insects, Cowie and Krebs (1979) suggested that a mechanism of "sliding memory window" might be used by animals which exploit an unknown environment continuously and use recent experience to make decisions about how long to stay in future patches. By employing this mechanism, an animal can average its recent experience in deciding when to leave the current patch. In this Chapter, I compare my experimental data with the patch leaving rules and the mechanism mentioned above, to show the possible rules that could be employed by the parasitoid *A. asychis*.

Materials and Methods

Here I give a brief description of my experiments only, since the details have been described in Chapter II. An open petri dish (14 cm diam) was used as the experimental habitat. I placed broad bean leaflets into each petri dish, one in the centre and four spaced around it, each leaflet defined as a patch. I placed one, two, four, six, or eight second-instar pea aphids on the central leaflet, and marked them with water-coloring pens, each with a different color, to enable their identification, using 45, 6, 28, 4, and 23 replications for host densities of 1, 2, 4, 6, and 8, respectively. After introducing a female of *A. asychis* into the petri dish, I recorded its behavior with a video camera until the wasp either reached the habitat boundary (*i.e.*, the edge of the petri dish) or left it. Ovipositions into hosts were confirmed by dissection of hosts that had ovipositor insertion time exceeding 1 min. According to Bai and Mackauer (1990), the probability that less than 1 min of insertion time would result in successful oviposition is very low.

For each of the observations, I gathered the data from the video tapes for patch residence time, numbers of parasitisms, host feedings, rejections, GUT, the sequences of host acceptance decisions and the host qualities.

The fixed number assumption (Gibb, 1962) and the fixed time assumption (Krebs, 1973) were apparently not tenable rules for my experimental system (see Chapter V). This was because: if the fixed number assumption is true, the number of hosts parasitized should not vary under different host densities; if the fixed time assumption is true, the patch residence time should be independent of host density. We know that these are not true, since the patch residence time and the number of hosts parasitized are functions of host density (see Chapter V). Therefore, I focussed on the tests of GUT assumptions and the sliding memory window mechanism.

To test the assumptions of use of a GUT rule, we had first to ascertain whether the GUT was independent of a function of host density. To test the mechanism of the sliding memory window, I assumed that the parasitoid used the window to remember qualities of the most recently encountered hosts to decide whether or not to leave the current patch. If the assumption is true, there must be some appropriate length of the window, by which the wasp makes patch-leaving decisions. Then, the question becomes: how many memory units should the wasp use to make patch leaving decisions. I used a memory vector $m_i(t)$ for characterizing the memory window, where positions in the vector describe host types recently encountered in chronological order. Thus, m_1 defines the host most recently encountered, and m_n defines the type of host encountered in the most distant past that the individual can still remember, where the subscript n is the size of the memory vector, *i.e.*, the length of the memory window. For example, an individual with $n = 5$ will always remember the identity of the last five hosts encountered. As the wasp encounters a new host, the identity of the new aphid is entered into the memory vector and the fifth, or most distant memory is lost.

Results

(1) Test of GUT assumptions:

Krebs *et al.* (1974) found a fixed GUT patch leaving rule from their study of the black-capped chickadee, *Parus atricapillus*, searching for mealworms on artificial pine cones. As predicted by their fixed GUT assumption, a parasitoid species has an intrinsic, constant GUT, and individuals leave a patch accordingly. If this is true, then the GUT should be independent of host density. Waage (1979) showed that the parasitoid wasp, *Nemeritis canescens*, employed a dynamic GUT for making patch leaving decisions. McNair (1982) deduced that an animal's GUT in a particular patch should be related to the host density. In general, GUT should be longer in patches that are consistently better than others. My data, in Fig. 4.1, show the GUT to be an increasing function of host density. The linear regression equation is

$$\mathrm{GUT} = 5.7162 + 0.5991 \times \text{host density} \qquad (4.1)$$

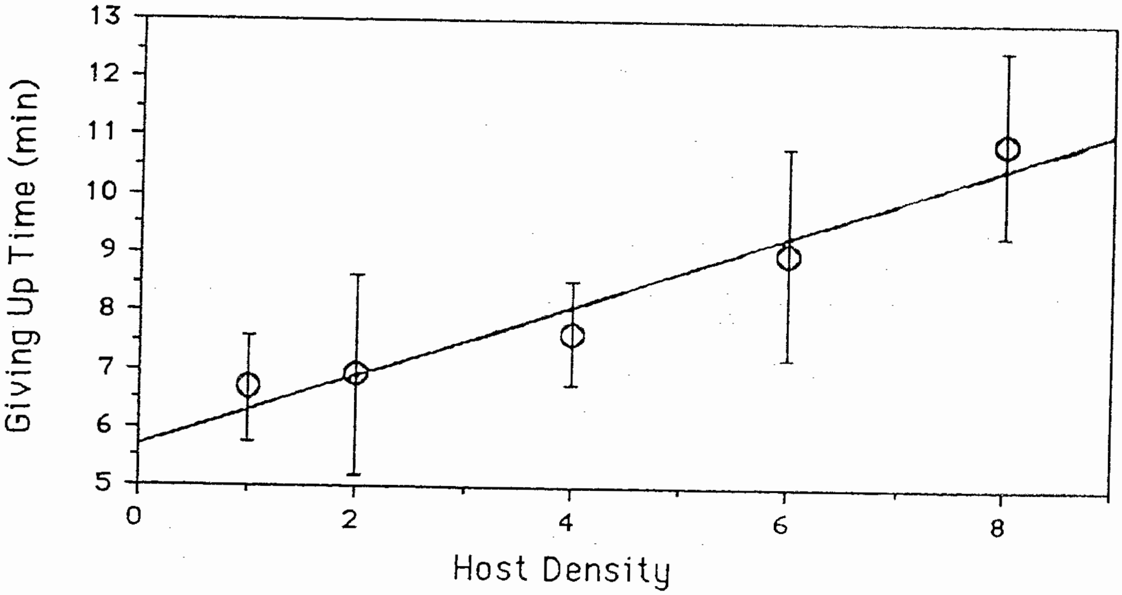
with $r = 0.9749$. Thus, with a positive slope of the regression line, my data are in agreement with McNair's (1982). I conclude that the fixed GUT assumption should be rejected, and the dynamic GUT assumption should be accepted.

The fact that the GUT is not constant across different host densities suggests that the patch leaving decision rule used by *A. asychis*, may include adaptive behavior such as learning, for coping with a changing environment.

(2) Test of sliding memory window:

The optimal value for the length of a memory window, n, is determined by the mechanism used by the animal for processing the information stored in the memory window. Roitberg and Prokopy (1984) found that the fruit-attacking tephritid flies "remember" five qualities of recently encountered hosts in making host acceptance decisions. Because these decisions, in general, depend upon the density of hosts and the

Fig. 4.1. The giving up time (GUT) ± SE at different host densities. The regression equation is $y = 5.7162 + 0.5991 \times$ host density per leaflet, $r = 0.9749$.


Giving Up Time (min)
13
12
11
10
9
8
7
6
5
0
2
4
6
8
Host Density

mixture of unparasitized and previously parasitized hosts, Roitberg and Prokopy used the time since the last oviposition as a proxy of host density, and the fraction of previously parasitized hosts in the previous five encounters as a measure of the mixture of unparasitized and parasitized hosts. I used a similar method but applied it to the patch leaving decisions, rather than to host acceptance decisions.

I assumed that *n* memory units had been used by the wasp for making patch leaving decisions, and the information, which represented the qualities of hosts recently encountered and stored in the memory window, would be updated after each host encounter. Since the intervals between encounters were almost always the same (31 ± 3 sec, mean ± SE, sample size = 737), I considered only the proportion of parasitized hosts (*i.e.*, not the host density) in *n* memory units to form an index of current patch quality, M, *i.e.*,

$$M = \frac{\text{number of parasitized hosts in the memory window}}{\text{length of the memory window, } n.} \qquad (4.2)$$

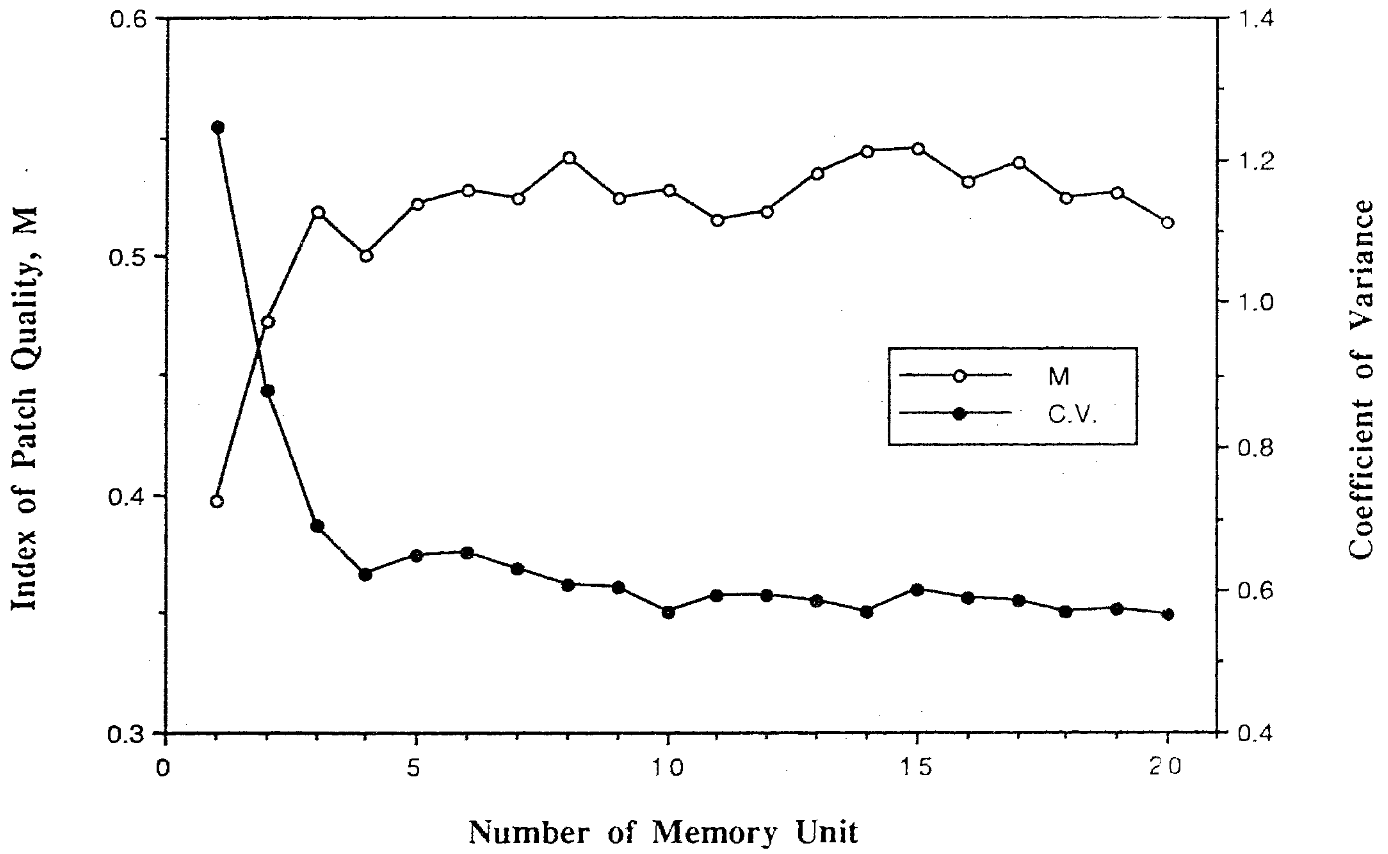
When the value of M reached to a certain level, the wasp should leave the current patch, because its quality is no longer adequate for continued searching within it. So, the question becomes: what is the critical value of M, or M_{crit}, above which the wasp should leave the current patch? As a patch leaving rule for a species, the value of M_{crit} should be relatively robust, *i.e.*, with the least variation under different combinations of conditions. Under natural conditions, wasps will experience different patches with different host densities and qualities while foraging, because hosts are generally non-uniformly distributed. The encounters of a wasp with its hosts can be seen as the samples the wasp makes within a given patch. If too few units of memory are used by the parasitoid, then sample errors could result in misjudgement of the patch quality, leading to incorrect decisions. By increasing the number of units, the parasitoid can reduce this risk (refer to the central limit theorem). But too many units of memory may not contribute to accurate assessment of environmental changes, since the correlation between the identity in distant memory and future host quality might be small. Thus, wasps that employ long windows would respond slowly to changes in environment. In other words, if the wasps used a mechanism of sliding memory window for making patch leaving decisions, the coefficient of variance (representing the sampling error) among parasitoid individuals will be gradually reduced to a certain level, with increasing memory units. There must be some value of n, beyond which a relative constant value of M and coefficient of variance among wasp individuals will appear in an ideal situation. For *A. asychis* females, each encounter with a host requires a relatively long time, *e.g.*, feeding needs about 40 min, and oviposition needs 1 min (see Chapter V). Also, the total number of encounters with hosts is influenced by the host density within that patch, *e.g.*, a wasp will make about 11 and 33 encounters before leaving the patch when host densities are 4 and 8 respectively (personal observation, unpublished data). Therefore, a moderate number of memory units be used for making patch leaving decisions, seems to be the reasonable solution.

I tested a series of sub-hypotheses about different numbers of memory units that are used for judging patch quality for finding the most suitable value of n. For example, one sub-hypothesis was that the wasp uses 5 memory units to make patch leaving decisions, so that the tested data come from the last 5 hosts encountered before leaving the patch in each observation. Thus, the value of M and C.V. (coefficient of variation) among wasp individuals can be easily calculated. My analysis considered up to 20 memory units. The results are shown in Fig. 4.2. From the figure, we know that when the parasitoid uses fewer memory units than 3, the values of the C.V. are large, and when more than 3 memory units are used, the C.V. values are relatively small and stable, and the M values are also relatively stable. Thus, $n = 3$, and I concluded that the parasitoid uses at least 3 memory units to make a patch leaving decision, and when the percentage of parasitized hosts in the memory window is greater than 0.5 (M_{crit} value), then the parasitoid will leave the patch. This could be another possible patch leaving rule employed by the parasitoid.

Discussion

The concept of patch is a complex issue, and has been discussed extensively in the literature (*e.g.*, Addicott, *et al.* 1987). In addition to the definition of Hassell and Southwood (1978) and Bell (1990) adopted here, other definitions are also possible. For example, a patch may be theoretically defined as a discontinuity in environmental states where the discontinuity matters to the organism (Wiens, 1976); or as any place in the environment where the abundance of either resources or organisms is high or low relative to its surroundings (Roughgarden, 1977); or practically defined as the territory of an animal (the amakihi territory of Kamil 1978); or as a whole plant (elementary unit of foraging of Ayal 1987); or as a part of

Fig. 4.2. The patch quality index M (line with open circle), and corresponding coefficient of variance (line with solid circle) when different numbers of memory units were used for making patch leaving decisions. The sample size is 18.


0.6
0.5
0.4
0.3
1.4
1.2
1.0
0.8
0.6
0.4
0
5
10
15
20
Index of Patch Quality, M
Coefficient of Variance
Number of Memory Unit
M
C.V.

a plant (bean leaflet; as in the present study); or as a single prey item (Cook and Cockrell 1978; Yamamura and Tsuji 1987). Krebs (1978) pointed out that environments can simultaneously exhibit patchiness at different spatial scales, from millimeters to kilometers. Holling (1992) showed that animals demonstrate attributes of size and behavior that are scaled by the discontinuous architecture of the landscapes in which they live, since ecosystems have a discontinuous architecture. He analyzed how animals make decisions in a discontinuous environment, and found that animals of different body sizes encounter different discontinuities in their environment, and thus the decisions are in accordance with the scales of sampling and measurement.

The appropriate size of a particular patch for studies on foraging behavior should be determined by the characteristics of the animal studied. The characteristics include: body size, speed of movement, reaction distance to hosts, etc., for parasitoid wasps; and body size, distribution, dispersal, etc., for the hosts. Thus, the concept of patch size is a relative one (Southwood, 1977).

The consequences of possible choices of different patch sizes differ. If the physical size of the patches relative to the wasps is small, as in this study, then host distribution tends to be Poisson, wasps search randomly, encounter hosts randomly, and find hosts easily; their encounter rates are often high, and the time interval between encounters is almost uniform if the wasps remain active. The time interval is influenced by factors such as the host's distribution, and the physiological status of the parasitoid. For example, if a longer interval is caused by the wasp's stopping to rest or groom, then its contribution to patch leaving decisions should be different from one caused by actively unsuccessful search.

If the physical size of the patches relative to the wasps is large, the hosts may be aggregatively distributed (clustered in parts of the patches), so the wasp's encounter rate with hosts will change with time, and thus the time interval between encounters will also change. That is to say, when wasps are foraging among clustered hosts, the time interval will be small; when wasps are foraging in other parts of the patches, the interval will be large. So, we can expect a large variation among intervals. Under these circumstances, the wasp's searching pattern may not always be random, because random searching is not always an optimal strategy.

The two possible patch leaving rules indicated in this study, show that the wasp makes its decisions based on the patch quality that it perceived through sampling. If a dynamic GUT rule is employed, then we can imagine that the wasp assesses patch quality by counting the density of unparasitized but not parasitized hosts. If a sliding memory window mechanism is employed, then the wasp detects the patch quality mainly by the percentage of unparasitized hosts in the total host population. In parasitism, the patch depletion process only changes the percentage of unparasitized and parasitized hosts in the total host population. In small patches, the encounter rate with hosts, either unparasitized or parasitized, is relatively fixed. Thus, the patch leaving decisions are made upon the qualities of hosts that are successively encountered. But in large patches, the encounter rate with hosts is not fixed, because of the large variation in intervals between encounters. Therefore, the patch leaving decisions are determined by both intervals between encounters and qualities of hosts successively encountered. Under this circumstance, if a long window is employed by the wasp, then a large C.V. value and the variation of M values among individuals could be expected.

Conclusion

When *A. asychis* searches for its pea aphid hosts in broad bean leaflet patches, there are two possible patch leaving rules:

(1) the wasp should leave the current patch when the GUT has elapsed, and the GUT should increase with host density by 5.7162 + 0.5991 × host density;

(2) a sliding memory window with a length of at least 3 units, and when the proportion of parasitized hosts in the memory window is more than half, the wasp should leave the current patch.

References

Addicott, J. F., Aho, J. M., Antolin, M. F., Padilla, D. K., Richardson, J. S., and Soluk, D. A. 1987. Ecological neighborhoods: scaling environmental patterns. - *Oikos*, 49:340-346.

Ayal, Y. 1987. The foraging strategy of *Diaeretiella rapae*. I. The concept of the elementary unit of foraging. - *Journal of Animal Ecology,* 56: 1057-1068.

Bai B. and Mackauer, M. 1990. Oviposition and host feeding patterns in *Aphelinus asychis* at different aphid densities. - *Ecological Entomology*, 15: 9-16.

Bell, W. J. 1990. Searching behavior patterns in insects. - *Annual Review of Entomology,* 35: 447-467.

Cook, R.M. and Cockrell, B.J. 1978. Predator ingestion rate and its bearing on feeding time and the theory of optimal diets. - *Journal of Animal Ecology,* 47: 529-547.

Cowie, R. J., and Krebs, J. R. 1979. Optimal foraging in patchy environments. - In: *Population Dynamics* (R.M. Anderson, B. D. Turner, L. R. Turner, eds.) Blackwell Press.

Gibb, J. A. 1962. Tinbergen's hypothesis of the role of specific searching images. - *Ibis*, 104: 106-111.

Hassell, M. P., and Southwood, T. R. E. 1978. Foraging strategies of insects. - *Annual Review of Ecology & Systematics*, 9: 75-98.

Holling, C. S. 1992. Cross-scale morphology, geometry and dynamics of ecosystems. - *Ecological Monograph,* (In Press).

Kamil, A. C. 1978. Systematic foraging by a nectar-feeding bird. - *Journal of Comparative and Physiological Psychology*, 92: 388-396.

Krebs, C. J. 1978. *Ecology: The Experimental Analysis of Distribution and Abundance*. 2nd Ed. Harper & Row, New York.

Krebs, J. R. 1973. Behavioural aspects of predation. - In *Perspectives in Ethology*, Eds. by Bateson, P. P. G. and Klopfer, P. H.. Plenum Press, N.Y.

Krebs, J. R., Ryan, J. C., and Charnov, E. L. 1974. Hunting by expectation or optimal foraging? a study of patch use by chickadees. - *Animal Behaviour*, 22: 953-964.

Mangel, M. 1992. Descriptions of superparasitism by optimal foraging theory, evolutionarily stable strategies and quantitative genetics. - *Evolutionary Ecology*, 6: 152-169.

McNair, J. N. 1982. Optimal giving-up times and the marginal value theorem. - *The American Naturalist.*, 119: 511-529.

Roitberg, B. D. and Prokopy, R. J. 1984. Host visitation sequence as a determinant of search persistence in fruit parasitic tephritid flies. - *Oecologia* (Berlin), 62: 7 - 12.

Roughgarden, J. D. 1977. Patchiness in the spatial distribution of a population caused by stochastic fluctuations in resources. - *Oikos*, 29: 52-59.

Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? - *Journal of Animal Ecology,* 46: 337-365.

van Alphen, J. J. M., and Visser, M. E. 1990. Superparasitism as an adaptive strategy. - *Annual Review of Entomology*, 35: 59-79.

Visser, M. E., van Alphen, J. J. M., and Nell, H. W. 1990. Adaptive superparasitism and patch time allocation in solitary parasitoids: The influence of the number of parasitoids depleting a patch. - *Behaviour*, 114: 21-36.

Waage, J. K. 1979. Foraging for patchily-distributed hosts by the parasitoid, *Nemeritis canescens*. - *Journal of Animal Ecology,* 48: 353-371.

Wiens, J. A. 1976. Population responses to patchy environments. - *Annual Review of Ecology & Systematics*, 7: 81-120.

Yamamura, N. and Tsuji, N. 1987. Optimal patch time under exploitative competition. - *The American Naturalist*, 129(4): 553-567.

CHAPTER V

PATCH RESIDENCE TIME AND PARASITISM: A SIMULATION MODEL*

Abstract

I describe the development and use of a simulation model to predict the patch residence time and rate of parasitism of the wasp *Aphelinus asychis* Walker (Hymenoptera: Aphelinidae), a solitary parasitoid of the pea aphid. I use the model to test the hypothesis that a wasp's decision to leave a patch or to accept or reject a host is based on information about previously encountered hosts that are stored in a sliding "memory window". The model incorporates the foraging behavior of individual wasps, including a simplified learning process of the proportions of parasitized and unparasitized hosts among all hosts encountered. Optimal foraging theory predicts that an animal should spend more time in high-quality than low-quality patches. The simulation results are consistent with this prediction as well as with empirical laboratory data. I propose that searching females of *A. asychis* store information about a changing environment in five units of a sliding "memory window".

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Introduction

The amount of time an animal spends in a patch may affect its rate of food intake and its predation risk (Pyke, 1984). van Alphen (1988) found that the subject of patch time allocation received surprisingly little attention, though it may be of crucial importance in understanding population dynamics of host-parasitoid systems (Comins and Hassell, 1979). Improved understanding of a parasitoid's searching behavior (including patch allocation, search patterns etc.) can also contribute to the models used for describing the dynamics of host-parasitoid and prey-predator interactions (Bernstein *et al.*, 1991). Two levels of searching behavior of a parasitoid species can be identified, (1) within patches and (2) between patches, as shown in Chapter II. For searching behavior within patches, patch residence time and the number of hosts parasitized are the most important features that characterize a wasp's foraging efficiency. My interest here, is to show how a parasitoid's foraging can be translated into predictions about parasitism within a particular patch, by using a theory-driven simulation model.

Patch residence time, which is defined as the time from which a parasitoid enters a patch until it leaves that patch, is an important feature of a parasitoid's searching strategy. Once a female parasitoid wasp enters a patch, it is likely to evaluate the quality of the patch by sampling, and to "decide" whether it should continue to search in the patch or leave for other patches. Since a parasitoid will rarely have perfect information on the qualities of other patches, and must bear the cost of movement between patches, it may remain in its current patch even if there are other patches with higher quality. As a wasp accepts unparasitized hosts, the quality of the patch, in terms of proportion of unparasitized hosts in the total, will be decreased. The higher the quality of the patch, the stronger such a tendency, as suggested by Charnov's (1976) marginal value theorem. The parasitoid may remain in the patch until patch quality has declined to a certain level. Therefore, the problem is: to what extent does a parasitoid remain in a particular patch under different patch qualities, rather than leaving the patch for an unknown environment. I shall test the predictions from optimal foraging theory as discussed by Krebs *et al.* (1974), Charnov (1976) and Hassell (1978).

Oster and Heinrich (1976) showed that it pays to invest time in sampling less profitable areas in unpredictable environments in case the distribution of prey changes. Two general strategies for sampling an unknown environment could be employed by animals (Cowie and Krebs, 1979). One strategy is to divide the total foraging time into an initial period of pure sampling, followed by an exploitation period. The alternative is to exploit continuously and use recent experience to make decisions about how long to stay in future patches. Cowie and Krebs demonstrated a specific mechanism for the alternative, called a sliding "memory window", which allows the animal to average its recent experience in deciding when to leave the current patch. Mangel and Roitberg (1989) showed that the plasticity in oviposition site selection by the apple maggot fly (*Rhagoletis pomonella* Walsh) could be successfully interpreted by introducing variables of its physiological state (egg complement) and its information state (sliding memory window).

In a previous study (Roitberg *et al.* 1992), we assumed that parasitoids make host acceptance decisions based on the qualities of recently encountered hosts which are stored in a sliding memory window. We defined the memory state as a memory vector $m_x(t)$ where positions in the vector describe, in chronological order, host types recently encountered at time t. Thus, m_1 defines the host most recently encountered, and m_{max} defines the type of host encountered in the most distant past that the individual can still remember, where max is the number of units in the memory vector. For example, an individual with max = 5 will always remember the identity of the five hosts most recently encountered. As individuals encounter new hosts the identity of those individuals are entered into the memory vector with the most distant memory being lost. A host acceptance decision matrix was calculated by using the dynamic modeling technique of Mangel and Clark (1988). This matrix contained optimal host acceptance decisions that maximize lifetime reproductive success as a function of two dynamic variables, memory and eggload, and parasitoid age. By running a simulation model that incorporated this matrix, we showed that during a fixed period, the parasitoid would perform better (*i.e.*, realize higher lifetime reproduction fitness) if more units of memory window were used. But the physiological cost of such memory windows would almost certainly also increase. Thus, we concluded that there must be a trade off between the benefit and the cost of information retention, and that a short memory window might be appropriate for *A. asychis*, because of its small body size and its fast environmental rate of change. A shorter memory window would enable the parasitoid to detect more sensitively the rapid changes of its environmental quality than would a longer memory window.

Along this line, I shall first simplify the memory model we used previously and adapt it to the situation of *A. asychis*. Then, I show the influences on the structure of the decision matrix of different relative fitness values for a wasp accepting a parasitized host. A stepwise regression analysis of results from my laboratory experiments provided the costs in time for each kind of host acceptance decision. Based on the host acceptance decision matrix of *A. asychis*, I built a detailed simulation model to test hypotheses about the number of memory units used and the patch leaving rules, in terms of the patch residence time and the number of hosts parasitized under different initial host densities. In this way, I showed the potential consequences at the patch level by comparing the simulation results with my experimental results.

Simplifying the Learning Model

In our model (Roitberg *et al.* 1992), we considered the probability that a wasp in each time step encounters one of three host types (λ_1 , λ_2 , and λ_3, corresponding to good, moderate, and poor host qualities, respectively), or encounters nothing (empty) λ_0. Thus we had $\lambda_1 + \lambda_2 + \lambda_3 + \lambda_0 = 1$. The number of possible states of memory window, and also the number of elements in the decision matrix, exponentially increases with increasing numbers of memory units. The matrix harbours optimal host acceptance or rejection decisions when such decisions maximize lifetime reproductive success. For example, if a wasp has 30 eggs each day, and 100 time steps used in the calculation, then there will be $3^3 \times 30 \times 100 = 81{,}000$ elements in the decision matrix when 3 units of memory are used (where base value, 3, indicates the number of host types, and power value, 3, denotes the number of memory units used), 729,000 elements when 5 units of memory are used, 6,561,000 elements when 7 units are used, and 59,049,000 elements if 9 units are used, etc. That is what Mangel and Clark (1988) called the limitation of dimensionality in the learning models. And that was the reason why we were limited to examining up to only 7 memory units in our 1992 paper.

In order to examine the effects of a large number of memory units on behavioral decisions, I simplified the learning model and adapted it to the situation of *A. asychis* as follows: At each time step, a wasp could encounter: a good (unparasitized) host with a probability of λ_g, or a bad (parasitized) host with a probability of λ_b, or nothing (empty) with a probability of λ_0. Thus we have $\lambda_g + \lambda_b + \lambda_0 = 1$. Considering the fact that the values of λ_g and λ_b did not include the information of sequences of host types that occurred in the memory window, we can account only for all the possible combinations of λ_g and λ_b values, *i.e.*, all the possible combinations of proportions of unparasitized and parasitized hosts in the memory window. Again, if a wasp has 30 eggs each day and 100 time steps were used in the calculation, then the number of elements in the decision matrix would linearly increase with the increase of memory units used. For example, $(3 + 1) \times 30 \times 100 = 12{,}000$ elements which would be in the decision matrix if 3 memory units were used (where 3 is the number of memory units used, and 3 + 1 indicates the possible combinations of values for each pair of λ_g and λ_b); 18,000 elements if 5 memory units were used, 24,000 elements if 7 were used, and 30,000 elements if 9 were used. The simplified memory model makes it possible to examine the effects on the behavioral decisions of different numbers of memory units used by the wasp. It also provides an opportunity to look at the effects on the structure of the decision matrix of different behavioral parameter values such as fitness payoffs. But before the calculations are discussed, we must obtain some real estimates of time costs for each kind of behavioral decision including oviposition, host feeding and rejection. These values were obtained from my laboratory experiments.

Patch residence time measurement

The detailed description of my experiments was given in Chapter II. I gathered data on each kind of host encounter decision, including external and internal examinations, oviposition, rejection, host feeding, and time spent on each kind of behavior within each observation, for a stepwise regression analysis (sample size = 107).

The result from a stepwise regression (equation 5.1) provides a picture of the components of patch residence time, and help us to understand how the wasp allocates its patch time:

$$Y = 1.7945 + 43.6566\,X_1 + 4.4907\,X_2 + 0.1512\,X_3 \qquad (5.1)$$

where Y (in min) is the active patch residence time, which equals the total patch residence time minus resting and grooming time, X_1 is the component of host feedings, X_2 is the component of ovipositions, and X_3 is the component of rejections ($R^2 = 0.7951$, $F_{3,103} = 133.1886$, $p = 0.0001$). All the independent variables are significant contributors to the regression equation. This equation predicts that the average time for feeding on a host is 43.66 min, for laying an egg is 4.49 min, for rejection is 0.15 min, and the wasp should leave an empty patch at about 1.79 min. From these values, I am able to calculate the optimal host acceptance decision matrix for *A. asychis.*

Host acceptance decision matrix

The decision matrix is a table that contains the optimal responses of *A. asychis* after encountering a host and examining it. Because of its strong ability in host discrimination (Bai and Mackauer, 1990), I assume that the wasp can acurately assess the quality of the host, either as good (unparasitized) or as poor (parasitized). The three possible decisions it can make are: laying an egg into the host; feeding on the host; or rejecting the host. Host feeding occurs periodically (Bai and Mackauer, 1990), thus we can represent it by a periodic function (equation 2), where x varies from 0 to π/2/period, and the period is from 20 to 24 h, *i.e.*, sin(x) can be from 0 to 1. When the probability of feeding, or a tendency to feed, reaches a certain threshold level, the parasitoid will feed on the next host it encounters. Once feeding has occurred, the hunger level of the wasp reverts to 0. After that, the probability of feeding, or the tendency to feed, will increase again with time. In this way, we can simplify the three possible decisions to two: acceptance or rejection.

$$\text{Probability of feeding occurrence} = \sin(x) + \text{random term} \qquad (5.2)$$

I assume that the wasp acts as if it "knows" the number of eggs it still holds, the probability of encountering a good or a bad host, the consequences of each decision, and the time left before it dies. Except for these conditions, I also specify the consequences for each kind of decision: *e.g.*, laying an egg into a good host, the direct fitness is 1.0, and laying an egg into a bad host, the direct fitness is 0.1; feeding on the host, causes the wasp to renew the egg status, *i.e.*, it will have maximum eggs in the near future; rejecting the host, causes a loss of a small amount of time. Here, I define the lifetime fitness (F) of the wasp as:

F(egg, t, T) = maximum expected fitness from the host exploitation between t and T when egg states at time t are defined as egg, where T is the terminal period.

The calculation for lifetime fitness considers three different, mutually exclusive, events and weights them according to their probabilities. These events and their effects are:

The wasp does not encounter any host, with a probability of λ_0. The future fitness is defined as the probability of surviving from one time period to the next, ρ, multiplied by future reproductive fitness F(egg, t +1, T);

The wasp encounters a good host. If it accepts the host, it obtains direct fitness of f_g (= 1.0), and future fitness of $\rho^{t(ovip)} * F(egg-1, t + t(ovip), T)$, where t(ovip) is the time required for laying an egg (= 5.0). If it rejects the host, it accrues 0 direct fitness and future fitness of ρ * F(egg, t +1, T).

The wasp encounters a bad host. If it accepts the host, it accrues direct fitness f_b (in this case 0.1), and future fitness of $\rho^{t(ovip)} * F(egg-1, t + t(ovip), T)$. If it rejects the host, it receives only future fitness expressed as ρ * F(egg, t +1, T).

There are two ways of including the probability of a successful attack on a host, τ, caused by the extent of the hosts' defensive behavior, into the foraging dynamics. One way is to add it through the simulation, which I shall describe in the next section, thus the dynamic modeling equation can be summarized as follows:

$$\begin{aligned}
&F(egg, t, T) = \lambda_0 * F(egg, t+1, T)\\
&+ \lambda_g * \Sigma \max[f_g + \rho^{t(ovip)} * F(egg-1, t+t(ovip), T); \rho * F(egg, t+1, T)]\\
&+ \lambda_b * \Sigma \max[f_b + \rho^{t(ovip)} * F(egg-1, t+t(ovip), T); \rho * F(egg, t+1, T)]
\end{aligned} \tag{5.3}$$

with condition of $F(egg, T, T) = 0$.

Another way is to include the probability of successful attack τ into the equation, thus:

$$\begin{aligned}
&F(egg, t, T) = \lambda_0 * F(egg, t+1, T)\\
&+ \lambda_g * \Sigma \max[\tau * (f_g + \rho^{t(ovip)} * F(egg-1, t+t(ovip), T)) +\\
&(1 - \tau) * \rho * F(egg, t+1, T); \rho * F(egg, t+1, T)]\\
&+ \lambda_b * \Sigma \max[\tau * (f_b + \rho^{t(ovip)} * F(egg-1, t+t(ovip), T)) +\\
&(1 - \tau) * \rho * F(egg, t+1, T); \rho * F(egg, t+1, T)]
\end{aligned} \tag{5.4}$$

with condition of $F(egg, T, T) = 0$.

Equations (5.3) and (5.4) are descriptions of decisions within one-day periods. Thus, the feeding events are not included. The equations can be solved "backwards in time" starting with $t = T - 1$ to $t = 1$. The maximization terms in the equations indicate that the decision (oviposition or rejection) is made to give the highest expected lifetime fitness.

I calculate the optimal decision matrices according to equation (5.3), because the successful attack probability t is not a constant, but varies instead with different defensive responses of local host populations to the attacks and with the parasitoid's own physiological status, which is readily included in the simulation. The results are: when encountering a good host, the wasp always lays an egg in the host because the host quality is already as good as it will find. When encountering a bad host, the wasp's decisions will change with the value of λ_g or λ_b which equals $(1 - \lambda_g)$, with the number of eggs, and the time available. [Note actual $\lambda_g = (1 - \lambda_0) \times \lambda_g$, and actual $\lambda_b = (1 - \lambda_0) \times \lambda_b$]. The contour graphs for the decision matrix are shown in Fig 5.1. When the quality of environment becomes better (*i.e.*, λ_0 decreases), the probability of accepting a bad host will decrease. In addition, if the direct fitness payoff for accepting a bad host increases, then more bad hosts are accepted (Fig. 5.2). Based on this host acceptance decision matrix, I can simulate the major characteristics of the parasitoid within a particular patch, and make corresponding testable predictions.

Simulation

Details of my stochastic (Monte Carlo) model are described in Appendix 1. My simulations are based on the following scenario: The wasp uses a sliding memory window to store the host qualities recently encountered. The contents of the memory window are renewed after each encounter as described in Roitberg, Reid, and Li (1992). The initial host qualities stored in the memory window are about half good and half bad, which means that the wasp came from a patch of average quality. Table 5.1 shows the parameter values used in the simulation model. The wasp always accepts a good host, and makes host acceptance decisions based on the decision matrix when encountering a bad host. The probability of encountering a good or bad host, λ_g or λ_b, is the proportion of good or bad hosts in the total number. That is to say, the values of λ_g and λ_b are based on

Fig. 5.1: Host acceptance and rejection decisions at different times and egg reserves. The fitness value for accepting a bad host is 0.1, and for a good host is 1. Lines from top to bottom represent the probabilities of encountering unparasitized hosts 0.8, 0.5, and 0.2 respectively. The wasp should accept a bad host when egg reserve value falls above the line, and reject it when below the line.

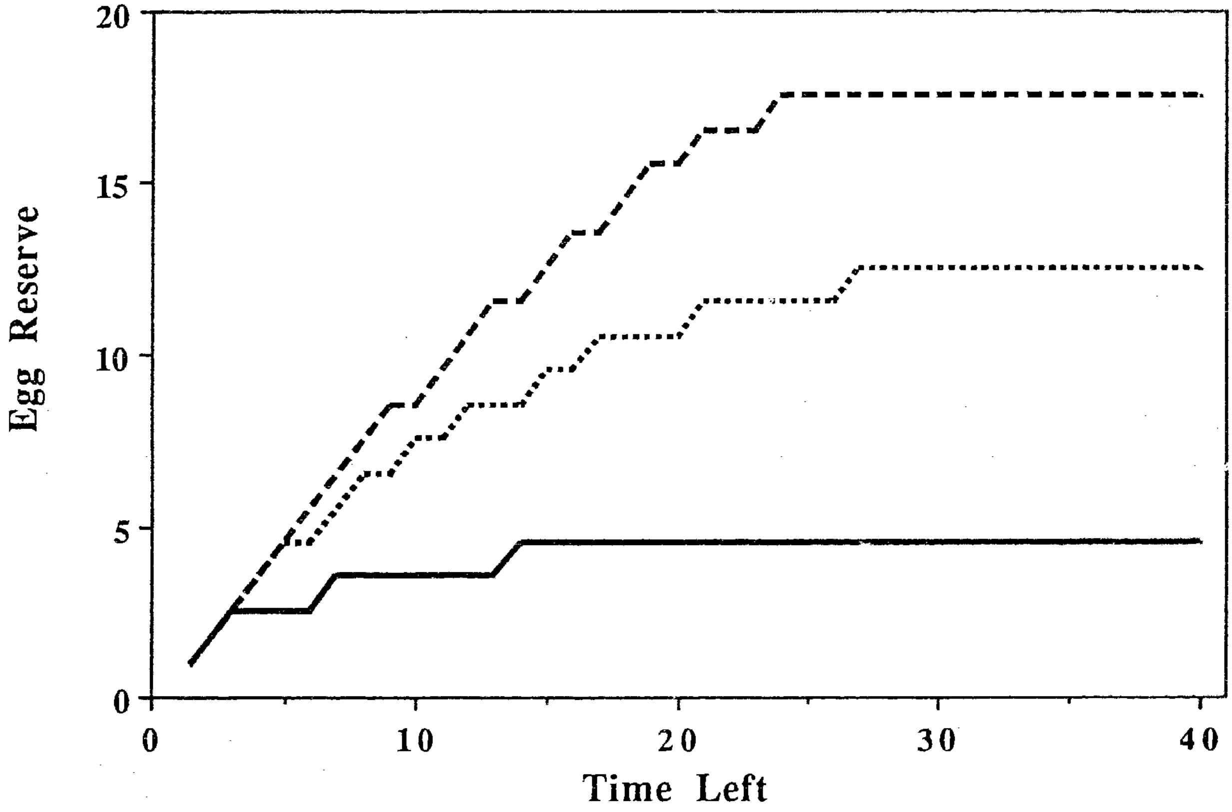

20
15
10
5
0
Egg Reserve
0
10
20
30
40
Time Left

Fig. 5.2: Host acceptance and rejection decisions at different times and egg reserves. The fitness value for accepting a bad host is 0.5, and for a good host is 1. Lines from top to bottom represent the probabilities of encountering unparasitized hosts 0.8, 0.5, and 0.2 respectively. The wasp should accept a bad host when egg reserve value falls above the line, and reject it when below the line.

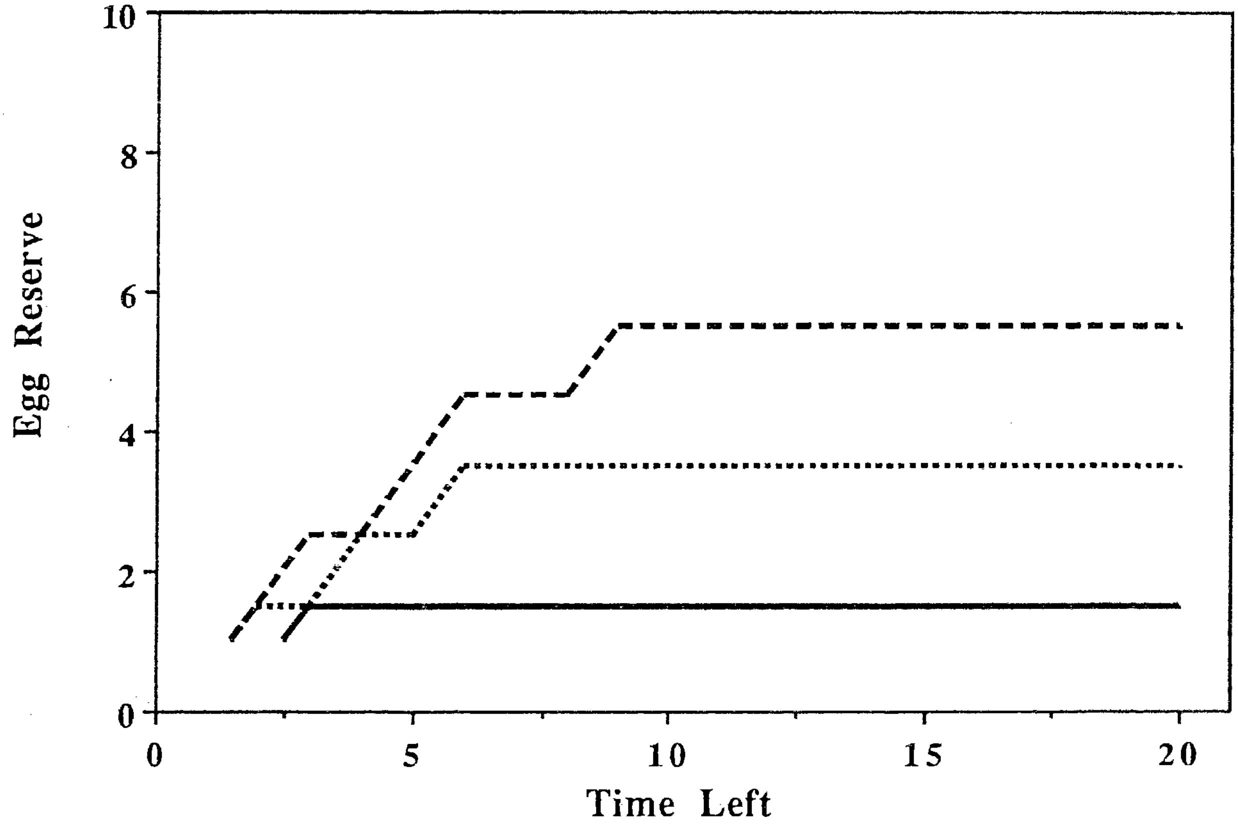

Egg Reserve
0
2
4
6
8
10
0
5
10
15
20
Time Left

Table 5.1. Parameter values used in the simulation model.

Item	Value
Time for laying an egg	5 min
Time for feeding on a host	40 min
Time for rejecting a host	1 min
Probability of not encountering any hosts, λ_0	0.1
Probability of successful attack, τ	0.2

the information stored in the memory units. The wasp searches randomly within patches (see Chapter II). The program was written in MicroSoft QuickBASIC, and run on a Macintosh Plus computer.

The hypotheses tested here concern the number of memory units used by the wasp and the patch leaving rules. A wasp should leave the current patch when the patch quality it experienced has changed to a value lower than its expectation. I assume that the indication of patch quality lower than the wasp's expectation is that the host qualities stored in about half of the memory units are bad. This assumption came from Chapter IV.

Monte Carlo simulations were run 50 times for each host density for wasps using different numbers of memory units. The results (Fig.5.3) show that with increasing host density and number of memory units used, the patch residence time and the number of hosts parasitized also increases. At a low host density, the patch residence times and the number of hosts parasitized do not vary much regardless of the different number of memory units used by the wasp. No significant difference was detected when using the decision matrix generated by using $f_b = 0.1$ *vs* 0.5. Fig. 5.4 shows the comparison of the predictions and experimental results for patch residence time and number of hosts parasited. We can see that the predictions are close to the experimental results. To select the best descriptor of patch residence time and the number of hosts attacked, I used the minimum sum of squares, R^2, as a criterion. Results from the comparisons show that the values of R^2: for patch residence time, 5 units (97.17) < 7 units (219.37) < 9 units (396.67) < 3 units (522.99); for the number of hosts parasitized, 5 units

Fig. 5.3: Patch level consequences under different host densities and numbers of units used in a sliding memory window: (a) patch residence time; (b) number of eggs actually being laid.

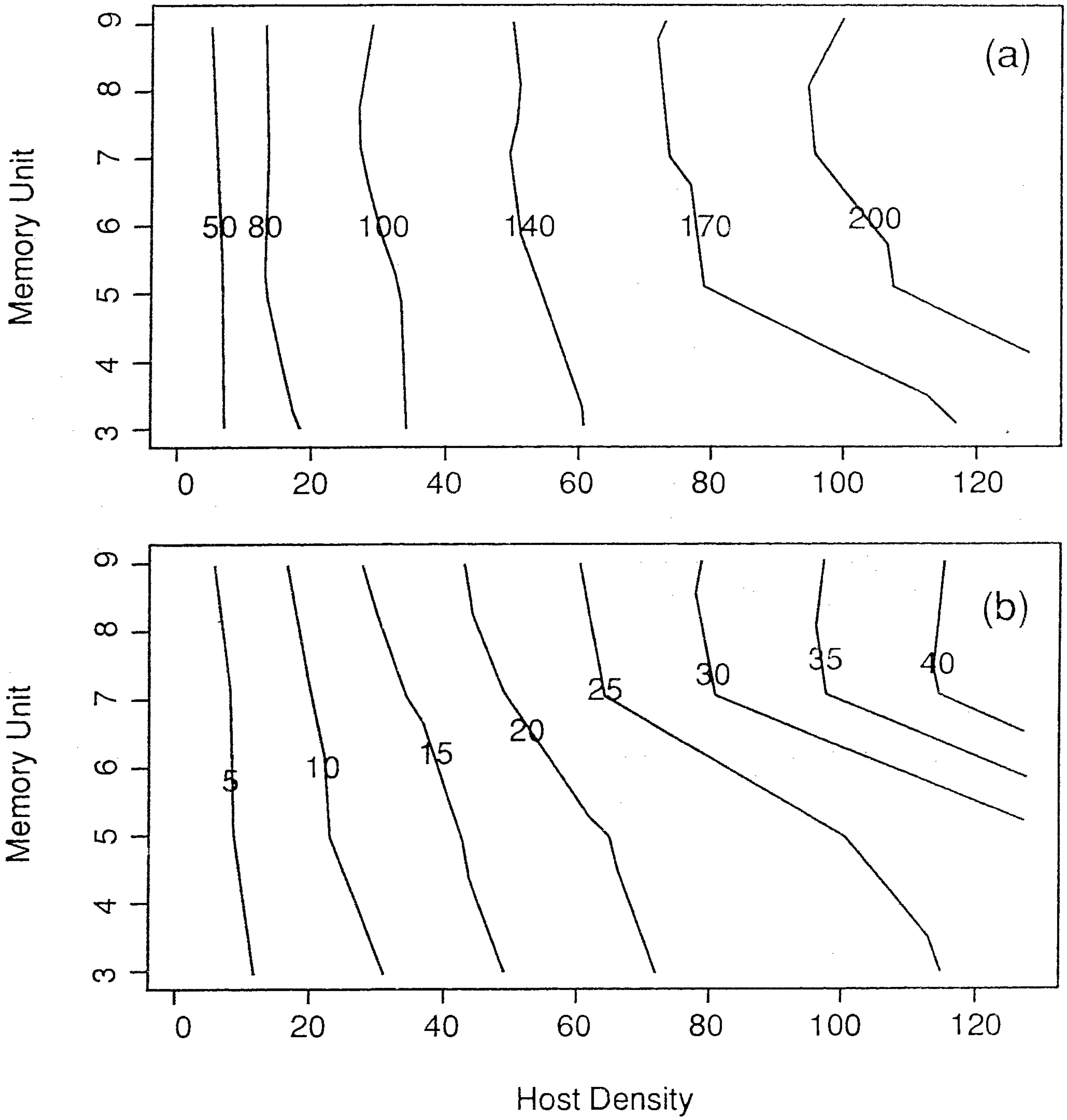
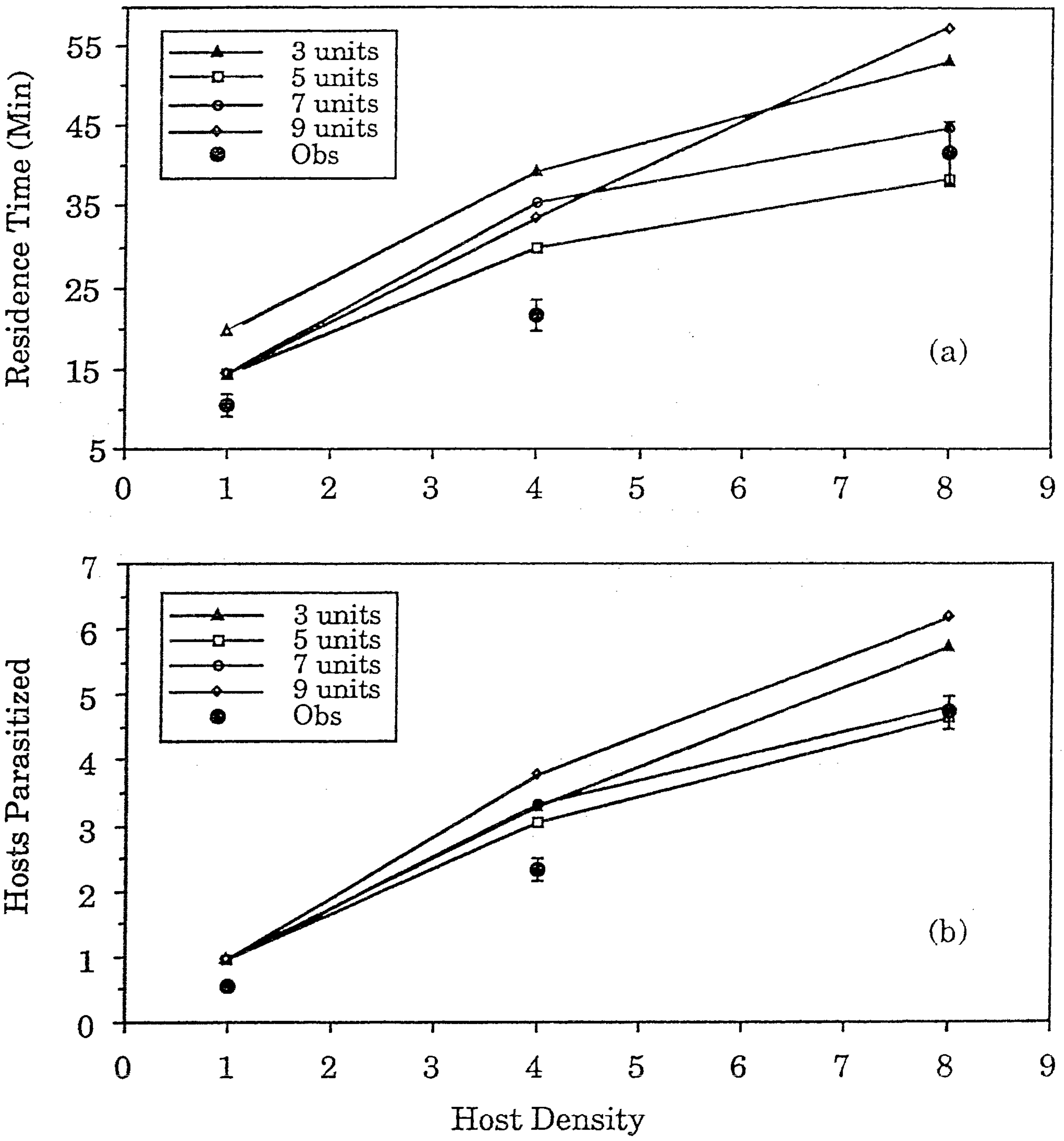

(a)
Memory Unit
3
4
5
6
7
8
9
50
80
100
140
170
200
0
20
40
60
80
100
120
(b)
Memory Unit
3
4
5
6
7
8
9
5
10
15
20
25
30
35
40
0
20
40
60
80
100
120
Host Density

Fig. 5.4: Comparisons of predictions from the simulation results and observed values: (a) patch residence time; (b) number of parasitized hosts.


Residence Time (Min)
55
45
35
25
15
5
3 units
5 units
7 units
9 units
Obs
(a)
0
1
2
3
4
5
6
7
8
9
Hosts Parasitized
7
6
5
4
3
2
1
0
3 units
5 units
7 units
9 units
Obs
(b)
0
1
2
3
4
5
6
7
8
9
Host Density

(0.68) < 7 units (1.16) < 3 units (2.04) < 9 units (4.34). The results confirmed what we inferred: that a short memory window might be appropriate for *A. asychis*, and indicate that a better prediction cannot be obtained by using more than 5 memory units. Therefore, I conclude that 5 units would be the appropriate estimation for the length of a sliding memory window.

Discussion

In the present study, the patch residence time of the parasitoid is a function of host density per patch, a result consistent with the prediction from optimal foraging theory (Krebs *et al.*, 1974; Charnov, 1976; Hassell, 1978). My results further confirm that a memory vector could be a possible mechanism employed by a parasitoid for making host acceptance decisions to cope with its changing environment as indicated by Roitberg, Reid, and Li (1992). My conclusion that *A. asychis* uses 5 units of memory to judge the patch quality by making both host acceptance and patch leaving decisions, is consistent with that of Roitberg and Prokopy (1984) for fruit-attacking tephritid flies. A parasitoid probably should not use many units in a sliding memory window for making behavioral decisions. Long memory windows may be expensive to maintain and may retard a wasp's ability to adapt to fast changing environments. We know that animals are generally non-uniformly distributed within a particular habitat, thus wasps will experience different patches with different host densities and qualities, while they are foraging. The encounters of a wasp with its hosts can be seen as the samples the wasp makes within a given patch. If too few units of memory are used by the parasitoid, then possible sample errors could result in the misjudgement of the patch quality, leading to incorrect decisions. By increasing the number of units, the parasitoid certainly can reduce this kind of risk. But too many units of memory may not increase its ability to judge environmental changes correctly, since the correlation between the identity in long distance memory and future host quality would be weak.

A black box approach such as stepwise regression can provide information (equation 5.1) which will tell us that the total patch residence time is a function of different kinds of behavior, and the average time devoted to each. But we still do not know the frequencies of each kind of behavior that will occur under different initial host densities. This means that a good regression equation such as equation (5.1), is still not good enough for making predictions at the patch level, or at the higher levels. We can only make predictions, based on the detailed simulation and according to the mechanism of host acceptance and patch leaving.

The rate of successful attack is determined to a great extent by the host's defensive behavior which depends upon its developmental stage and physiological status. This rate will vary among different host individuals and local populations. From the laboratory experiments of Gerling *et al.* (1990), the wasp rejects about 80% of 1st and 2nd instar pea aphids and about 95% of 3rd and 4th instar pea aphids. These results are from hosts with good qualities. In reality, the average successful attack rate should be low. In my simulation, I choose 20%.

The speed of renewal of egg status after feeding should be a function of time. But for simplification, I assumed that the renewal process was completed during a single step in min. In cases including the renewal speed in the calculation of the decision matrix and in the simulations, we can expect that the proportion of rejection will be increased. Thus, we can make a better prediction from the simulation than those in Fig. 5.4.

My simplified memory model can solve the computational difficulties involved in the models of learning by greatly reducing the demand for computer memory. It will benefit most microcomputer users, but what is the cost of this simplification? McNamara and Houston (1985) considered a more realistic situation, *i.e.*, information values are to be weighted differently depending upon the sequence of entering the memory window. Since only the proportions of encountering good or bad hosts are to be considered in my present method, the chance of directly weighting information values stored in a memory window would be lost. Thus, some other ways have to be used, if we want to test the situation proposed by McNamara and Houston (1985).

The results presented in this Chapter are at the patch level though they arise from host acceptance decisions and patch-leaving rules. Such results will influence parasitism at the habitat level and thus population dynamics. My next work is to evaluate the consequences of these results.

References

Bai, B. & Mackauer, M., 1990. Host discrimination by the aphid parasitoid *Aphelinus asychis* (Hymenoptera: Aphelinidae): when superparasitism is not adaptive.- *The Canadian Entomologist*, 122: 363-372.

Bernstein, C., Kacelnik, A., and Krebs, J. R. 1991. Individual decisions and the distribution of predators in a patchy environment. II. The influence of travel costs and structure of the environment. - *Journal of Animal Ecology*, 60: 205-225.

Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. - *Theoretical Population Biology*, 9: 129-136.

Comins, H. N., and Hassell, M. P. 1979. The dynamics of optimally foraging predators and parasitoids. - *Journal of Animal Ecology*, 48: 335-351.

Cowie, R. J., and Krebs, J. R. 1979. Optimal foraging in patchy environments. - In: *Population Dynamics* (R.M. Anderson, B.D. Turner, L.R. Turner, eds.) Blackwell Press.

Gerling, D., Roitberg, B. D., Mackauer, M. 1990. Instar-specific defense of the pea aphid, *Acyrthosiphon pisum*: influence on oviposition success of the parasite *Aphelinus asychis* (Hymenoptera: Aphelinidae). - *Journal of Insect Behavior*, 3(4): 501-514.

Hassell, M. P. 1978. *The Dynamics of Arthropod Predator-Prey Systems*. Princeton University Press. Princeton, New Jersey.

Krebs, J. R., Ryan, J. C., and Charnov, E. L. 1974. Hunting by expectation or optimal foraging? a study of patch use by chickadees. - *Animal Behaviour*, 22: 953-964.

Mangel, M. & Clark, C. W. 1988. *Dynamic Modeling in Behavioral Ecology*. Princetion University Press, Princeton, New Jersey. 308 pages.

Mangel, M. and Roitberg, B. D. 1989. Dynamic information and host acceptance by a tephritid fruit fly. - *Ecological Entomology*, 14: 181-189.

McNamara, J. M. and Houston, A. I. 1985. Optimal foraging and learning. - *Journal of Theoretical Biology*, 117: 231 - 249.

Oster, G. and Heinrich, B. 1976. Why do bumblebees major? A mathematical model.- *Ecological Monograph*, 46: 129-133.

Pyke, G. H. 1984. Optimal foraging theory: a critical review. - *Annual Review of Ecology & Systematics*, 15: 523-575.

Roitberg, B. D. and Prokopy, R. J. 1984. Host visitation sequence as a determinant of search persistence in fruit parasitic tephritid flies. - *Oecologia* (Berlin). 62: 7 - 12.

Roitberg, B. D., Reid, M. and Li, C. 1992. Choosing hosts and mates: the value of learning. - In *Insect Learning*, Eds., Papaj, D. R. and Lewis, W. J. Page 174-194.

van Alphen, J. J. M. 1988. Patch-time allocation by insect parasitoids: superparasitism and aggregation. - In *Population Genetics and Evolution*, Ed. by G. de Jong. pp.215-221. Springer-Verlag Berlin Heidelberg.

CHAPTER VI

MOVEMENT PATTERNS BETWEEN PATCHES

Abstract

Parasitism dynamics within patches and movement patterns between patches are the important components for describing the parasitism of the wasp, *Aphelinus asychis*, on its pea aphid hosts on bean plants. I present the parasitism dynamics of the wasp within patches, in terms of the patch residence time and the numbers of hosts parasitized, by two descriptors. I found that the wasp had a tendency to search patches in the same horizontal layer. When the wasp has been forced to search on a surface, its pattern of movement between patches can be described by area-restricted search or a random walk. I built a three dimensional simulation model to predict the parasitism of the wasp to its pea aphid hosts on broad bean plants, and to investigate why such movement patterns were used by the wasp. The results showed that by employing these movement patterns, the wasp was able to find its pea aphid hosts more efficiently when the hosts were non-uniformly distributed than when they were uniformly distributed. Different modelling approaches are discussed on the relative sizes of animals, goals of studies, and scales at which observations are made.

Introduction

How an animal searches for a resource patch, in order to maximize the use of its limited available time and energy for foraging and reproduction, is an important feature contributing to its reproductive success (Bell, 1991). For a parasitoid species, it becomes a question of how to move between patches.

Theoretically, there are two major types of movement or search patterns: (1) random search, which is most often assumed in mathematical models, where the animal does not require, store, or process any information about host distribution in making the decision for the direction of the next movement, and the length of time step is equal in all movements, so that it can be well described as a random walk (Berg, 1983); and (2) non-random search, which includes three strategies: systematic, or aggregative, or area-restricted search. Systematic search means that the animal starts searching from a particular point and continues by moving over the environment until the entire area has been covered without retracing its path (see Chapter II). Examples are spiral orientation in homing birds, expanding squares, parallel sweeps, and spiral searches (Haley and Stone, 1980). Aggregative search is often assumed in mathematical models as negative binomial search (*e.g.*, May, 1978; Hassell, 1985; May and Hassell, 1988; Hassell and Anderson, 1989). Hence the animals concentrate on searching for hosts in high density areas, and spend less time on searching in low density areas. This kind of search has often been referred to as optimal foraging, and is predicted by the marginal value theorem of Charnov (1976). The theorem leads to the conclusion that aggregation of predators and parasitoids will contribute to system stability (Hassell and May, 1974; Hassell, 1978; May, 1978; Comins and Hassell, 1979; Chesson and Murdoch, 1986). Area-restricted search is the tendency of predators and parasitoids to remain in the vicinity of recent encounters before continuing a wider-ranging exploration (Kareiva and Odell, 1987), and it leads to an aggregated spatial distribution of captures per attack. Examples are numerous among coccinellids, syrphids, neuropterans, blackbirds and thrushes, and even houseflies "preying on" sugar droplets (see review of Kareiva and Odell, 1987).

There are two ways of analyzing the dynamics of parasitism processes, and they can be distinguished by considering small or large patches proportional to the size of animal studied (see Chapter IV). A large-patch-size-approach is to define a parasitoid's universe as a patch, then the whole process can be expressed as within patch dynamics. A small-patch-size-approach is to break a parasitoid's whole universe down into a number of subunits with each defined as a patch, then the whole process will be explained at two different levels: within and between patches. A small-patch-size-approach is appropriate for my experimental system, because of the architecture of the broad bean plant and the small body size of *A. asychis*; an animal's searching strategy is normally in accordance with an animal's environmental architecture (Holling, 1992). I divided the bean plants into sub-areas such as leaflets, and assumed that the host distribution within each of the host-containing sub-areas could be described as a Poisson distribution. In this way, I broke down the analysis into two levels (or scales): within and between patches (or leaflets). Within patches, *A. asychis* females have been shown to search randomly for their pea aphid hosts (Chapter II). In this Chapter, I concentrate on the movement patterns of the wasps between patches. I first present a description based on a detailed simulation of the foraging dynamics of a wasp under different initial host densities and qualities within a patch. Second, I show the movement patterns of *A. asychis* from laboratory observations. Finally, I use a three-dimensional simulation that links most of the information available from my study and from the literature, using a systems ecology approach to investigate the question of why such movement patterns may be used by *A. asychis* for finding pea aphid hosts on broad bean plants.

The objective of this Chapter is to develop a method that could be used in syntheses from the information available about an experimental system to demonstrate how we can scale information at a lower level (within patches) up to a higher level (between patches), and thus provide a useful tool for exploring the possible population consequences of foraging processes involved in the system.

Foraging dynamics within patches

In Chapter V, I presented a model which can predict foraging dynamics within patches when initial conditions are favorable, *i.e.*, all hosts are unparasitized. In the present Chapter, I generalized the simulation model to include varying initial patch qualities. I indexed the patch quality from 0 to 1 which represents the proportions of unparasitized hosts in total. Thus, index 1 denotes the best patch quality, and index 0 indicates the worst patch quality. The foraging dynamics within patches can then be represented by the number of hosts parasitized and the patch residence time as in Chapter V. I ran my simulation model as follows: each patch quality varied from 0 to 1 with increments of 0.1 which I defined as a series; for each series, host densities 1, 2, 4, 8, 16, 32, and 64 were given as initial values of the simulations; 100 Monte Carlo simulations were applied to each of these runs; I recorded the number of hosts parasitized and the patch residence time for each of the initial patch qualities and host densities. The results for each series were fitted to three equations, (6.1) to (6.3), by Marquardt's nonlinear parameter estimation method (Marquardt, 1963) on a Unix computer system (SAS Institute Inc., 1988):

$$Y = b_0 / (1 + \exp(b_1 - b_2 \times X)) \qquad (6.1)$$

$$Y = b_0 + X / (b_1 + b_2 \times X)) \qquad (6.2)$$

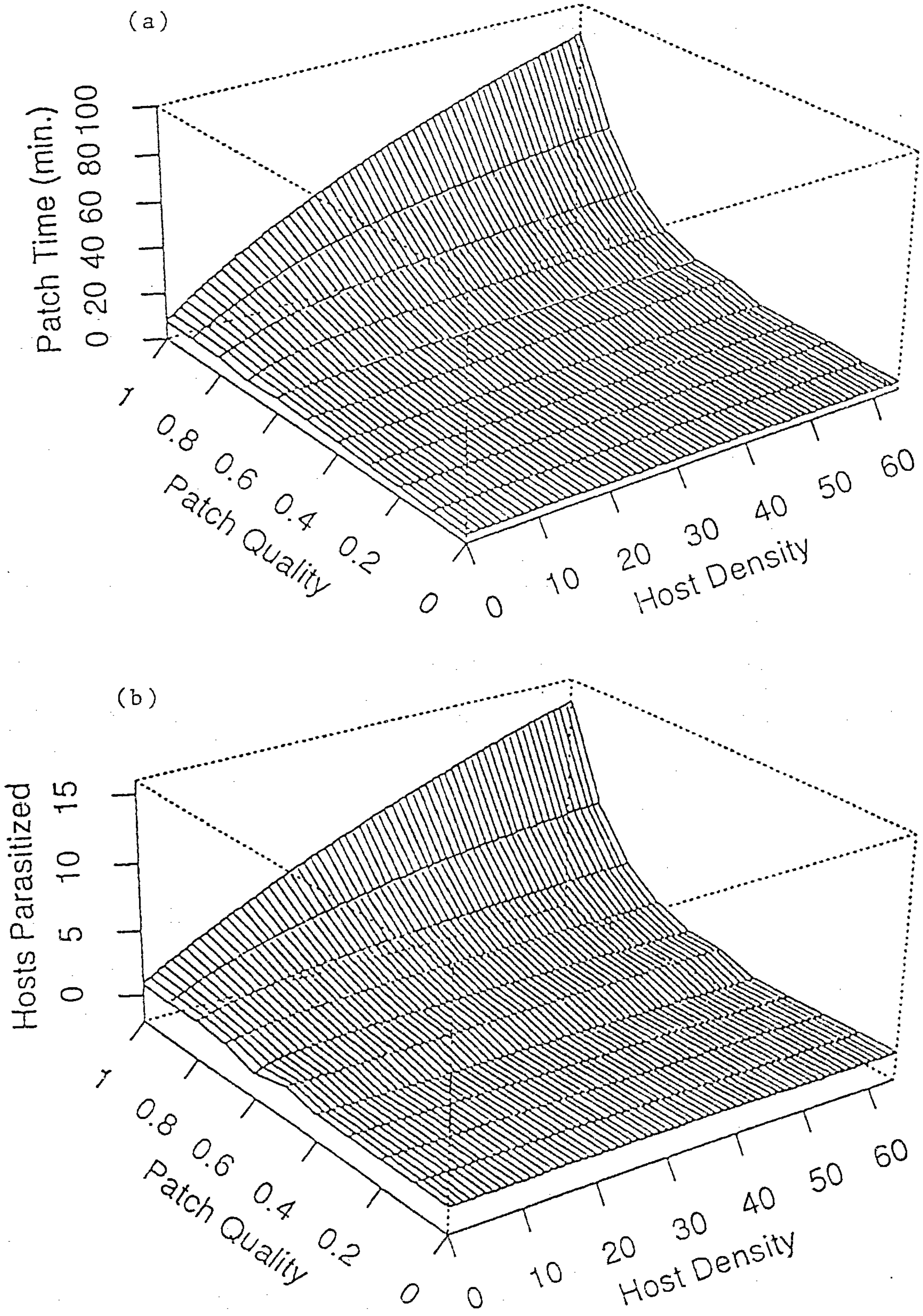
$$Y = X / (b_1 + b_2 \times X)) \qquad (6.3)$$

where X is the initial host density, and Y is either the number of hosts parasitized or the patch residence time. I chose equation (6.2) to present my results, due to the smallest squared sum of residuals. Then, I summarized the results from all the series to form two foraging dynamics descriptors within patches, one for the number of hosts parasitized and another for the patch residence time. Fig. 6.1 shows the behavior of these descriptors.

Movement patterns of the wasp

There are two ways to deal with movement patterns of a predator or parasite. The first one is to trace its path of movement, *i.e.*, to study the search path between patches, its turn angles, and movement speed, which are used to decide the next patch to be visited. In this way, one expects to be

Fig. 6.1. The average patch residence time (a); and the average number of hosts parasitized (b); under different initial host densities, and initial host qualities.

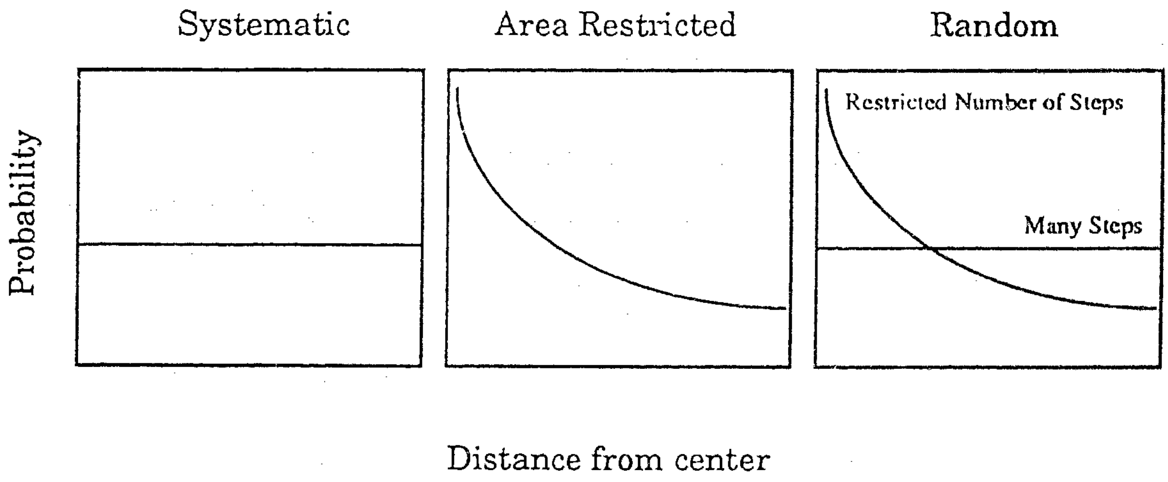

(a)
Patch Time (min.)
0 20 40 60 80 100
Patch Quality
1 0.8 0.6 0.4 0.2 0
Host Density
0 10 20 30 40 50 60
(b)
Hosts Parasitized
0 5 10 15
Patch Quality
1 0.8 0.6 0.4 0.2 0
Host Density
0 10 20 30 40 50 60

able to predict the animal's detailed movements, and thus the whole foraging process. However, these details make the mathematical analysis more difficult and they complicate both the design and interpretation of field observations (Kareiva, 1985). The second way is a simplification of the first, *i.e.*, to study the probability of a given patch being visited. I defined the first patch visited as the central patch, even though it may or may not be the real central patch of the host distribution. Then, each of the other patches is measured in terms of distance from the central patch, and the probability of a given patch being visited is determined according to its distance from the central patch. In this way, one can plot and express different movement patterns (or searching strategies) by curves of different shapes, on the probability of a given patch being visited, *vs* the distance from the central patch. The consequence of this simplification is that it is hard to predict the exact position of the searching animal at a given time except with systematic search patterns. Fig. 6.2 shows the curves of the three different searching strategies: systematic, area-restricted, and random. For random search, different numbers and lengths of step will generate different shapes of the curve (Berg, 1983; Casas, 1990).

Note from Fig. 6.2 that aggregated spatial distribution of parasitism (curved lines) might be generated from two mechanisms: area-restricted search and random walk.

To identify the mechanism employed by *A. asychis*, I conducted two series of experiments to elucidate the vertical and horizontal movement patterns.

Fig. 6.2. The probability of a given patch being visited as a function of its relative position in terms of the distance from the central patch, defined as the first patch visited by the searching animal.

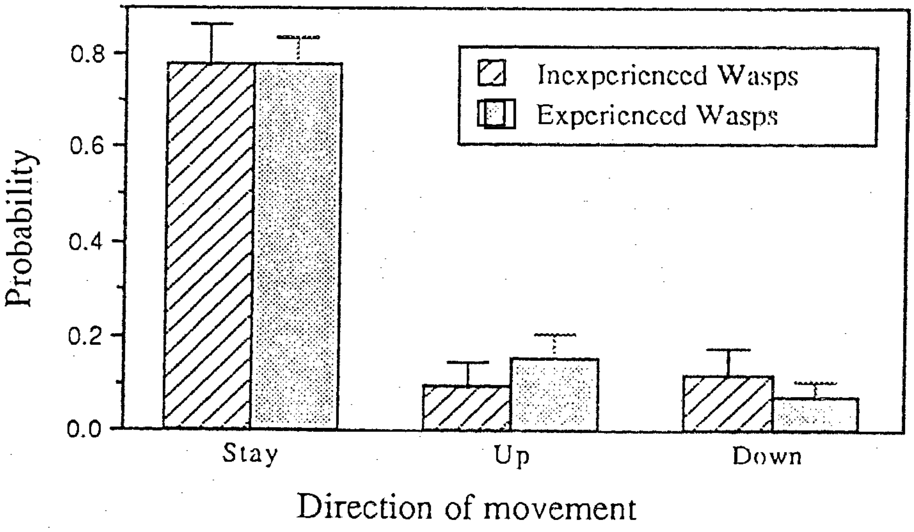

Systematic
Area Restricted
Random
Restricted Number of Steps
Many Steps
Probability
Distance from center

(1) Vertical movement patterns:

The first series of my experiments were carried out on bean plants to study the wasp's vertical movements. I chose plants with 10-12 leaflets, 15 cm in height, then numbered each leaflet starting from the bottom for each of the plants. The bean plants were horizontally divided into three layers: lower (leaflets 1-4), middle (leaflets 5-8), and upper (leaflets 9-12). In my experiments, no aphids were present on the plants, since I assumed the movement patterns would not change with host density. I released a single female wasp onto one of the bean leaflets of the middle layer. I then observed its movements on the plant, and recorded the sequence of numbers of bean leaflets visited. Each observation ended when the wasp jumped or flew away from the plant. The wasps used in the experiments were from two groups: experienced or inexperienced at assessing patches, using 20 replications for each group. The preparation of these two groups of wasps was the same as in Chapter III.

The experimental results showed that four movement patterns could be observed: the wasp searched the middle layer then left the plant; it searched at the middle and upper layers and then left the plant; it searched at the middle and lower layers and then left the plant; or it searched the whole plant and then left. Unable to identify a dominant pattern of the four, I pooled the data to obtain the probabilities that the parasitoids moved upwards (number of upward moves / total number of moves), downwards (number of downward moves / total number of moves), or stayed at the same horizontal layer (1 - probabilities of movement upwards and downwards).

Fig. 6.3. The probabilities that the wasps, experienced or inexperienced, would move upwards, downwards, or stay on the same horizontal layer.


0.8
0.6
0.4
0.2
0.0
Probability
Inexperienced Wasps
Experienced Wasps
Stay
Up
Down
Direction of movement

The results are shown in Fig. 6.3. in which, we see that the wasp had a tendency to search patches on the same horizontal layer. There was no significant difference between wasps with and without patch experience in their tendency to search at a mid-layer, or to move up, or down. However, the tendency to move upward was slightly greater with experienced than with inexperienced wasps.

(2) Horizontal movement patterns:

The second series of experiments was carried out on an artificial two-dimensional surface to study the wasp's horizontal movements. Sixteen aphid-free leaflets of bean plants were placed on a piece of squared paper, as shown in Fig. 6.4. A small amount of glue fixed the leaflets to the paper and I numbered each bean leaflet for identification. One wasp from either the experienced or inexperienced group was released onto leaflets 6 or 7. A video camera recorded each wasp's behavior starting from the release of the wasp. Replicates were terminated when the wasp flew or jumped or walked away from the experimental environment. The numbers of replications for experienced and inexperienced groups were 35 and 20 respectively.

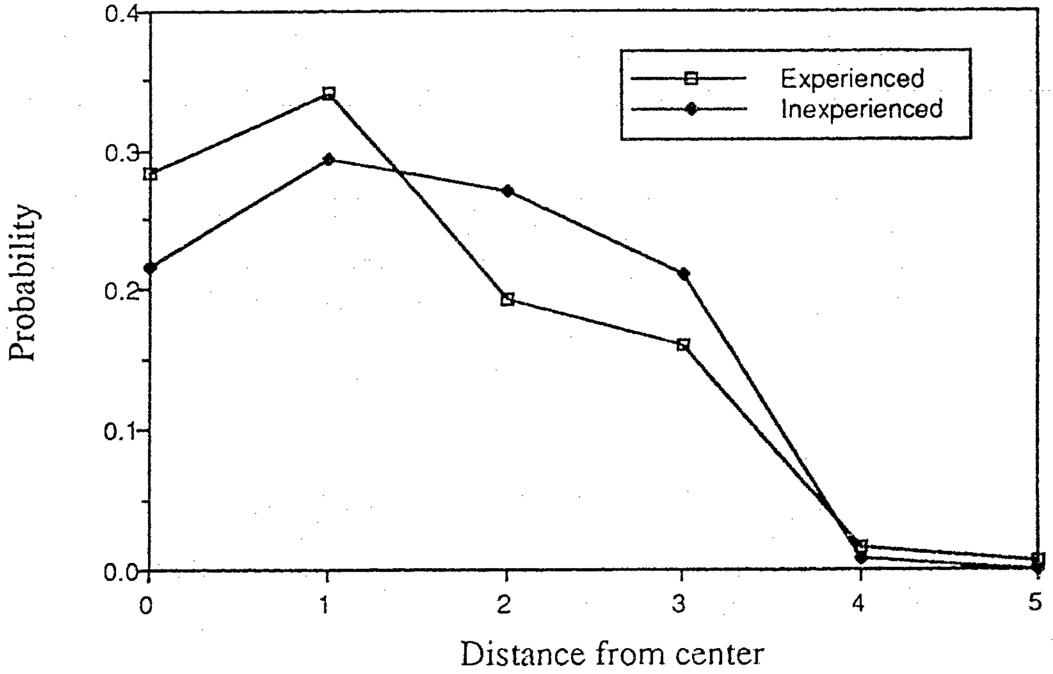
I also made a few observations on wasps when aphids were placed on bean leaflets (with one aphid per leaflet, or two aphids on half the bean leaflets but the other half with none), but similar results were obtained with regard to movement pattern.

The probability that a given patch will be visited, in relation to its distance from the central patch, is shown in Fig. 6.5. It suggests that the pattern in which a wasp moves between patches can be described by non-

Fig. 6.4. The configuration of experiments on the wasp's horizontal movements on an artificial surface. Shaded squares with numbers indicate the bean plant leaflets. The grid lines were about 2 cm apart.

		1		2		3		4	
	5		6		7		8		
		9		10		11		12	
	13		14		15		16		

Fig. 6.5. The probability that a given patch will be visited in relation to its relative position distant from the central patch.


0.4
0.3
0.2
0.1
0.0
Probability
Experienced
Inexperienced
0
1
2
3
4
5
Distance from center

systematic searching, either an area-restricted search or a random walk with limited time steps, with the length of each time step being small relative to the environment (Berg, 1983; Casas, 1990; see also Fig. 6.2) when the wasp has been forced to search on a surface.

For the next section, I developed a simulation model, based on the information presented in the previous two sections, to determine the foraging consequences of these movement patterns. I expected that these movement patterns were the ones favored by natural selection, *i.e.*, by using them, the wasp was able to find its pea aphid hosts more efficiently when the hosts were non-uniformly distributed than when they were uniformly distributed.

Simulation Model

Simulation description:

(1) The simulated plant upon which a female wasp foraged for pea aphids was divided into an upper, a middle, and a lower layer; each layer consisted of 10 × 10 patches, with each patch containing a potential colony of pea aphids.

(2) The movement patterns of the wasps were based on the results described in this Chapter which are summarized as follows:

(a) if a wasp had just left a host-containing patch, it would remain at the same horizontal layer to forage for hosts, *i.e.*, the location of the next patch it would visit is determined by the random walk process with a distance of one patch;

(b) if a wasp left a non-host-containing patch, then it would be 80% likely to visit a patch located on the same horizontal layer in the next step, and be

(b1) 10% likely to move up or down respectively, if it was at the middle layer;

(b2) 20% likely to move up, if it was at the lower layer;

(b3) 20% likely to move down, if it was at the upper layer.

(3) When the wasp moved away from the experimental space, then the program stopped.

(4) The maximum time available for each run of the simulation model was 720 min. The length of each simulation step was 1 min. The wasp spent 40 min to feed on a host, 5 min to lay an egg in a host, and 1 min to reject a host.

Fig. 6.6 is the flowchart of my simulation model.

Simulation results:

(1) Searching time allocation:

My simulation results are shown in Fig. 6.7. On uninfested plants, the wasp spent about 62% of its searching time in the patches of the middle layer. Since the wasp did not find hosts in every patch of the plants, there were many opportunities to move up and down. During such movements, it would be forced to pass through some patches in the middle layer, either when it was moving from the upper to lower layer, or reverse. Thus, the patches in the middle layer will have the most chances of being searched. But when hosts are present on the plants, the wasp will have a higher

Fig. 6.6. The flowchart of my simulation model of the parasitism of the wasp to its pea aphid hosts on broad bean plants.

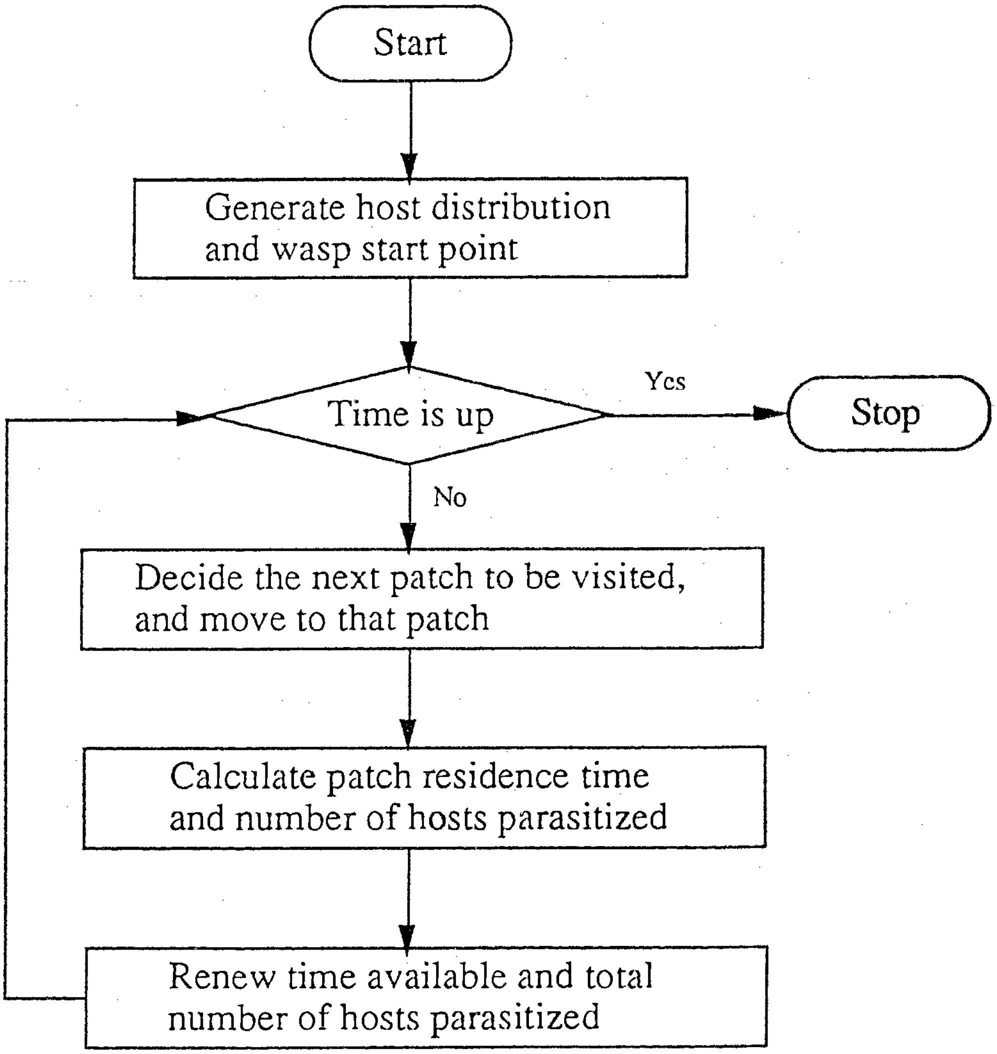
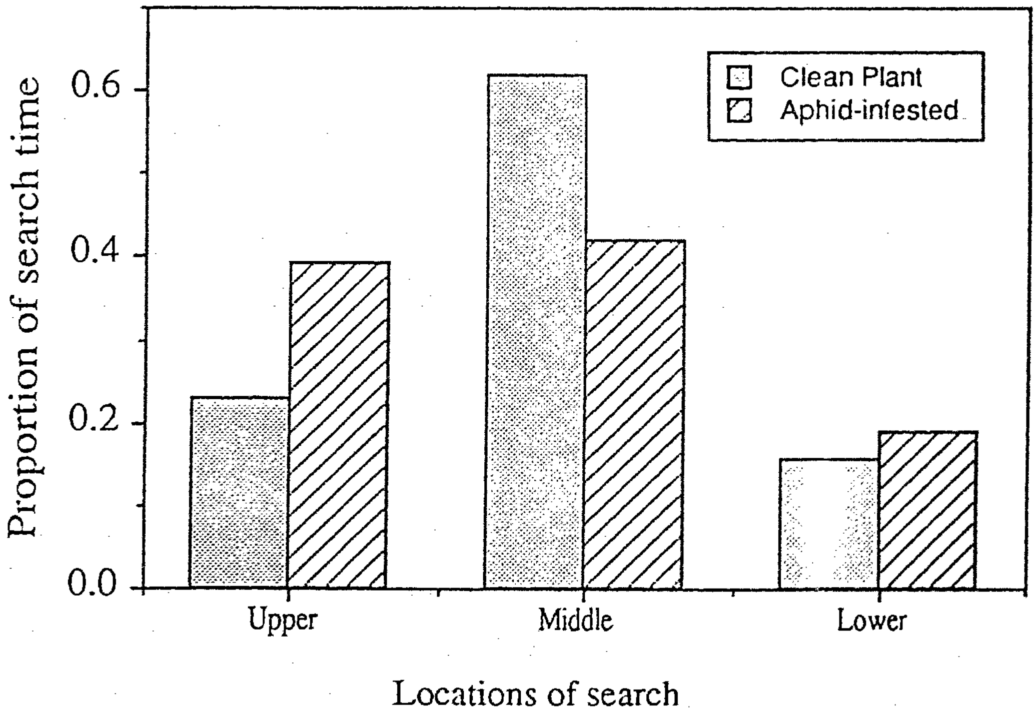

Start
Generate host distribution and wasp start point
Time is up
Ycs
Stop
No
Decide the next patch to be visited, and move to that patch
Calculate patch residence time and number of hosts parasitized
Renew time available and total number of hosts parasitized

Fig. 6.7. The proportion of searching time allocated by female wasps on clean and aphid-infested plants.


Proportion of search time
0.0
0.2
0.4
0.6
Clean Plant
Aphid-infested
Upper
Middle
Lower
Locations of search

probability to continue searching patches in the upper than in the other two layers because of host distribution, so that the wasp will allocate a large percentage of its searching time (about 40%) to the upper layer, and another (about 40%) to the middle layer. These results are consistent with Cloutier and Bauduin's (1990) observations that the aphid parasitoid, *Aphidius nigripes*, spent a significant proportion of search time on the youngest leaflets of aphid-infested potato plants. But on uninfested plants, the parasitoids concentrate their search efforts on middle leaflets as well as the stem. The agreement of searching time allocation between model behavior and experimental data partially indicates that the mechanisms embodied in my model are reasonable. Furthermore, we need to look at the model's predictions on parasitism to ensure that my descriptors are working well.

(2) Parasitism:

Here, I compare my experimental data with the simulated results of the number of hosts parasitized under different initial host densities and distributions.

The data used for validating the simulation model were obtained from the experiments carried out in cages (30 × 30 cm wide and 40 cm high). In each cage, I placed one plastic pot (10 cm diam.) in which a single broad bean plant was growing. The size and height of the plants, and the method for numbering the leaflets were the same as for the first series of my experiments. Different numbers of pea aphid hosts (Table 6.1) were put onto leaflets of different layers at the beginning of each observation. Then I released a female wasp with experience in patch treatment onto a leaflet of

Table 6.1. The initial numbers of second instar pea aphids which were put onto leaflets at different layers of bean plants for each observation.

Experimental group	Number of aphids in plant layer Upper	Middle	Lower
1	1/leaflet	1/leaflet	1/leaflet
2	3/leaflet	3/leaflet	3/leaflet
3	5/leaflet	5/leaflet	5/leaflet
4*	30	30	30
5	40	20	10
6	20	5	5
7	20	0	0
8	40	0	0
9	60	0	0

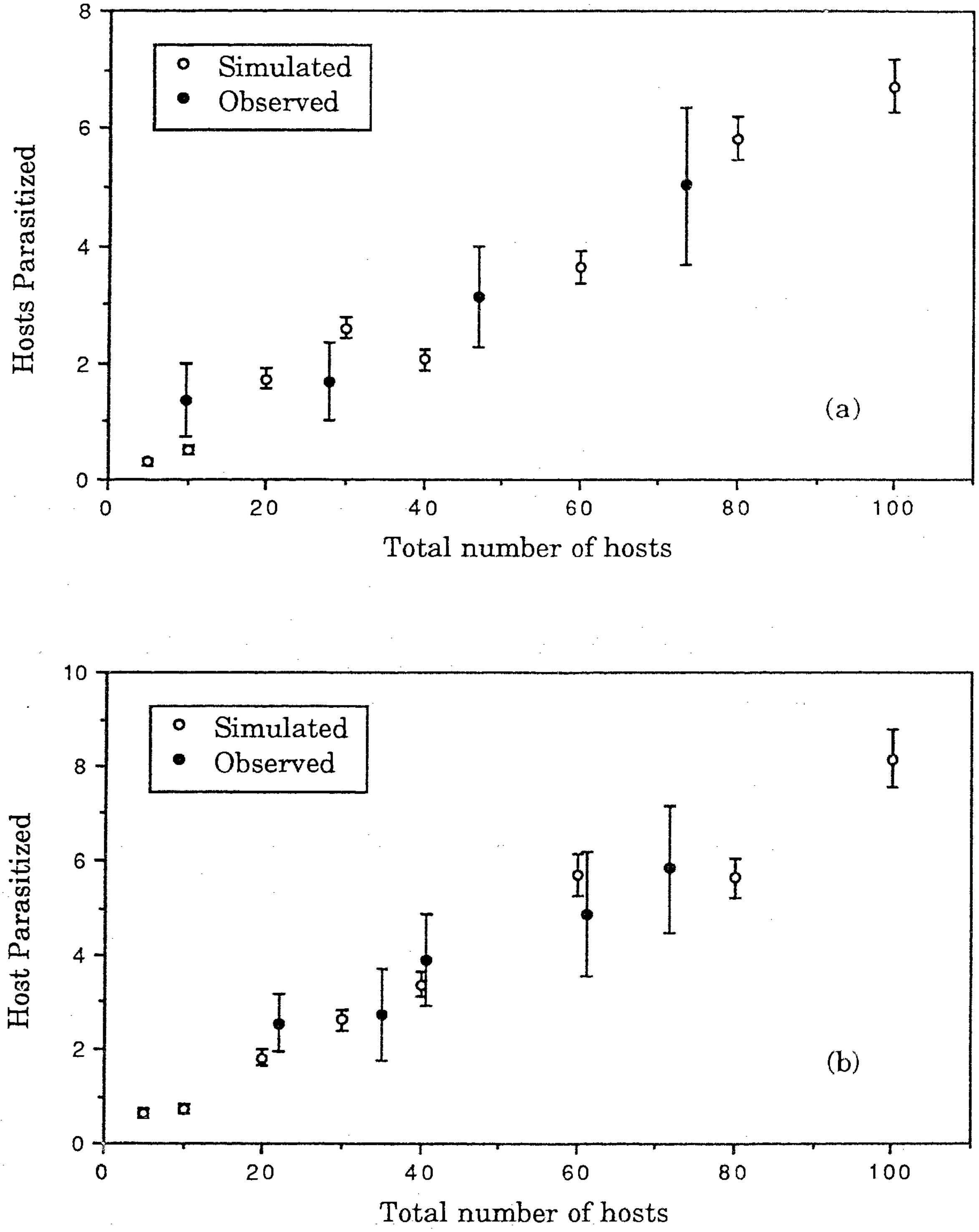
* Total aphids at the layer, from groups 4 to 9.

the middle layer. After 24 h, I removed the wasps from the cages, and checked the number of aphids remaining on the plants. The aphids were then allowed to move freely on the plants. I recorded the number of mummies on the plants 10 days later. There were 12 replicates in each group.

Fig. 6.8 shows the comparisons between the predictions of parasitisms from the simulation model and those observed in my experiments, when the hosts were uniformly (group 1-4) (Fig. 6.8a) or non-uniformly (group 5-9) (Fig. 6.8b) distributed among the leaflets. From Fig. 6.8, we can see that most experimental results were consistent with my predictions, but when total host number per plant was low, the observed hosts parasitized were slightly higher than predicted. This probably was because the wasp was allowed to visit the plant only once in my simulation model, but was able to revisit the plant in the cage experiments, as long as time was available. Since the total patch time was less at low than at high host density, the wasp would have more of a chance to revisit the plant when host density was low than when host density was high.

A non-parametric test for the parallelism of two regression lines was applied to my simulation results shown in Fig. 6.8a and Fig. 6.8b. The tested hypothesis is that the slopes of the two regression lines, the number of hosts parasitized *vs* total hosts provided under uniformly or non-uniformly host distributions, are equal. If this hypothesis is true, then the wasp would achieve the same foraging efficiency under different host distributions. The non-parametric test used here is a variation on the Wilcoxon matched-pairs signed-ranks test (Daniel, 1978). When the

Fig. 6.8. Comparisons between predicted and observed parasitism, under different host distributions: (a) less clustered, *i.e.*, more or less uniformly distributed among all patches; and (b) clustered, *i.e.*, hosts distributed more on upper and less on lower layers.


Simulated
Observed
Hosts Parasitized
0
2
4
6
8
0
20
40
60
80
100
Total number of hosts
(a)
Simulated
Observed
Host Parasitized
0
2
4
6
8
10
0
20
40
60
80
100
Total number of hosts
(b)

hypothesis is true, the probability of a value of the statistic T as extreme as 1 (4 pairs of data) should be greater than 0.125 (two-sided probability). However, the calculated statistic T was 0.0856. This means that these data do not provide convincing evidence in favor of the hypothesis that the numbers of hosts parasitized were equal when the hosts were either non-uniformly or uniformly distributed. If the wasps also showed a similar trend in my laboratory observations, *i.e.*, the wasp parasitized more pea aphids in groups 5-9 than in groups 1-4, then the tested hypothesis should be rejected. A Student's *t* test, described by Zar (1984) for comparing the two slopes of linear regressions, was used to test the hypothesis mentioned above. The result showed a significant difference between the two slopes at the level of $\alpha = 0.1$ ($t = 2.077$). This indicated that the wasp tended to parasitize more hosts when the hosts were non-uniformly distributed rather than uniformly distributed. This result was expected. Because hosts are most probably non-uniformly distributed under natural conditions, such movement pattern would probably by favored by natural selection. I thus conclude that the movement pattern between patches presented in this Chapter could be one of the mechanisms used by *A. asychis* females.

Discussion

Overall, the results indicate that my simulation model could be used as a descriptor of the wasp's foraging behavior on bean plants. The results also show that the theory-driven modelling approach can be used as a tool for analyzing the foraging process of a parasitoid species.

The patch concept plays a key role in the study of parasitoid foraging (Hassell and Southwood, 1978; Waage, 1979; Cloutier and Bauduin, 1990). A patch can be defined as a functional area of the arresting stimulus, which may be a physical structure or a contact semiochemical (Waage, 1979). However, as pointed out by van Alphen and Vet (1986), this definition cannot be applied to cases when wasps ignore potential arresting stimuli or such stimuli do not exist. Thus, ecologists have generally resorted to the arbitrary choice of a single physical structure or a size of area (Rosenheim *et al.*, 1989), reflecting the relative property of the patch concept (Southwood, 1977).

The appropriate size of a particular patch for studying foraging behavior should be determined by the characteristics of the animals studied (see Chapter IV). For *A. asychis* females, their movements are restricted by body size and their habit of walking and jumping, thus the appropriate size of a patch should be small. Normally, a large animal can move farther than a small one, so that the appropriate patch size should be larger than that for a small animal. Furthermore, the choice of a large patch size will bring many problems together, make analysis more complex, and a good prediction difficult (Kareiva and Odell, 1987), but with the advantage of solving several problems at the same time. On the other hand, by using small patch size, the analysis is simplified, but the insights are limited.

Different modelling approaches should be used for different scales (see Chapter IV). An analytical modelling approach may be suitable for considering large patches. By contrast, a numerical simulation approach appears to be proper when small patches are defined. Rosenheim *et al.* (1989) have shown that, for a given system, the observed patterns of aggregation in parasitism will be shaped to a greater extent by demographic than by behavioral processes, as the spatial scale of observation increases. Therefore, the choice of patch size, reflects how people want to solve the problem, and serves as a window through which the researchers look for answers to the questions.

Methodology depends heavily on the goals of any study. There are two goals in studies of foraging behavior. One is the pure behavior study itself, *i.e.*, an attempt to give the best description of an animal's foraging behavior, and to find why animals forage in specific ways. The other is to look at the population consequences of particular behaviors. Not all the characteristics of foraging behavior significantly contribute to an understanding of subsequent population dynamics, which raises a question as to what modelling approaches are suitable for these two goals. For pure behavioral studies, it depends on how much detail the researcher wishes to understand. When the intention is not prediction, since it is too hard to know the true processes of an animal's behavioral decision-making, a descriptive model, such as a regression, is the best choice. Under such circumstances, the more independent variables that are recorded and the more observations made or samples taken, the better the results could be. If, however, the goal is to find possible mechanisms that the animals may actually use so as to look at the population consequences, then a mechanistic modelling approach such as numerical simulation would be better than a regression model. For looking at population consequences of a particular behavior, the predictability of the model is an important precondition. In this case, a numerical simulation model may serve well, because it can easily include the stochastic information and the background knowledge of the interacting system, so as to express the consequence of behavioral plasticity. In contrast, regression models often fail to do that, because they are usually deterministic, and basically are of "black box" type in that they do not specify the biological mechanisms.

In the present study, random encounter and almost the same time intervals between encounters at the level of within-patches simplify the analysis (see Chapter IV), because the encounter rate with hosts used here accounts only for the proportions of good or bad quality hosts, and does not include the interval between encounters. At the level of between-patches, the most important component is the movement patterns of the wasps, and that is closely related to host distribution, which in turn usually corresponds to the architecture of the landscape. This approach can be called the "small-patch-size-approach". The opposite approach, which has already been used in behavioral studies such as that of Driessen and Hemerik (1991), can be called the "large-patch-size-approach". In their studies, the hosts were not evenly distributed within patches, the animals were able to choose between parts of a patch with or without hosts or kairomone. Thus the parts of patches containing hosts would be intensively searched, and the parts of patches not containing hosts would not be searched thoroughly. In their study, the intervals between encounters will change with time: small changes when searching parts of patches containing hosts; large changes when searching parts of patches not containing hosts, since the depletion process does not change host density but only changes the proportions of acceptable to unacceptable hosts. In dealing with this situation, it would be appropriate to apply a discount rate to the contributions of each of the encounters, to patch-leaving decisions. But this approach makes analysis more difficult, although the whole problem can be solved at once. Thus, we can expect that the modelling approaches should differ, based on the patch sizes chosen.

There is another constraint on the choice of patch, *viz.*, behavioral observations made on different sized patches which may lead to different conclusions. In the Oregon shrub-steppe habitat, Wiens (1985) observed that increased patch size was associated with the time spent by sage sparrows, *Amphispiza belli*, on foraging in a patch, up to a certain point; beyond that, the visit time became largely independent of patch size. This example suggests that any conclusion must be closely associated with the specific scale at which the investigation was made, so that one must take the scale into account when coming to a conclusion.

By dividing the whole analysis into two levels, within and between patches, we were actually dealing with the problem of cross-scale dynamics. The logic behind my analysis was that animals perceive only certain scales of their environment; foraging decisions made for various scales are different; and the information upon which these decisions are based is also different. The time when a parasitoid actually switches its foraging decision-making from one scale to another is critical for understanding the cross-scale process. We can expect some similarities between ecosystem and foraging processes, thus the methodologies used in studying both could be exchanged. Since local processes can not simply be added together to show large scale processes, the challenge to researchers is how to scale the information gathered at lower levels up to higher levels. My present study demonstrates that theory-driven simulation models can serve this purpose well.

References

Bell, W. J. 1991. *Searching Behaviour. The Behavioural Ecology of Finding Resources*. Chapman and Hall, University Press, Cambridge.

Berg, H. C. 1983. *Random Walks in Biology*. Princeton University Press, Princeton, New Jersey.

Casas, J. 1990. Multidimensional host distribution and nonrandom parasitism. a case study and a stochastic model. - *Ecology*, 71(5): 1893-1903.

Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. - *Theoretical Population Biology*, 9: 129-136.

Chesson, J. and Murdoch, W. W. 1986. Aggregation of risk: relationships among host-parasitoid models. - *The American Naturalist*, 127: 696-715.

Cloutier, C. and Bauduin, F. 1990. Searching behavior of the aphid parasitoid *Aphidius nigripes* (Hymenoptera: Aphidiidae) foraging on potato plants. - *Environmental Entomology*, 19(2): 222-228.

Comins, H. N., and Hassell, M. P. 1979. The dynamics of optimally foraging predators and parasitoids. - *Journal of Animal Ecology*, 48: 335-351.

Daniel, W. W. 1978. *Applied Nonparametric Statistics*. Houghton Mifflin Campany, Boston.

Driessen, G. and Hemerik, L. (1991) *Studies on larval parasitoids of Drosophila: from individuals to populations*. - Ph.D. Thesis. University of Leiden, Netherlands.

Haley, K. B., and Stone, L. D. (eds.) 1980. *Search Theory and Applications*. Plenum Press, New York.

Hassell, M. P. 1978. *The Dynamics of Arthropod Predator-Prey Systems*. Princeton University Press. Princeton, New Jersey.

Hassell, M. P. 1985. Insect natural enemies as regulating factors. - *Journal of Animal Ecology*, 44:

Hassell, M. P., and Anderson, R. M. 1989. Predator-prey and host-pathogen interactions. In: *Ecological Concepts: The Contribution of Ecology to an Understanding of the Natural World*. Ed. by J.M. Cherrett. Blackwell Scientific Publications. Oxford.

Hassell, M. P. and May, R. M. 1974. Aggregation in predators and insect parasites and its effects on stability. - *Journal of Animal Ecology*, 43: 567-594.

Hassell, M. P. and Southwood, T. R. E. 1978. Foraging strategies of insects. - *Annual Review of Ecology & Systematics*, 9: 75-98.

Holling, C. S. 1992. Cross-scale morphology, geometry and dynamics of ecosystems. - *Ecological Monograph*, In Press.

Kareiva, P. 1985. Patchiness, dispersal, and species interactions: consequences for communities of herbivorous insects. - Pages 192-206 in J. Diamond and T. Case, eds. *Community Ecology*. Harper & Row, New York.

Kareiva, P. and Odell, G. M. 1987. Swarms of predators exhibit "preytaxis" if individual predators use area restricted search. - *The American Naturalist*, 130: 233-270.

Marquardt, D. W. 1963. An algorithm for least squares estimation of nonlinear parameters. - *Journal of Society of Industrial Applied Mathematics*. 11: 431-441.

May, R. M. 1978. Host-parasitoid systems in patchy environments: a phenomenological model. - *Journal of Animal Ecology*, 47: 833-843.

May, R. M., and Hassell, M. P. 1988. Population dynamics and biological control. - *Philosophical Transactions of the Royal Society, London B*, 318,129-169.

Rosenheim, J. A., Meade, T., Powch, I. G., and Schoenig, S. E. (1989) Aggregation by foraging insect parasitoids in response to local variations in host density: determining the dimensions of a host patch. - *Journal of Animal Ecology*, 58: 101-117.

SAS Institute Inc. 1988. *SAS/STAT™ User's Guide, Release 6.03 Edition*. Cary, NC: SAS Institute Inc., 1028pp.

Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? - *Journal of Animal Ecology*, 46: 337-365.

van Alphen, J. J. M. and Vet, L. E. M. 1986. An evolutionary approach to host finding and selection. - In *Insect parasitoids* (J. Waage and D. Greathead, eds) pp. 23-61. Academic Press, New York.

Waage, J. K. 1979. Foraging for patchily-distributed hosts by the parasitoid, *Nemeritis canescens*. - *Journal of Animal Ecology*, 48: 353-371.

Wiens, J.A. 1985. Vertebrate responses to environmental patchiness in arid and semiarid ecosystems. Page 169-193. - In *The Ecology of Natural Disturbance and Patch Dynamics*. Eds. Pickett, S.T.A. & White, P.S. Academic Press, Inc., Orlando, Florida.

Zar, J.H. 1984 *Biostatistical Analysis*. (2nd Ed.) Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

CHAPTER VII

GENERAL CONCLUSION AND DISCUSSION

In this thesis, I have studied the parasitism by the wasp *Aphelinus asychis*, using a mechanistic modelling approach. I divided the wasp's foraging processes into two levels, within and between patches, although three kinds of basic foraging decisions were considered, namely patch allocation, patch leaving, and host acceptance.

Within patches, the wasp's search patterns, host acceptance decisions, and patch leaving rules were considered in detail because of their importance for parasitism dynamics. A random search assumption seems appropriate for *A. asychis* females because the wasps' encounter rate with aphids agreed with the expected random distribution. This result indicates that *A. asychis* females tend to employ the least energy-requiring search strategy for their within-patches foraging activities. Furthermore, a stochastic simulation model was used for finding the general conditions under which a random or a systematic search pattern would be favoured by natural selection. The results of the simulation showed that systematic search was the best strategy if hosts did not move within the patch, whereas random searching was the best strategy for a forager searching for random-moving hosts.

A state variable dynamic programming model was employed to determine the optimal host acceptance decisions for the wasp under different conditions, such as host density, which was expressed by the probability of not encountering a host per unit time, and patch quality which was indicated by the probability of encountering a parasitized or an unparasitized host per unit time. These optimal host acceptance decisions might not be realized due to stochastic factors. For *A. asychis*, the actual result of a host encounter was determined by the optimal decision, and an unsuccessful attack rate caused by the defensive behavior of the aphids.

The patch leaving decision rules for the wasp were experimentally tested on host-free and host-containing patches. On host-free patches, the IGUT (initial giving-up time) of wasps that had experience with hosts was significantly shorter than in those without experience. However, the experienced wasps remained on patches with honeydew, or on clean patches, for a similar periods of time. The results suggest that the contact kairomone presented by aphid honeydew served as the first cue for inexperienced or naive wasps to locate their hosts, but honeydew was used less as the wasps gained foraging experience. Thus, the mechanisms of making patch leaving decisions might not be based on whether the contact kairomone was present or not. On host-containing patches, two possible mechanisms could be employed by the wasp for making patch leaving decisions: the wasp should leave its current patch (1) when its GUT has elapsed and the GUT (min) should increase with host density according to the relationship $5.7162 + 0.5991 \times$ host density per leaflet; and (2) when, with a sliding memory window of at least 3 units (encounters), the proportion of acceptable, unparasitized hosts stored in the memory window drops below one half. Nevertheless, the second mechanism was assumed in my simulation, because the information required was the one used in making host acceptance decisions. By comparing simulation results, in terms of the patch residence time and rate of parasitism of the wasp, I found that five units was the number that best fitted my experimental data. This indicated a sliding memory window with five units could be employed by *A. asychis* as its mechanism for making patch leaving decisions.

An important component at the between-patches level is the movement pattern of the wasp. My data showed that the parasitoid tends to keep searching for its aphid hosts on the same layer of plants. Within a layer, the wasp used an area-restricted search. These results are reasonable because area-restricted searching is less energy-consuming. The *A. asychis* first searched in the same layer as the arrival patch. In this way, the wasp can reduce its risk of not locating a new patch, and lessen its energy cost for moving, since the cost of moving between layers is generally greater than moving to an adjacent patch in the same layer. The next patch the wasp would visit is dependent upon the quality of the current patch. If the patch quality is good, then the wasp would have a higher probability of keeping searching for its aphid hosts in the same layer rather than searching in another layer. However, if the patch quality is bad, then the wasp would be more likely to search a new patch in another layer than one in the same layer

A synthesis of all the information available was used in a three-dimensional simulation model. The model predicted well the parasitism when a wasp foraged for its pea aphid hosts in a cage using different host densities and distributions. This indicates that the information collected at a lower level, within patches, could be scaled up to a higher level, between patches, through the linkage of the movement patterns of the wasps between patches.

Throughout the modelling work, I found that, first, the choice of modelling approach depended heavily on the goal of the study. The descriptive approach has the power to describe a particular phenomenon and offers convenience of mathematical treatment, but it was not suitable for this study. The mechanistic approach, which uses the concepts of individual ecology (such as behavioral ecology) as the basis for constructing a theoretical framework with which to interpret the phenomena of population ecology (Schoener, 1986) can serve as a research tool for scaling lower-level information up to a higher-level. Thus, it was appropriate for this study.

Second, the simulation modelling approach is useful to understand and to explain the mechanisms in detail, but it imposes simplicity, sacrifices generality and requires much computer time. Thus, to develop symbolized, simple mechanical models that faithfully represent mechanisms operating in nature is important in ecological theory (Levin, 1989; Pulliam, 1989).

Third, it is necessary to use some kinds of approximations or descriptors to summarize the results of time-consuming lower-level simulation, otherwise it would be too complex to obtain an explanatory relationship between lower-level theory and upper-level phenomena.

Fourth, in the study of animal behavior, especially for tiny parasitoid species, researchers must concentrate on a small number of variables by which the animal's decision-making processes can be determined. This is not only for convenience of mathematical treatment, but also for the biological meaning because a tiny parasitoid is less likely to keep track of many variables. It is reasonable to believe that animals make their foraging decisions by employing relatively simple rules in addition to some environmental and biotic stochasticities.

References

Levin, S. A. 1989. Challenges in the development of a theory of community and ecosystem structure and function. - Pages 242-255 in J. Roughgarden, R. M. May, and S. A. Levin, eds. *Perspectives in ecological theory*. Princeton University Press, Princeton, N.J.

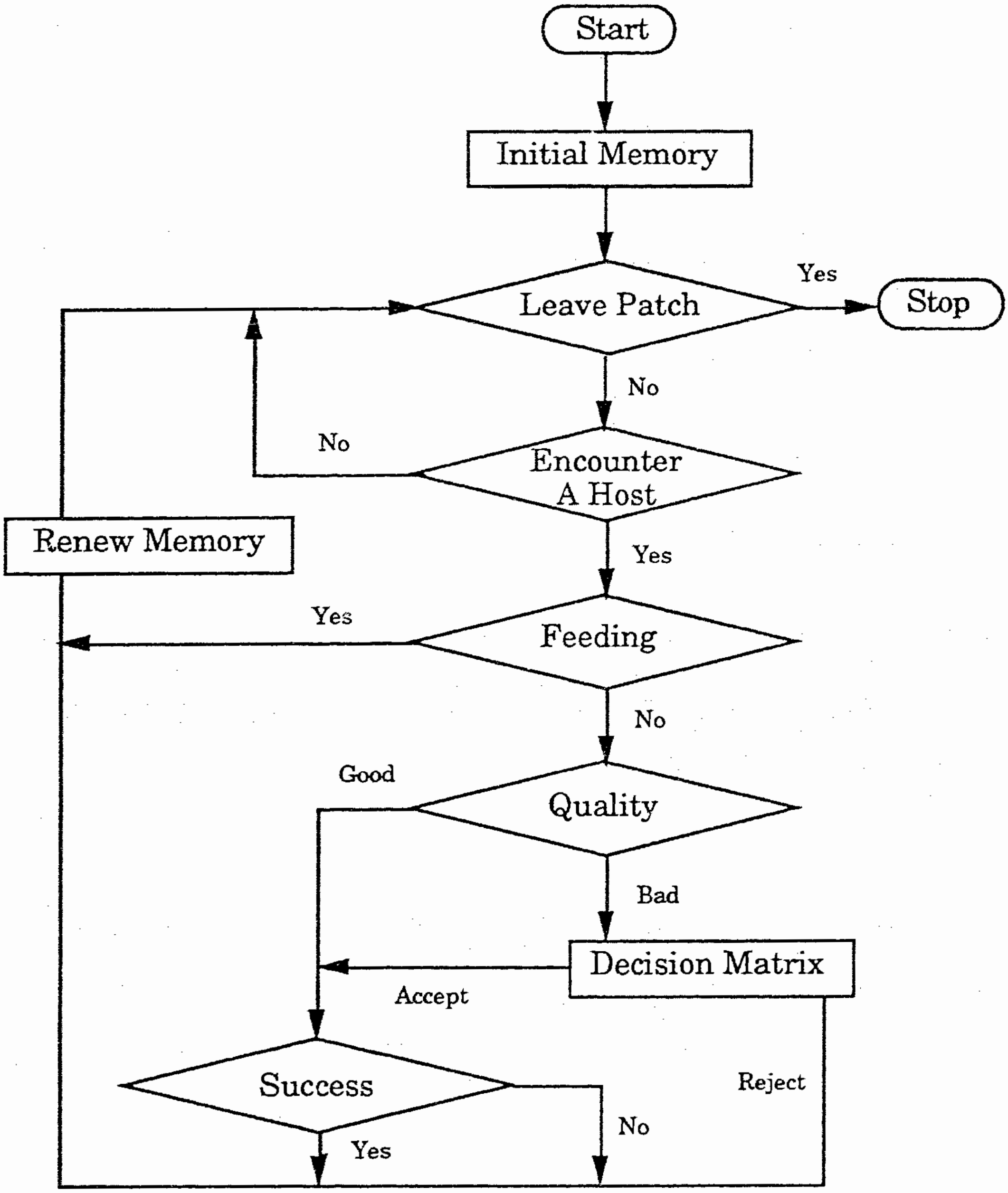
Pulliam, H. R. 1989. Individual behavior and the procurement of essential resources. - Pages 25-38 in J. Roughgarden, R. M. May, and S. A. Levin, eds. *Perspectives in ecological theory*. Princeton University Press, Princeton, N.J.

Schoener, T. W. 1986. Mechanistic approaches to community ecology: a new reductionism? - *American Zoologist*, 26(1): 81-106.

APPENDIX

My simulation model begins with initialization of a wasp's sliding memory window, which gives the host quality values the wasp originally carries. Once the time loop begins, a wasp will continue to search for hosts until the time when it decides to leave the patch, not including stop or grooming time. If the wasp does not leave the patch, then by comparing a random number generated from a uniform distribution between 0 and 1 to the value of λ_0, the model determines whether a host is encountered. Random numbers greater than the value of λ_0, are scored as host encounters. We also have to consider a special case where the host density is very low, which would result in a high probability of the wasp not encountering any hosts. Here, I introduce an initial time for the wasp to give up, following Morrison and Lewis (1981) (details in Chapter III), *i.e.*, the wasp should leave the current patch if it does not encounter any hosts in the first 3 min after entering a new patch. Once it encounters a host within the first 3 min, the patch-leaving decision will be made only when the quality of the patch is lower than what it expected, as mentioned above. When wasps encounter hosts, random numbers are generated to determine whether host feeding occurs according to equation 5.2. Once the probability of feeding becomes greater than 0.8, then the feeding occurs. If not, another random number from 0 to 1 with uniform distribution is generated for comparson with the proportion of unparasitized hosts in the total number of hosts. If the random number is not greater than that proportion, then the quality of the encountered host is unparasitized, otherwise it is parasitized. The next step is to obtain an optimal host acceptance decision: for unparasitized hosts, the decision is always to accept it; for parasitized hosts, the accept or reject decision is drawn from the decision matrix according to the current wasp's physiological status (egg and memory state) and age. If the host is to be accepted, then a random number again from 0 to 1 with uniform distribution is compared to the value of τ, (a probability of a successful attack). When the random number is greater than the value of t, then the wasp fails to parasitize the host, otherwise an egg is deposited into the host body. After each encounter, the memory vector is renewed, that is to say, the identity of the host encountered is entered into the memory vector with the most distant memory being lost. This process is shown in the Fig. A.1.

Fig. A.1: Flowchart of the simulation model of the parasitism of the wasp to its pea aphid hosts within a broad bean leaflet.


Start
Initial Memory
Leave Patch
Yes
Stop
No
Encounter A Host
No
Renew Memory
Yes
Yes
Feeding
No
Good
Quality
Bad
Decision Matrix
Accept
Success
Reject
No
Yes