MICHIGAN STATE UNIVERSITY LIBRARIES
3 1293 00675 9934

This is to certify that the

thesis entitled

A BEHAVIORAL ANALYSIS OF OVIPOSITIONAL DISCRIMINATION IN THE CABBAGE BUTTERFLY (PIERIS RAPAE (L.))

presented by

BETH ANN BISHOP

has been accepted towards fulfillment of the requirements for

MASTER OF SCIENCE degree in ENTOMOLOGY

Stuart H Gage
Major professor

James R. Miller

Date 11/11/86
11-14-86

O-7639

MSU is an Affirmative Action/Equal Opportunity Institution



RETURNING MATERIALS:
Place in book drop to remove this checkout from your record. FINES will be charged if book is returned after the date stamped below.

A BEHAVIORAL ANALYSIS OF OVIPOSITIONAL DISCRIMINATION IN THE CABBAGE BUTTERFLY (*PIERIS RAPAE* (L.))

By

Beth Ann Bishop

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Entomology

ABSTRACT

A BEHAVIORAL ANALYSIS OF OVIPOSITIONAL DISCRIMINATION IN THE CABBAGE BUTTERFLY (PIERIS RAPAE (L.))

By

Beth Ann Bishop

The sequence of behaviors resulting in Pieris rapae oviposition on hosts was divided into four consecutive stages and each stage subdivided into component behaviors (steps). Comparison of transitional probabilities between successive stages and steps for sequences performed in response to different plant species revealed that:
1) significant discrimination between hosts and non-hosts occurred at virtually every sequence stage and step,
2) significant discrimination between different species of hosts occurred only during the movement stage,
3) discrimination among different non-host species occurred only while a butterfly fluttered above the plant, and
4) reputed "repellent" plants deterred further response only while the butterfly fluttered above the plant. The relative discrimination between hosts and non-hosts increased as the sequence progressed. Additionally, for most sequence steps and stages, more discrimination occurred between hosts and non-hosts than between hosts or among non-hosts. The most important stimuli eliciting an ovipositional response to a plant are inferred to be host-specific.

ACKNOWLEDGEMENTS

Writing this section has been long anticipated. For one thing, it represents the completion of a very long, sometimes painful, sometimes rewarding process. Second, it affords me the opportunity to express my appreciation to those whose help was indispensible.

I'd like to break with tradition and thank my family first. They are the persons most responsible for what I am (aside from myself), so this project has also been their creation.

Sincere appreciation also goes to my major professors. Thanks to Dr. Stuart Gage for taking me on as an unproven graduate student, for giving me the freedom to develop my own project, and for the patient help he has given me throughout my program. Thanks, also, to Dr. Jim Miller for his infectious enthusiasm, for continually challenging me, and for his time and expert advice, which was always available and frequently used.

The committee is a very important part of the success of a graduate program and I was very fortunate to have an excellent one. Like my major professors, Dr. George Ayers and Dr. Al Putnam provided me with time and advice whenever it was needed. Special thanks, also, goes to all of my

committee members for their careful reading of such a lengthy Thesis.

Sincere thanks goes to Dr. Fred Stehr who served as my major professor while Dr. Gage was on sabbatical. Thank you, Dr. Stehr, for your help and advice, for your tolerance of my spontaneous, often untimely interruptions, and for your expert editorial comments both during and after this time.

Other members of the Entomology Department also deserve special mention. Thanks goes to Dr. Ed Grafius for both his advice and for the use of his equipment. Thanks to Dr. Stan Wellso for allowing me space in the insect rearing room and in the greenhouse. Thanks, also, to Elizabeth Morrow and Paul Love for their help at Collins Road.

A special note of appreciation goes to Department Chairperson Dr. Jim Bath for helping to create a department in which student concerns are a top priority, and for his advice and council to me.

My friends also deserve a mention of thanks, for, to successfully complete a project such as this, one depends on emotional support and friendship. Thanks to my fellow entomology students: Susan Jawitz, Bob Kriegel, Aubrey Moore, and others, for your advice, for allowing me to toss ideas back and forth, and for your friendship. Special thanks to Kathe Sharpe for getting me into this in the first place, and for helping me through the rough times. Thanks to Dr. Charles Anderson for being my confidant and for being

an objective observer from whom to seek advice. Sincere thanks goes to my long-time friend and editor, Dr. Victoria Kingsbury, for her friendship and support, and for her assistance in getting this Thesis in its final form.

Last, but not least, thanks to Robert, for tolerating caterpillars in my living room, for his unswerving faith in my ability to complete this project, and for being my rock of support.

TABLE OF CONTENTS

LIST OF TABLES x

LIST OF FIGURES xiii

LIST OF TERMS xvii

INTRODUCTION 1

LITERATURE REVIEW 7

The Animal 7

Host Plants 14

Response to Plant Stimuli 20

Acceptability of Host Plants 27

Deterrents 30

MATERIALS AND METHODS 32

Establishment and Maintenanace of the Butterfly Culture 32

The Plants 37

Field Cage 40

Sequence Description 48

Sampling Procedure 57

Experiments 59

Methods of Analysis 62

RESULTS AND DISCUSSION 74

Establishing where Discrimination Occurs 74

Level I: Acceptability of Plants for Oviposition 74

Results: Broccoli 74

Results: Comparisons 77

Level II: Transitions between Successive Stages of Oviposition 79

Level III: Transitions between Successive Steps of Oviposition 89

IIIA: Movement to Response Transition 89

Proportion of butterflies entering the target area from above vs the proportion entering via the soil space (Ap vs s) 94

Proportion of visiting butterflies vs method of entry 97

Distance from which butterflies perceive and respond to hosts 100

IIIB: Response to Alight Transition 103

Proportion of lands vs contacts 111

IIIC: Alight to Curl Transition 113

Results: Broccoli 113

Results: Comparisons 117

Level IV: The Visit Sequence 130

Effect of Step Number 132

Effect of Key Events 136

Determination of the Order of the Chain 140

Visits to Different Target Plant Species 143

IVB: Post-Curl 149

Relative Discrimination 151

Comparisons within a Sequence 151

Level II: Relative Discrimination at Different Stages of the Ovipositional Sequence 156

Level III: Relative Discrimination at Different Steps of the Ovipositional Sequence 158

Degree of Discrimination Occurring between Different Plant Types 161

Level II: Stages of Oviposition 163

Level III: Steps of Oviposition 165

Miscellaneous Results and Discussion 168

Correlation of Number of Visits to Number of Eggs 168

Increase in Butterfly Responsiveness over the Season 169

Ending Behavior 177

Total Time 181

GENERAL DISCUSSION 185

Methods 185

Hypotheses and Results 190

Hosts vs Non-Hosts 190

Hosts of Differing Acceptabilities 194

Different Species of Non-Host 198

Repellent vs Non-Repellent Plants 202

The Sequence 206

Pre-Alighting Discrimination 208

Post-Alighting Discrimination 216

Further Questions 217

Control Implications 223

CONCLUSIONS 224

LIST OF REFERENCES 226

APPENDIX A: Sampling dates during which different plant comparisons were tested. 238

APPENDIX B: Number of butterflies entering each stage of the ovipositional sequence for the plant species in each comparison. 239

APPENDIX C: Number of butterflies performing the behaviors in the movement stage of oviposition for the plant species in each comparison. 244

APPENDIX D: Number of butterflies fluttering, contacting, landing, and ending as the first two behaviors in visits to the plant species in each comparison. 249

LIST OF TABLES

1. Percent coverage of wild plants growing in the field cage. 42

2. Cut flowers used to feed Pieris rapae in the field cage. 46

3. Description of Pieris rapae behavior patterns recorded in the target area. 49

4. Plant comparisons--The plant types between which discrimination was assessed in the 5 experiments. 63

5. Hypotheses and predictions tested in determining where in the ovipositional sequence discrimination occurs. 70

6. Mean number of eggs received per sampling interval by each plant species in the five comparisons. 78

7. Number of butterflies entering the target area ending (seq-->end) and visiting (seq-->V) for different plant species. 80

8. Number of visiting butterflies alighting (V-->l-c) and ending (V-->end) for different plant species. 84

9. Number of alighting butterflies curling (l-c-->cu) and ending (l-c-->end) for different plant species. 87

10. Number of butterflies entering the soil space that entered the plant space (s-->p) and that ended (s-->end) for different plant species. 90

11. Number of butterflies entering the plant space visiting (p-->V) and ending (p-->end) for different plant species. 93

12. Number of butterflies entering the target space via the soil space (s) and from above (Ap) for different plant species. 96

13. Number of butterflies fluttering, contacting and landing as the first act in visits to different plant species. 105

14. Number of butterflies contacting, landing and ending following an initial flutter above different plant species. 109

15. Number of butterflies contacting and landing on their initial alight on different plant species. 112

16. Number of butterflies ending and continuing after their first alight on different non-host species. 125

17. Number of butterflies performing a flutter, a contact, a land, a land-curl, or an end on steps 1 through 4 of visits to the broccoli target (comparison I). 134

18. Number of butterflies performing specified transitions to all possible behaviors following a flutter, a contact, and a land as a function of step number. 135

19. Number of butterflies performing specified transitions to all possible behaviors following a flutter, a contact, a land, and a land-curl as a function of "experience". 137

20. Chi-Square test for quasi-independence of preceding behavior from following behavior on table including an impossible transition (flutter-to-flutter). 142

21. Percentage of butterflies making the same transition between behaviors for the same plant (broccoli or tansy) in different comparisons (different sampling dates). 174

22. Mean length of time of sampling intervals (time taken to record sequences) for different target plant species. 184

23. Summary of the hypotheses, predictions, and results from the first section of the results for hosts vs non-hosts. 191

24. Summary of the hypotheses, predictions, and results from the first section of the results for hosts of differing acceptabilities. 195

25. Summary of the hypotheses, predictions, and results from the first section of the results for different non-host species. 199

26. Summary of the hypotheses, predictions, and results from first section of the results for repellent vs non-repellent plants. 203

LIST OF FIGURES

1A. Female Pieris rapae. 13

1B. Male Pieris rapae. 13

2. Hydrolysis reaction of thioglucosides to isothiocyanates
a) R=CH2=CH-CH2--Sinigrin,
b) R=p-HOC6H4CH2--Sinalbin.
(From Kjaer 1963, 1976) 17

3. Map of the Field Cage Interior. T=target plant, P=plant area, S=soil area, RH=reserve host, F=cut flowers. 43

4A. Spatial representation of hypothetical sequence of behaviors of Pieris rapae in target area. S=soil space, p=plant space, A=enter target area from above, V=visit, f=flutter, l=land, c=contact, cu=curl, end=leave target area. 52

4B. Diagramatical representation of hypothetical sequence of behavior of Pieris rapae in target area. S=soil space, p=plant space, A=enter target area from above, V=visit, f=flutter, l=land, c=contact, cu=curl, end=leave target area. 53

5. Organization of the analysis in first part of the Results. Data is analyzed on successive Levels (I through IV). Each subdivision of a level represents one test. Statistical test used is given in lower right corner of box (G = G test, ANOVA = Analysis of variance). Seq=sequence, V=visit, end=leave target area, l=land, c=contact, f=flutter, cu=curl, Ap=enter target area from above, s=soil space, p=plant space, cont=continue (no curl but reland). 65

6. Distribution of the number of eggs laid per sampling interval on the broccoli target plant (comparison I). 75

7. Percentage of butterflies entering the plant area from above (Ap) and via the soil space (s) that visited broccoli, tansy, sage and mustard. Percentages shown under the same letter are not significantly different at the .05 level. 99

8. Percentage of butterflies entering the soil space that left the target area without visiting the plant, for the broccoli and tansy target plants (comparison I). 102

9. Number of butterflies performing each behavior in the alight stage of oviposition for the broccoli target (comparison I). The width of the boxes is proportional to the number of butterflies performing the designated behavior (this number is given in the box). The width of the arrows is proportional to the transitional probabilities (shown next to the arrow). The total area of the boxes is insignificant. 114

10. Percentage of butterflies curling, continuing and ending on successive alights on broccoli (comparison I). 116

11. Percentage of butterflies performing their first curl on the first through fifth alight on broccoli (comparison I). 118

12. Percentage of alighting butterflies that rested only on differpent plant species. Percentages shown under the same letter are not significantly different at the .05 level. Br=broccoli, T=tansy, S=sage, M=mustard, L=lettuce, Sy=soybean, BT=broccoli-tansy, *=data not analyzed due to the low number of visits occurring. 120

13. Number of butterflies curling, continuing and ending after the first three alights on broccoli and tansy (comparison I). The number in parentheses is the percentage of butterflies making that particular alighting that performed the designated behavior. 121

14. Percentage of butterflies curling, continuing, and ending after the first three alights on broccoli and mustard (comparison III). 123

15. Percentage of butterflies curling, continuing, and ending after the first three alights on broccoli and broccoli-tansy (comparison V). 126

16. Percentage of butterflies curling, ending, and continuing after making their first alight on the broccoli leaves, and on the tansy leaves of the broccoli-tansy target. 128

17. Percentage of butterflies fluttering, contacting, landing, and landing with a curl as the first behavior: 1) in a visit, 2) following the first alight, 3) following the first curl, and 4)following the second curl. 139

18. The visit sequence to the broccoli target (comparison I). The size of the boxes is proportional to the relative frequency of the behavior. The width of the arrows is proportional to the transitional probability between behaviors (given next to the arrow). The relative proportion of the behavior as the first act in a visit is shown by the arrow in the upper right corner of each box. 144

19. The visit sequence to the tansy target (comparison I). The size of the boxes is proportional to the relative frequency of the behavior. The width of the arrows is proportional to the transitional probability between behaviors (given next to the arrow). the relative proportion of the behavior as the first act in a visit is shown by the arrow in the upper right corner of each box. 145

20. The visit sequence to the mustard target (comparison I). The size of the boxes is proportional to the relative frequency of the behavior. The width of the arrows is proportional to the transitional probability between behaviors (given next to the arrow). The relative proportion of the behavior as the first act in a visit is shown by the arrow in the upper right corner of each box. 146

21. Percentage of butterflies ending (not making additional curls) after curling on broccoli and mustard as a function of curl number. 150

22. Percent communication from plant to butterfly during different stages of the ovipositional sequence. 157

23. Percent communication from plant to butterfly during different steps in the ovipositional sequence. 160

24. Percent relative discrimination between hosts and non-hosts, hosts of differing acceptabilities, and different species of non-hosts during different stages in the ovipositional sequence. 164

25. Percent relative discrimination between hosts and non-hosts, hosts of differing acceptabilities, and different species of non-hosts during different steps in the ovipositional sequence. 166

26. Eggs laid per sampling interval vs visits per sampling interval for broccoli (comparison I). r=.758 170

27. Eggs laid per sampling interval visits per sampling interval for mustard (comparison III). r=.856 171

28. Eggs laid per sampling interval vs visits per sampling interval for broccoli-tansy (comparison V). r=.866 172

29. Percentage of butterflies performing ending behaviors in the feeding, oviposition, and ending categories as a function of how far they progressed through the sequence. 180

30. Percentage of butterflies exhibiting ending behavior classed as "ovipositional" that directed their ending behavior toward hosts rather than toward non-hosts as a function of how far they progressed in the ovipositional sequence. 182

LIST OF TERMS

Term	Definition
Alight Stage	A sequence stage. Behaviors performed after the first alight up to the first abdominal curl
Curl Stage	A sequence stage. Behaviors performed after the first abdominal curl
Movement Stage	A sequence stage. Behaviors performed before the visit.
Plant Space	The inner cylinder of space in the target area.
Reserve Hosts	Host plants that were placed in the field cage among the wild vegetation to provide the butterflies with suitable ovipositional sites and to collect eggs for maintenance of the butterfly culture.
Response Stage	A sequence stage. Behaviors performed from the first visit behavior up to the first alight (land or contact).
Sampling Date	A day on which sequences were observed and recorded.
Sampling Interval	The period of time during which behavioral sequences performed in response to a single target plant were observed and recorded.

Sequence Stage	A group of consecutive behaviors in the ovipositional sequence. Four sequence stages were identified: the movement stage, the response stage, the alight stage and the curl stage.
Sequence Step	Corresponds to the performance of one behavior in the ovipositional sequence.
Soil Space	The outer cylinder of space in the target area.
Target Area	The area inside the field cage in which the behavior of butterflies was observed and recorded.
Target Plant	The plant used during an experiment. Butterfly behavior in response to the target plant was recorded.

INTRODUCTION

To a phytophagous insect, different species of plants are not equally acceptable as food. Even insect species that feed on a variety of plants consume some plant species heavily, others very little, and still others not at all. For example, larvae of the Colorado potato beetle (Leptinotarsa decemlineata [Say]) feed mainly on plants in the family Solanaceae, but will accept some species in the families Caesalpiniaceae, Asclepiadaceae, Cruciferae and Compositae. Other plants are not eaten (Hsiao and Fraenkel 1968). Even insects considered to be generalist feeders, such as grasshoppers, are selective in diet. For example, the sulfur-winged grasshopper (Arphia sulphurea [Fab.]) feeds mainly on grasses. Although A. sulphurea may consume some herbaceous species, others are not accepted (Gangwere 1965). Because insects are often apart from acceptable food, they must be able to find (Miller and Strickler 1984) and distinguish acceptable from non-acceptable plants. By so doing they discriminate among plants.

Discrimination among objects is based on perception. All information about the external environment that an animal has access to is received by its sensory organs and interpreted by its nervous system. If the information

received from two objects differs, and if the animal registers this difference physiologically, then the animal's perceptions of the two objects differ.

The perceptual basis of observed discrimination patterns in the Insecta has long intrigued humans. There are at least two reasons why understanding an insect's perceptions may be desirable. First, many species of phytophagous insects are pests of crops. By understanding the perceptual basis for discrimination, humans have the potential for manipulating relevant plant stimuli and thus changing the acceptability of a plant (Beck 1965).

Secondly, the realization that: 1) An animal's perceptions are influenced by the structure of its sensory and neurological equipment, and 2) that each species, by virtue of its unique evolution, possesses slightly different equipment, leads to the inference that the perceptions of our fellow animals may be fundamentally different from our own (von Uexkell 1957, Dethier 1969). An understanding of the perceptions of insects allows us to expand our own world by making theirs partially accessible to us.

Humans are incapable of knowing directly another animal's perceptions; but, we may gain knowledge about these perceptions by observing behavioral discrimination (e.g., differences in observed behavior toward two objects). Dethier (1969) loosely defines perception as "How the world looks", or "What things are the same and what things are different." He explains that we may infer perception when

an animal behaves "as though" objects are the same or "as though" they are different. For example, if a phytophagous insect exhibits identical behavior toward two different plant species then the possibility exists that they are perceived as essentially the same for that insect at that time. Any qualitative or quantitative differences in stimuli perceived by humans (either unaided or with the help of instruments) are either not perceived by the insect or do not influence behavior. Conversely, if the responses toward the two plant species differ, then we may assume that they are perceived differently by the insect. By examining characteristics that differ between the plant species, one may at least speculate as to the stimuli responsible for perceptual differences. In this way discrimination gives us a "window" on the perceptual world of phytophagous insects.

Discrimination between plants by insects is often assessed by comparing criteria (such as tissue damage or number of individuals per unit) that are the net result of all responses made by many individual insects of a given species toward a plant. As many authors have pointed out, the behavior that results in plant use is, in reality, a sequence of separate responses, each mediated by perceptions (Dethier 1953, Thorsteinson 1960, Beck 1963, 1965, Kennedy 1965). It is important to remember this sequence when investigating the perceptual basis of discrimination. One cannot assume that an insect's perceptions remain constant throughout the sequence. Certain stimuli may become more or

less important as the sequence progresses (Kennedy 1965). Because an animal's perceptions may change as the sequence progresses, so too may the observed degree of discrimination.

The present study investigates discrimination between plants during the ovipositional sequence of the cabbage butterfly (Pieris rapae [L.]), an oligophagous butterfly. Oligophagous butterflies pose several challenges to development of an understanding of the perceptual basis of discrimination. The first challenge lies with the nature of the animal. Because butterfly larvae are relatively small and immobile, survival depends, to a large extent, on a female's ability to place her eggs on the proper food plants. Since adults are nectar feeders, they usually do not maintain an association with larval food plants except during oviposition. Adults are relatively mobile; during daily flight a female usually encounters a great variety of plants, yet she is able to distinguish those species crucial to offspring survival.

The second challenge to understanding the perceptual basis of discrimination in oligophagous butterflies lies with the nature of oligophagy. Oligophagous insects feed on a limited range of plants, often taxonomically related (Thorsteinson 1958). Species of host plants are often diverse, appearing (to a human observer) to be morphologically as different from one another as they are from non-hosts. Yet there are sharp differences in the

number of eggs laid on hosts as compared with the number laid on non-hosts. P. rapae, for example, colonizes mostly plants within the family Cruciferae. Plants in this family are extremely diverse, yet a "mistake" by a P. rapae female (i.e., an egg laid on a non-host) is rare. This pattern implies that the butterflies discriminate behaviorally between hosts and non-hosts at one or more points in the ovipositional sequence.

The ability to respond appropriately to a diverse group of objects, such as host plants, must be due to a "class recognition" based upon the ability to perceive the constant and unique class characteristics despite variation in these characteristics and amid large amounts of extraneous information. Brues (1920) explained it this way: "Undoubtedly there is some attribute of such plants that insects can recognize in a general way and not as a specific characteristic of some single plant species or genus." Understanding just what this characteristic (or group of characteristics) is lies at the heart of understanding the perceptual basis of host plant discrimination by oligophagous insects.

For P. rapae this "class characteristic" has long been thought to be thioglucosides; secondary plant chemicals produced by hosts (Verschaffelt 1911). However, some recent research has suggested that a P. rapae female is able to perceive these host-specific chemicals only after alighting on a plant (Hovanitz and Chang 1964, Renwick and Radke 1983,

Traynier 1979). If so, then this question is raised: Is ovipositional behavior before alightment non-discriminatory? Does P. rapae alight randomly on plants, distinguishing hosts from non-hosts only after alighting has occurred?

The present study was designed to address the above questions. Emphasis was placed on the sequential nature of oviposition. The approach taken was to observe the ovipositional sequence of P. rapae in a semi-natural setting, with the goal of identifying the responses in the behavioral sequence where discrimination is exhibited, and analyzing the role played by discrimination during each response in determining the overall acceptability of the plant.

The specific objectives of the study were:

1. To describe the sequence of behaviors leading to P. rapae oviposition on a normal host plant. The temporal order of behaviors would then serve as a basis for comparing sequences performed in response to different plant species.

2. To determine where in the ovipositional sequence discrimination occurs. Discrimination was assessed between the following plant types: i) hosts vs non-hosts, ii) hosts of different acceptabilities, iii) different species of non-hosts, and iv) repellent vs non-repellent plants.

3. Comparison of the relative degree of discrimination: i) occurring between hosts and non-hosts at different points of the ovipositional sequence, and

ii) occurring among different plant types at the the same point in the ovipositional sequence.

In summary, the purpose of this study was to assess discrimination by comparing behaviors toward different plants. The nature of the stimuli influencing the performance of such behaviors is not directly addressed. However, a better understanding of discrimination patterns is the first step to discovering the nature of the stimuli involved.

LITERATURE REVIEW

The Animal

The cabbage butterfly, Pieris rapae (L.), is a member of the cosmopolitan family Pieridae, which includes mostly small to medium-sized butterflies. The family is represented by two North American subfamilies: Colianae, the sulfurs, most species of which feed as larvae on legumes, and Pierinae, the whites, most species of which are larval specialists on crucifers and capers (Opler and Krizek 1984). P. rapae belongs to the later subfamily, which includes a large number of genera and species (see Ehrlich and Raven 1964). As mentioned previously, most temperate species are crucifer specialists (Cruciferae) although plants in the related families, Caparidaceae, Resedaceae, and Tropaeolaceae are sometimes utilized. Eleven species of Pierinae are found in the Eastern U.S. alone. Where the

geographical distribution of different species overlaps, niche separation occurs by a variety of behavioral and ecological mechanisms including: adult habitat, range and acceptability of different species of potential host plants, and differences in the part of the plant utilized by larvae (Shapiro 1974, 1975; Chew 1977, Opler and Krizek 1984).

P. rapae is endemic to Eurasia and North Africa, but has been introduced to many other parts of the world, including New Zealand (Moss 1933), Australia, Bermuda, Hawaii, and other Pacific islands (Opler and Krizek 1984). The animal was accidentally introduced to the North American continent in 1860, near Quebec, Canada and its spread was rapid (Scudder 1887). By the early 1900's the invasion was so complete that one W. Virginia agricultural bulletin not only reported a serious effect of the larvae (i.e., "cabbage worms") on cole crops where none existed previously, but also reported that the invader was displacing and restricting native Pierinae species (Rumsey and Brooks 1909). The present day range of P. rapae in N. America extends from coast to coast and from central Canada to northern Mexico.

Pieris rapae has had a significant impact on cultivated cruciferous crops. Prior to the advent of modern insecticides, at least one tenth of the total cabbage crop was lost to larval feeding (Twinn 1924). Although today direct crop losses are probably minimal due to the use of insecticides, the cost of control is high, resulting in

significant increases in production costs. For example, in 1979 89,000 acres of cabbage were planted in the U.S. for the fresh market, 67,000 of which were treated for insect control (Ferguson 1984). Over 193,400 pounds of insecticides were used. At 1984 prices, this translates to a insecticide cost of approximately $3.5 million for cabbage alone (derived from data supplied by E. Grafius, personal communication). The primary damage to cabbage is done by the late-instar larvae which burrow into the head of the plant and deposit large amounts of green frass, thereby reducing market value (Harcourt 1963).

Although the success of species introduced into new areas without their biological control agents is well known, there is perhaps an additional reason accounting for the success of P. rapae as a colonizer. Despite a narrow range of acceptable food plants as larvae, the adult butterfly is very adaptable. Extremes in temperature seem to affect it much less than other butterfly species. Where occurring seasonally, P. rapae is among the first butterflies to emerge in the spring and among the last to disappear before winter; e.g., they occur between the middle of May and the first of September in Michigan's upper peninsula, from late March to early November in Virginia, and year round in Mississippi (Opler and Krizek 1984).

Where P. rapae occurs seasonally there is usually sufficient time for a number of generations to occur. Development from egg to adult requires between 37 days

(at 17 degrees C) to 22 days (at 27 degrees C) (Richards 1940). Females lay eggs as long as temperatures and the presence of hosts permit. In some regions of the Southern United States as many as 6 to 7 generations a year may occur (Opler and Krizek 1984).

During the average 3 weeks or 156 degree days (base 10 degrees C) (Gossard and Jones 1977), a female has the potential to lay a large number of eggs; laboratory counts of the total number of eggs laid range from 300 to 500 (Moss 1933, Rahman 1968, Twinn 1924). Gossard and Jones (1977) measured egg production in a field cage and found that it ranged up to fifty eggs per female per day, depending on age and temperature.

As a result of this high fecundity, in combination with the propensity of females to cover up to 700 meters per day (Jones et al. 1980), an individual female is able to distribute her eggs over a wide area. Females are reported to fly in a great diversity of habitats, being rare or absent only in canopied forests and in open areas not supporting crucifers (Opler and Krizek 1984). Adaptability in food and host requirements is probably responsible for this. P. rapae is reported to visit a large number of flower species, even those not believed to possess nectar (Opler and Krizek 1984). Additionally, eggs are laid on a large number of host species. In this respect, P. rapae is less restricted than most other Pieris species which

oviposit on a limited number of crucifer species (Opler and Krizek 1984).

Given the mobility of females, the high reproductive potential, and the relative non-specificity of adult food and habitat requirements, it is easy to understand the success this insect has achieved as a colonizer.

The life cycle of P. rapae has been described by several authors including: Twinn (1924), Richards (1940), and Harcourt (1963). Eggs are laid singly on host plants. Oogenesis requires 4 to 9 days, depending on temperature (Moss 1933, Richards 1940). There are 5 larval instars. First instar larvae are less than 4 mm long and feed primarily on the outer leaves of plants. The last two instars feed mainly on younger leaves, burrowing into the heads of plants such as cauliflower, cabbage, and broccoli. Older larvae are capable of moving to another plant upon consumption of the original host.

Approximately one day prior to pupation, the caterpillar stops feeding and begins to move to a pupation site. Although some may pupate on the same host plant, larvae more commonly move to another object, such as a fence post, outbuilding, or another plant, climb it, and then pupate.

Pupae are green or brown, pointed on either end with three ridge-like projections on the dorsal and lateral surface, and are attached to the substrate by a silken

girdle. Pupation may take from 6 to 11 days depending on temperature (Richards 1940).

Adults are mostly white, with black markings on the tips of the forewings, one black spot on the dorsal side of the hind wing, and one (males) or two (females) black spots on the dorsal surface of the forewing (Figure 1). The underside of the wings is speckled with yellow.

Females usually mate and begin to oviposit within 24 hours of emergence (weather permitting). Males patrol a home range, mating with females emerging from pupation in this area (W.G. Wellington, personal communication in Jones et al. 1980). Males are probably stimulated to approach females, at least from close range, by visual stimuli (Obara and Hidaka 1968, Obara 1970).

Egg laying begins shortly after mating. A female lands on a plant, curls the tip of her abdomen downward until it touches the (usually) underside of the leaf, and then withdraws, leaving a single egg glued to the leaf surface. Approximately 85% of the eggs are laid on the underside of leaves (Richards 1940). Most of the time, successive ovipositions are separated by at least a short intervening flight.

Jones et al.(1980) and Root and Kareiva (1984) both found that individual females were highly directional, tending to fly in the same general direction over the course of a day's flight. An individual's "preferred" direction



Figure 1A. Female Pieris rapae.



Figure 1B. Male Pieris rapae.

varied from day to day and was not dependent on any environmental cues such as sunlight or wind direction.

Host Plants

The host plant range of P. rapae includes a large number of morphologically diverse plants, mostly within the families Capparidaceae, Resedaceae, Tropaeolaceae and Cruciferae (Twinn 1924). Members of the latter family are the usual hosts of most temperate Pierinae species (including P. rapae). Tropical Pierinae species mostly utilize capers (Capparidaceae).

The family Cruciferae is large and diverse, containing approximately 350 genera and 2,500 species, most of which are annual or bienniel herbs distributed in the cooler regions of the northern hemisphere (Lawrence 1951). Most crucifers, as members of this family are commonly known, are adapted to disturbed habitats. They include many common weeds of roadsides and cultivated fields. In addition, several species have been selectively bred and cultivated by humans. The most well-known cultivated species include varieties of Brassica oleraceae: cauliflower (B. oleracea var. botrytis), collards (B. oleracea var. acephala), kale (B. oleracea var. acephala), cabbage (B. oleracea var. capitata), broccoli (B. oleracea var. italica), brussel sprouts (B. oleracea var. gemmifera), and other species including: mustard (B. juncea), turnip (B. campestris, radish (Rhaphanus spp), and watercress (Nasturtium

officianale). Varieties of B. oleraceae have been cultivated for hundreds, perhaps thousands of years (Nieuhof 1969). Long-term selective breeding programs have resulted in the creation of "infraspecific complexes and artificial hybrids", making taxonomic relationships difficult to decipher (Kjaer 1976).

To humans crucifers share few morphological characteristics; only the anatomy of the flowers is common to all species. Most species also have simple, alternate leaves and many are characterized by the presence of forked or stellate unicellular hairs (Lawrence 1951).

Biochemically, all crucifers are characterized by the presence of thioglucosides in living tissue. Thioglucosides are sulfur-containing chemicals synthesized by the plant (for biosynthesis, see Kjaer 1976) and present in parenchyma cells (Stevens 1924). Since their discovery over 100 years ago, more than 70 naturally-occurring thioglucosides have been identifi[illegible] (Kjaer 1976). Thioglucosides are considered to be present [illegible] plants in the families Cruciferae, Resedaceae, Ca[illegible]ridaceae, and Moringaceae; and in at least some species of several other families, including Tropaeolaceae (Kjaer 1963).

A typical piece of cruciferous tissue contains a complex of different thioglucosides, the composition of which varies from organ to organ (Josefsson 1967). There is evidence that the qualitative pattern of thioglucosides is under genetic control (Hemingway et al. 1969).

Thioglucoside pattern varies between species, and between varieties in the case of cultivated varieties of B. oleracea (Josefsson 1967, Nair et al. 1976, Rodman and Chew 1980). Environmental and developmental factors may also affect thioglucoside composition quantitatively. Younger leaves contain higher concentrations of thioglucosides than older leaves (van Emden and Bashford 1969). Nutrient regimes deficient in sulfur and those deficient in nitrogen reduce and increase thioglucoside concentration, respectively (Wolfson 1980).

When plant tissue is damaged, thioglucosides may undergo enzymatic hydrolysis to glucose, sulfuric acid and a volatile isothiocyanate (Kjaer 1963) (see Figure 2). Each thioglucoside yields, upon hydrolysis, a unique isothiocyanate (Josefsson 1967). The reaction is catalyzed by the enzyme myrosinase, which is contained in specialized idioblasts (Esau 1977) and is known to be present in all thioglucoside-containing plants (Bjorkman 1976). The enzyme has also been identified in a fungus (Aspergillus sydowii), a bacterium (Paracorobactrium aerogenoides), the cabbage aphid (Brevicoryne brassicae), and mammalian tissue (Bjorkman 1976).

A number of different myrosinase isoenzymes have been identified, but individual enzymes do not appear to be adapted to particular thioglucosides (Bjorkman 1976). As with the parent compounds, different isoenzymes co-occur in plant tissue, forming complexes that vary from one organ to

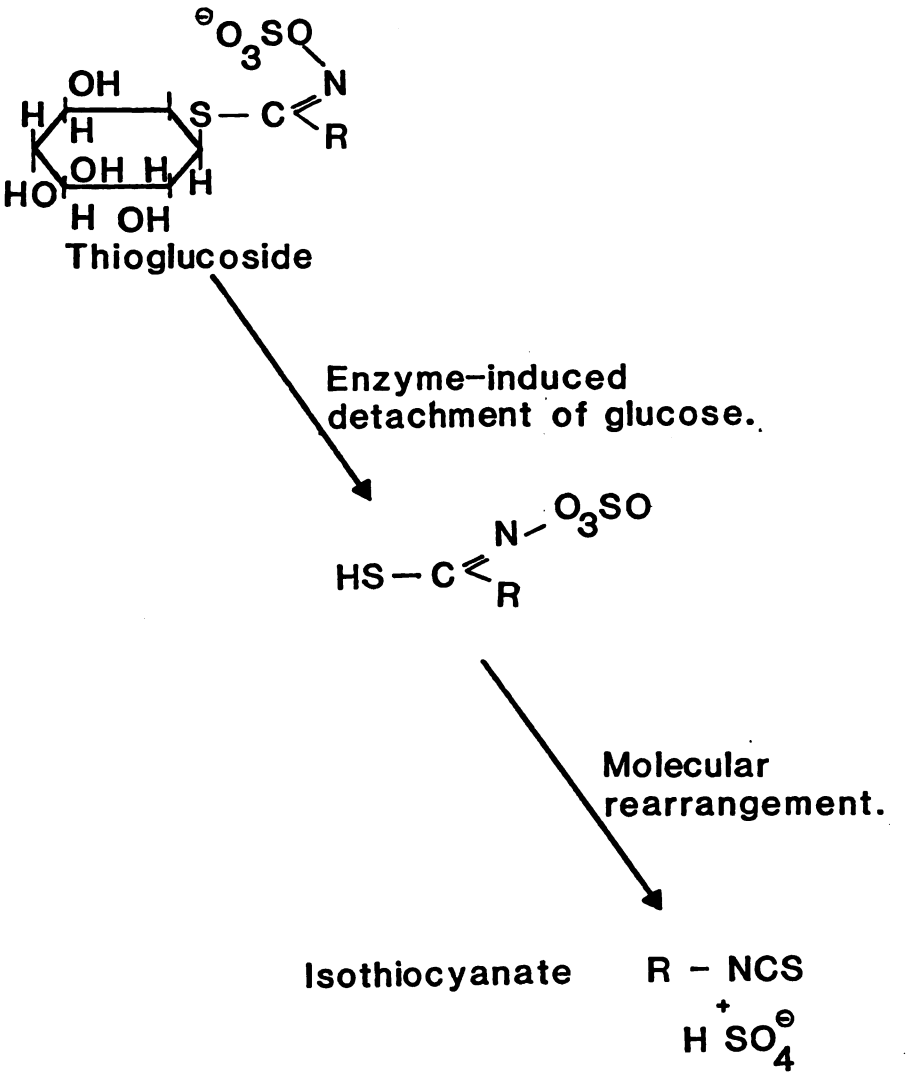


Figure 2. Hydrolysis reaction of thioglucosides to isothiocyanates
a) R= CH2=CH-CH2--Sinagrin, b) R= p-HOC6H4CH2--Sinalbin.
(from Kjaer 1963, 1976)

the next (Macgibbon and Allison 1970). Nutrition and habitat seem to influence the abundance of myrosinase-containing idioblasts a plant possesses. When development is checked, the abundance of these cells increases (Solereder 1909). In addition, there may be a genetic component to enzyme activity, as it varies from species to species (Bjorkman 1976).

Because of the multitude of factors resulting in differences between plants in both substrate and enzyme, major differences in isothiocyanate production are not surprising. Different parts of a single plant may vary in the amount of isothiocyanate produced (Bjorkman 1976). Growing conditions may affect isothiocyanate production; cabbage plants grown earlier in the season produce over 100 times more allyl isothiocyanate (the hydrolysis product of the thioglucoside sinigrin) than plants grown later in the season. Also, brussel sprout and cabbage plants grown 1 ft apart produce 20 times more allyl isothiocyanate than those spaced 3 ft apart (MacLeod 1976).

In summary, the total thioglucoside picture is exceedingly complex. Different plant species may have unique gentically- determined chemical profiles subject to modification by numerous environmental factors. Yet all plants serving as hosts for P. rapae contain thioglucosides. As might be expected, thioglucosides play an important role in the host specificity of P. rapae and other insects specializing on crucifers. Over the years, the relationship

between crucifer chemistry and crucifer-specialist insects has been well studied and documented. Thioglucosides in crucifers are one of the the best supported examples of a plant secondary compound originally evolving as a defense against predators and pathogens and later becoming a releasing stimulus to insect species able to overcome the defensive barrier. As evidence for a defensive function, thioglucosides (and/or isothiocyanates) have been found to function as a fungicide, an antibiotic, a mammalian digestional irritant (Feeny 1977), and an insect feeding inhibitor (Eriksonand Feeny 1974). Furthermore, some cruciferous species (Lepidium spp and Thlaspi spp) contain atypical enzymes that degrade thioglucosides to the geometrical isomers of isothiocyanates, the thiocyanates (Kjaer 1976). Such plants typically support poor growth or are lethal to some Pieris species (Chew 1975).

A number of insects have overcome the thioglucoside defensive chemical barrier. For example, the green peach aphid, Myzus persicus, appears able to tolerate these compounds, although its growth is negatively correlated with the total allyl isothiocyanate content of the leaves (van Emden 1972). Other crucifer specialist insects actually require thioglucosides or isothiocyanates to initiate feeding or colonization. Besides influencing the ovipositional behavior and larval feeding behavior in Pieris rapae, thioglucosides and/or isothiocyanates have been found to play a role in the host specificity of cabbage aphids

(Brevicoryne brassicae, Wensler 1962), cabbage flea beetles (Phyllotreta cruciferae and P. striolata, Feeny et al. 1970), the cabbage root fly (Delia brassicae, Finch 1978), the diamondback moth, Plutella maculipennis (Thorsteinson 1952, Gupta and Thorsteinson 1960), and the large white butterfly, Pieris brassicae (David and Gardiner 1962, 1966).

Response to Plant Stimuli

Basic to understanding discrimination behavior in P. rapae is an understanding of the perceived plant characteristics that influence the behavior of ovipositing butterflies. Many studies have investigated the role played by selected stimuli in P. rapae ovipositional behavior. Most investigators use the number of eggs laid as the measured result. In such cases, it may be impossible to infer correctly which responses in the ovipositional sequence are involved (Jones 1977). Nevertheless, such studies form the basis of our knowledge.

The following discussion considers the influence of plant stimuli of two basic types--visual stimuli and chemical stimuli--on P. rapae ovipositional behavior.

Vision potentially plays a role in all phases of oviposition, but traditionally has been considered to be more important in the earlier stages (Dethier 1953, Beck 1965). Furthermore, visual stimuli were considered to play a relatively minor role in host-plant specificity because visual aspects of host plants, as compared with

chemical aspects, were believed to be too variable to enable insects to distinguish hosts from non-hosts.

More recently, emphasis has been placed on the interaction of several stimuli in determining host specificity (Dethier 1976, 1982, Schoonhoven 1977). Accordingly, vision has been accorded a more important role in ovipositional behavior. Prokopy and Owens (1983) state that "Numerous examples exist where both visual and chemical stimuli, operating sequentially or simultaneously, play a role in host plant location by a variety of insects."

Three different visually perceived characteristics of plants potentially influence P. rapae ovipositional behavior: plant color, plant size, and plant shape. Color influences courtship behavior (Obara 1970, Obara and Hidaka 1968) and feeding behavior (Miyakawa 1976) of P. rapae. That color has a role in the ovipositional behavior of P. rapae was shown by Hovanitz and Chang (1964) who found that most eggs were laid on blue-green artificial ovipositional substrates.

Because of their use of the end result of oviposition (eggs) as a criterion for comparisons, Hovanitz and Chang's (1964) study did not reveal which behavior(s) in the ovipositional sequence were influenced by color. Later studies suggest that color affects P. rapae movement behavior, post-alighting behavior, and the probability of landing on a plant. Miyakawa (1976) found that butterflies were more likely to approach and fly over green backgrounds

than non-green backgrounds. In addition, the flight paths of P. rapae butterflies flying over vegetation were characterized by considerably more turning than those over bare ground. This may have been due, in part, to a color difference between the two backgrounds.

The influence of color on the post-alighting behavior of P. rapae has been demonstrated by Fox (1966). When cabbage butterflies were held on differently colored pieces of paper, tarsal drumming only occurred on green paper.

The influence of color on the probability of alighting by P. rapae was first suggested by Ives (1978) and later confirmed by Traynier (1984). Ives (1978) found that more P. rapae eggs were laid on young plants than on older plants of the same size, and also on plants grown under low light intensities. This difference was in part explained by an increased probability of landing on the younger plants (Jones 1977). Ives noted that the plants grown under low light conditions were similar to the younger plants, having "fewer, larger leaves that were lighter in color, thinner and less fibrous." Thus, the difference in the probability of landing between young and old plants could have been due partially to a difference in color. Recently, Tranier (1984) has confirmed with laboratory experiments that alighting by P. rapae is influenced by color.

The size of a host plant also affects the number of P. rapae eggs a species or variety receives (Ives 1978, Latheef and Irwin 1979). Jones (1977) found that plant size

affected the probability of landing on a host, but not the probability of laying an egg after landing. The probability of landing was also affected by the variety or species of host. The response to variety was found to override the response to size in that bigger varieties did not necessarily elicit more landings (Ives 1978).

P. rapae ovipositional behavior may also be influenced by shape: either the overall shape of the plant (Prokopy and Owens 1983), or the shape of the leaves. Leaf shape is known to influence oviposition in the butterfly Battus philenor (Rausher 1978) and is believed to influence oviposition in other butterfly species (Stanton 1982, Feeny et al. 1983). Miyakawa (1976) found that shape affected P. rapae feeding behavior, but the effect of shape on oviposition has not yet been investigated.

The influence of chemicals on P. rapae ovipositional behavior has been intensely investigated. Particular emphasis has been placed on host-specific thioglucosides and isothiocyanates. Verschaffelt (1911) was the first to demonstrate a relationship between a phytophagous insect and the chemicals of its hosts when he noted that plants fed on by P. rapae larvae and the larvae of the closely related P. brassica contained thioglucosides. He also demonstrated that larvae could be induced to feed on normally unacceptable food if it was smeared with juice from a host plant or with solutions of sinigrin (a thioglucoside). While Verschaffelt could not determine the relative roles of

gustation (of soluble thioglucosides) and olfaction (of volatile isothiocyanates), he postulated that olfaction would be relatively more important for host recognition by ovipositing adults.

Since thioglucosides are soluble, they are presumably perceived only after contact. Butterflies are known to possess tarsal contact chemoreceptors that are usually more numerous in females than in males (Fox 1966). Presumably, these sense organs facilitate ovipositing females in identification of their host plants via characteristic chemicals perceived after landing. Perception of these chemicals may be enhanced by the drumming behavior often performed by females after landing (Ilse 1956). Since the tarsal chemoreceptor organs are always located beneath a tarsal spine, drumming presumably abrades the plant tissue, thereby releasing chemicals (Fox 1966).

The physiological effect of thioglucosides on tarsal chemoreceptors of the large white butterfly (Pieris brassicae) was studied by Chun and Schoonhoven (1973). They found two types of trichoid sensilla located on the tarsi. A cell in type "B" sensilla was found to be responsive to GTA, a thioglucoside.

Pieris rapae possesses tarsal hairs similar to P. brassicae (Fox 1966, Traynier 1979). Although the effect of thioglucosides on these hairs has not yet been investigated, it is assumed that they serve a similar function since both host plant extracts and commercial preparations of sinigrin

have been shown to elicit P. rapae oviposition (Hovanitz and Chang 1964, Renwick and Radke 1983, Traynier 1984), and because thioglucosides are not perceived via abdomenal contact chemoreceptors in either P. brassicae (Klijnstra 1982) or Pieris rapae (Traynier 1979).

The number of P. rapae eggs laid is influenced by the concentration of host-plant extract or sinigrin. The findings of Renwick and Radke (1983) suggest that, although a single thioglucoside, such as sinigrin, stimulates oviposition, other chemicals are probably involved in determining the overall ovipositional response. Since host plant tissue typically contains a complex of different thioglucosides, it is possible that it is the particular combination and relative quantities of thioglucosides and/or other constituents that determine overall response (Dethier 1976), but this has not yet been investigated for P. rapae.

Perception of host-specific chemicals via tarsal chemoreceptors affects Pieris rapae behavior for up to 72 hours after contact. Traynier (1979) found that P. rapae females that had previously contacted host foliage were more likely to land on plants and were also more likely to lay eggs on non-hosts than individuals that had, instead, previously contacted non-host foliage.

In contrast to thioglucosides, isothiocyanates are volatile compounds which butterflies are potentially able to perceive prior to landing. Perception of isothiocyanates could result in host-specific behavior prior to landing.

There is circumstantial evidence that the large white butterfly (P. brassicae) uses host volatiles in its host finding (Mitchell 1978, Rothschild and Schoonhoven 1977, Behan and Schoonhoven 1978). Results for P. rapae, however, have largely been negative. Traynier (1979) suggested that host plant volatiles played no role in P. rapae oviposition because his caged butterflies were observed to fly directly toward any green object placed in the cage (host foliage, non-host foliage, or yellow and green index cards). Allyl isothiocyanate (AITC) applied to artificial ovipositional substrates was found to elicit no more eggs than water (Hovanitz and Chang 1964). Ovipositional substrates possessing a source of host volatiles (cabbage leaves obscured from the butterflies' view) received no more eggs than those without (Renwick and Radke 1983). Additionally, high concentrations of AITC (Hovanitz and Chang 1964) and macerated cabbage (Renwick and Radke 1983) reduced the number of P. rapae eggs laid on artificial ovipositional substrates.

The conclusion that volatiles play no role in P. rapae ovipositional behavior is based on results obtained using butterflies confined to small cages. In such cases, butterflies are often deprived of normal releasing stimuli; this results in threshold lowering and a concomittent reduction in the degree of discrimination exhibited (Lorenz 1981, Singer 1982). In addition, both Hovanitz and Chang (1964) and Renwick and Radke (1983) obtained their results

by counting eggs, not by observing behavior. As a result, the behavior can only be inferred and such inferences may be wrong (Jones 1977). Consequently, whether host volatiles affect P. rapae ovipositional behavior has not been established, but any such effect is not likely to be strong.

Acceptability of Host Plants

An ovipositional "mistake" is relatively rare in P. rapae. However, plants within the host-plant range may differ in the number of eggs they receive. A number of studies have compared the number of eggs received by different species or varieties or plants, or by plants differing in intrinsic characteristics such as age or size. In reporting results of these studies the term acceptability, which refers to the relative number of P. rapae eggs a plant tends to receive in a choice situation, will be used. A highly acceptable host, on the average, receives more eggs than a host of lower acceptability, under similar conditions.

Different species or varieties of host may differ in acceptability. Varieties of Brassica oleraceae usually are more acceptable than other host species (Dickson and Eckenrode 1975, Radcliffe and Chapman 1966a, Ives 1978). In some cases, the acceptabilities of different B. oleracea varieties differ (Harrison and Brubaker 1943, Ives 1978). However, the rank order of acceptability among different varieties is not consistent among studies. Furthermore,

Radcliffe and Chapman (1966a), using several cultivars of each variety, found that acceptability was more dependent upon the particular cultivar used than on variety. For example, several kale cultivars had low acceptabilities (relative to other B. oleracea varieties), while other kale cultivars were highly acceptable. In addition, results varied from year to year (Harrison and Brubaker 1943, Latheef and Irwin 1979a), from a greenhouse to a field situation (Dickson and Eckenrode 1975), and within a single growing season (Radcliffe and Chapman 1966b, Latheef and Irwin 1979a).

Jones (1977) found that both the probability of landing on a particular host and the probability of laying an egg after landing was influenced by the variety of host involved. Thus, differences in acceptability are the result of differences in both pre-alighting and post-alighting ovipositional behavior.

Red cabbages are reported to be less acceptable than green cabbages, presumably because of the color of their foliage (Opler and Krizek 1984). Results of several studies confirm this (Dickson and Eckenrode 1975, Radcliffe and Chapman 1966a, 1966b). Other results, however, refute this finding (Harrison and Brubaker 1943, Radcliffe and Chapman 1965, Latheef and Irwin 1979a). In any case, even when shown to be less acceptable than green cabbages, red cabbages still received more eggs than other species of

(green) hosts, such as mustard (Radcliffe and Chapman 1966a).

This lack of consistency in results has led some investigators to suggest that overall host acceptability may be determined more by intrinsic plant characteristics such as size, maturity, height, or amount of foliage than by the variety of host (Harrison and Brubaker 1943, Latheef and Irwin 1979a). Both size and age have been found to affect acceptability. Latheef and Irwin (1979a) found a significant positive correlation between plant diameter and the number of eggs received by cabbages. Ives (1978) found that bigger plants (size was measured as total leaf surface area), received more eggs than smaller plants of the same variety. Other measures of plant size such as height and diameter were not associated with acceptability. The influence of plant size on acceptability, however, was valid only for comparisons within a single host variety. For example, kale plants, although bigger than cabbages, received fewer eggs. This finding is in agreement with results from Radcliffe and Chapman (1966a) who, when using different varieties of hosts, found that total leaf surface area was not correlated with acceptability.

The effect of age on acceptability is inverse to that of size. Younger plants tend to receive more eggs than do older plants of the same size (Ives 1978, Latheef and Irwin 1979a).

Deterrents

Plant chemicals functioning as deterrents are believed to play a major role in the host specificity of many insect species (Jermy 1966). The most extensively studied have been those chemicals acting as feeding inhibitors (Munakata 1977). While less attention has been paid to chemicals inhibiting oviposition, some non-host plant extracts, when applied to host foliage, have been found to reduce the number of eggs laid by P. rapae and other Pieris species (Lundgren 1975, Rothschild and Schoonhoven 1977, Rothschild and Fairbairn 1980).

Certain plants, mostly aromatic herbs, have traditionally been considered to have the ability to deter insects when planted near crop plants. Several of these so-called companion plants, including tansy, rosemary, tomatoes, sage, nasturtium, catnip, and hyssop, are reported to repel cabbage butterflies (McKillip 1973, Hunter and Hines 1971). Studies investigating these claims have yielded contradictory results. Some report no difference in number of eggs laid on hosts growing in a monoculture and those intercropped with various other species (Latheef and Irwin 1979b, Cranshaw 1984, Root and Kareiva 1984). Others report a significant increase in the number of eggs laid on intercropped hosts (Maguire 1984b, Mathews et al. 1983, Latheef and Ortiz 1983a, 1983b). This has led to the suggestion that, instead of being repellent, some non-host

species are attractive to P. rapae females, presumably via their odor (Latheef and Ortiz 1983b).

Interpretation of these results is, however, complicated by the confounding factor of patch size. Contrary to the predictions of Root's (1973) resource concentration hypothesis, the number of P. rapae eggs laid per plant increases as patch size decreases (Maguire 1983, 1984a, Root and Kareiva 1984, Cromartie 1975). Intercropping other species with hosts, in effect, results in the creation of many small host patches. Therefore, the increase in the number of eggs laid per plant on intercropped hosts may be due to a reduction in patch size rather than to an alleged attractiveness of non-hosts (Root and Kareiva 1984). Some results, however, cannot be reconciled with this explanation. For example, Latheef and Irwin (1983a) found that more eggs were laid on collard plants surrounded by various herb species than on non-boardered controls. In addition, significantly different numbers of eggs were laid on collard surrounded by different species of herbs. For example, significantly more eggs were laid on collard bordered by wormwood than on collards bordered by santolina. The possibility still exists, therefore, that companion plants do affect the behavior of ovipositing P. rapae.

MATERIALS AND METHODS

Establishment and Maintenance of the Butterfly Culture

The *P. rapae* butterflies used as experimental animals in this study were confined to a 1.8 m x 1.8 m x 1.8 m field cage set up over wild second-year vegetation at the Collins Road Entomology Field Research Center MSU, E. Lansing, MI. The field cage served both to house butterflies and as a confined area in which to conduct experiments. Flowers and potted host plants inside of the cage provided food and ovipositional sites, respectively, for the caged butterflies.

Butterflies were placed in the field cage as adults and were left until they died (or, on rare occasions, escaped). To maintain the relatively high density of butterflies necessary for experiments, butterflies were added almost daily. A total of 1,119 adult butterflies was placed in the cage during the course of the study (163 were captured from wild populations, 956 were reared from eggs indoors). An average of nine individuals per day was added.

Approximately 76% of the individuals added to the cage were female. Shortly after the cage population was established, I observed that males persistently flew at and attempted to copulate with unreceptive females, thus interfering with their ovipositional behavior. Maintaining a 76:24 male to female ratio reduced male "harassment," while still ensuring fertilization of virgin females.

The cage was initially stocked with wild butterflies captured from the local area. On June 2, 3, and 4, 17 wild butterflies from the first (overwintering) generation were captured and placed in the cage. These butterflies laid eggs readily on host plants (reserve hosts) placed in the cage for that purpose.

These butterflies were among the last individuals to emerge from the overwintering generation. Shortly after this capture, wild P. rapae could not be located. The initial cage population died out. The egg-laden hosts were removed from the cage and taken indoors for rearing.

Wild, second-generation adults were first observed flying approximately June 20. Individuals were captured and used to restock the cage. Like their predecessors, these individuals laid readily on reserve hosts.

A total of 147 wild second-generation butterflies was captured and placed in the cage from June 20 to July 14. During this period adults emerged indoors from the eggs laid by butterflies of the overwintering generation and were added to the cage.

By July 15, with the emergence of adults from eggs laid by the second-generation adults, a continuous culture had been established. After this date only adults reared from larvae indoors were added to the cage. Butterflies added to the cage at the end of the study were two to four generations removed from their wild, captured ancestors.

To maintain the culture, egg-laden reserve hosts were removed from the cage every 3 to 5 days, replaced with clean plants, and taken indoors for rearing. Larvae were reared in two different indoor rearing areas. The first was a controlled environment rearing room. The temperature in the controlled rearing room was maintained at approximately 22 degrees C, with a 16L:8D light cycle. The second rearing area was a room where light and temperature were not controlled. Each group of reserve hosts consisted of six plants, four plants of which were taken to the controlled environment rearing room and two of which were taken to the non-controlled rearing area.

Caterpillars were reared in two different environments for two reasons. The first was the threat of disease, which if it were to occur could destroy a culture. If a disease outbreak had occurred, experiments could have been delayed for three to four weeks (the time it would take to establish a new continuous culture). Raising caterpillars in two separate locations minimized the risk of losing the entire culture to disease. The second reason for rearing caterpillars in two different environments was to increase genetic variability in the culture and reduce inbreeding. Eggs laid on reserve hosts which belonged to the same group (i.e. were present in the cage during the same time interval) were the progeny of a single group of parents. There was a greater chance that two butterflies reared from one group of reserve hosts were siblings than for two

individuals raised from eggs laid on reserve hosts present in the cage at different times. Because eggs from one group of reserve hosts were all laid during the same three to five day interval, the chances were good that larvae would pupate and emerge at about the same time if they were exposed to the same environmental conditions. Raising the eggs from one group of reserve hosts under different temperatures resulted in increased variation in developmental time. During periods of relatively high external temperatures, caterpillars raised in the non-controlled area pupated two to five days earlier than those raised in the controlled rearing room. Likewise, during periods of cool temperatures, pupation occurred two to seven days later than in the controlled rearing room. The net effect was a greater "mixing" of individuals raised from eggs laid on different groups of reserve hosts. Such a mixing is desirable in that it may minimize the effects of inbreeding common to laboratory cultures.

Plants fed to larvae were mostly from reserve host stock grown in the greenhouse. All available species and varieties of hosts (see p 38) were used. No attempt was made to keep the food plant species or variety constant during the larval period. Thus, an individual caterpillar may have fed on all varieties of reserve host during its larval life.

There were two reasons for providing caterpillars with different varieties of food plants. First, although the

idea is not well accepted, there is some evidence that the food plant species fed to larvae influences adult oviposition (Yamamoto et al. 1969). Hovanitz and Chang (1963) developed different "strains" of P. rapae, that showed a marked "preference" for the host species on which they had been raised as larvae. Whether these strains were produced by unintentional artificial selection or whether larval experience influenced ovipositional "preference" is irrelevant. The fact remains that differences in larval food resulted in strains of butterflies differing in ovipositional "preference." Such artificially induced "strains" could have biased the results of this experiment.

A second reason for feeding larvae a variety of host plants concerns variation in developmental time. Chew (1975) found that raising Pieris napi larvae on a variety of host plant species increased the variance of the time to pupation. If the same phenomenon exists in P. rapae, then the degree of "genetic mixing" explained earlier would be increased by feeding larvae different host varieties.

Most of the time, whole, rooted, living plants were used to feed larvae. Eggs laid on reserve hosts were allowed to hatch and the larvae allowed to feed until they had consumed a major portion of the reserve host. At this point, larvae were transferred to new plants by cutting pieces of the original plant and placing them directly on the new plants. Young larvae were not handled directly because of potential injury (Stone and Midwinter 1975).

Food plants were changed in this manner as often as necessary.

When caterpillars were nearly mature (2.5 to 4 cm long) they were transferred to individual pupation chambers. These were constructed as follows: pieces of host plant leaves were cut into small pieces and placed in the bottom or top halves of petri dishes (9 cm). A caterpillar was then lifted off its food plant with forceps and carefully placed on top of the cut leaves. Finally, a 0.24 l plastic cup was inverted over the leaves and larvae. Caterpillars fed on the leaves on the bottom of the dish until ready to pupate, at which time they climbed the sides of the inverted cup and pupated. After pupation, the original petri dish was replaced by a clean one.

Emergence generally occurred from 7 to 14 days after pupation. Pupation chambers were kept in dimly lit areas, because under low-light conditions the adults did not attempt to fly. For transfer of adults to the field cage, pupation chambers containing emerged adults were placed in the bottom of a plant tray which was covered with a second inverted plant tray. This arrangement kept the trays dark and thus prevented adult injury.

The Plants

With the exception of soybean, all potted plants used in this study were grown from seed. Standard commercial potting soil was used as the growing medium. Seeds were

sown in flats and allowed to germinate. Following germination, plants were placed under fluorescent lights. After reaching the one to three leaf stage, the seedlings were transplanted into 2.5 cm square plastic "six-pack" containers and transferred to a greenhouse. The temperature, humidity, and light conditions in the greenhouse varied with external weather conditions. No supplemental lighting was provided.

Plants were transplanted two more times before being used in the field cage: the first time to 8 cm round plastic pots, the second time to 15 cm round clay pots. Transplanting occurred when the plants were judged to have outgrown their containers. Plants were fertilized with 10-30-10 soluble fertilizer at each transplanting, and every two to three weeks between transplantings.

Both host and non-host plants were grown in this manner. Host plants were used as food for caterpillars, to collect eggs for the maintenance of the butterfly culture (reserve hosts), and as experimental plants (target plants). The following varieties of host were used: cabbage (tastie), broccoli (italian green sprouting), mustard (tendergreen), cauliflower (snowball), brussel sprouts (long island improved), and collards (georgia). To avoid large differences in size and age between host plants used at the beginning and end of the study, three separate plantings were made. Seeds were first sown on April 16, and these plants were used as target plants and reserve hosts from

June 29 to August 15. Plants were 74 to 120 days old during this interval. The second planting occurred on May 14. These plants were used in the field cage from August 15 to September 6. Plants were 93 to 114 days old during this interval. The third planting was made on June 11. These plants were used in the field cage between September 6 and October 17. The plants were between 87 and 128 days old during this interval.

Non-hosts were used as experimental target plants. The non-host species used included tansy, sage, romaine lettuce and soybean. Tansy (Tanacetum vulgare) seeds were sown on March 23, 30 and April 2 and used in the experiments as target plants between July 12 to October 17 (age: 111 to 208 days). It was necessary, especially later in the season, to modify the size of the tansy plants. Initially, the tansy plants were pruned by pinching off the tops. Later in the season cuttings of the original tansy plants were used, in lieu of whole plants.

Sage (Salvia officinalis) seeds were sown on March 30 and were used in experiments from July 21 to Aug 21. Plants were between 113 to 115 days old during this interval. Romaine Lettuce (Lactuca sativa) was sown on June 11 and was used in experiments from August 14 to September 22. The plants were between 64 and 103 days old during this time.

Soybean (Glycine max) plants were obtained from a field of plants sown approximately July 1. Plants were dug out of

the ground, placed, along with potting soil, into 15 cm clay pots, and used in experiments within one to three days after transplanting. Soybean plants were used in experiments from August 30 to September 22.

Field Cage

The field cage was intially set up on June 1, 1984 and remained up for the duration of the study, being taken down on November 4 1984. As mentioned previously, the field cage was set up over a field of wild, second year vegetation. The dominant vegetation in this field included: yellow rocket (Barbarea vulgaris), aster (Aster spp), cinquefoil (Potentilla spp), thistle (Circium spp), and various grasses.

Although the vegetation surrounding the cage was mowed once in late July, the wild vegetation inside the cage was, for the most part, left to grow naturally. To provide a more uniform vegetational coverage, white dutch clover (Trifolium repens) and annual rye grass (Lolium persicum) were sown in bare areas of the cage on July 7, 1984. During extended dry periods the wild vegetation inside of the cage was watered, both to prevent dessication of the wild plants and to increase the humidity of the cage, humidity being an important factor in survival of butterflies in outdoor cages (Crane and Fleming 1953). Consequently, the cage interior provided a semi-natural habitat for the butterflies.

The percent coverage for each wild plant species inside the cage was determined at the end of the study season (Table 1). The method used to determine percent coverage was a modification of the line-intercept sampling method (Brower and Zar 1977). Eight line transects were established at vegetation height. Two were made by connecting string to diagonal corners of the cage. The remaining six were made by connecting string from each reserve host position to the target plant. The transect length of each plant or clump of the same species was recorded. The sum of the transect lengths for a single plant species divided by the total transect lengths covering vegetation was taken as the percentage coverage for that species. This measure provides an estimate of the percentage of the total vegetation area composed of each species.

Six host plants (reserve hosts) were present in the cage amid the wild vegetation at all times. These hosts were kept in holes dug in the ground for that purpose (Figure 3). The positions of the 6 reserve hosts (i.e., the holes dug in the ground) are shown in Figure 3. The position of each reserve host was 12 cm from the side of the cage, 24.5 cm from the nearest cage corner, and 70 cm from the center of the target area (target plant). In addition, all reserve host positions were 59 cm from the neighboring positions (with the exception of positions 1 and 6 which were 93 cm apart).

Table 1. Percent coverage of wild plants growing in the field cage.

Plant	Percent Coverage
Grasses and Clovers	53.6
Dandelion (*Taraxacum officinale*)	20.5
Cut flowers in bottles	10.6
Cinquefoil (*Potentilla* spp)	7.5
Dock (*Rumex* spp)	3.8
Prickly lettuce (*Lactuca serriola*)	1.2
White cocklebur (*Lychnis alba*)	1.2
Alfalfa (*Medicago sativa*)	1.0
Yellow Toadflax (*Linaria vulgaris*)	0.7

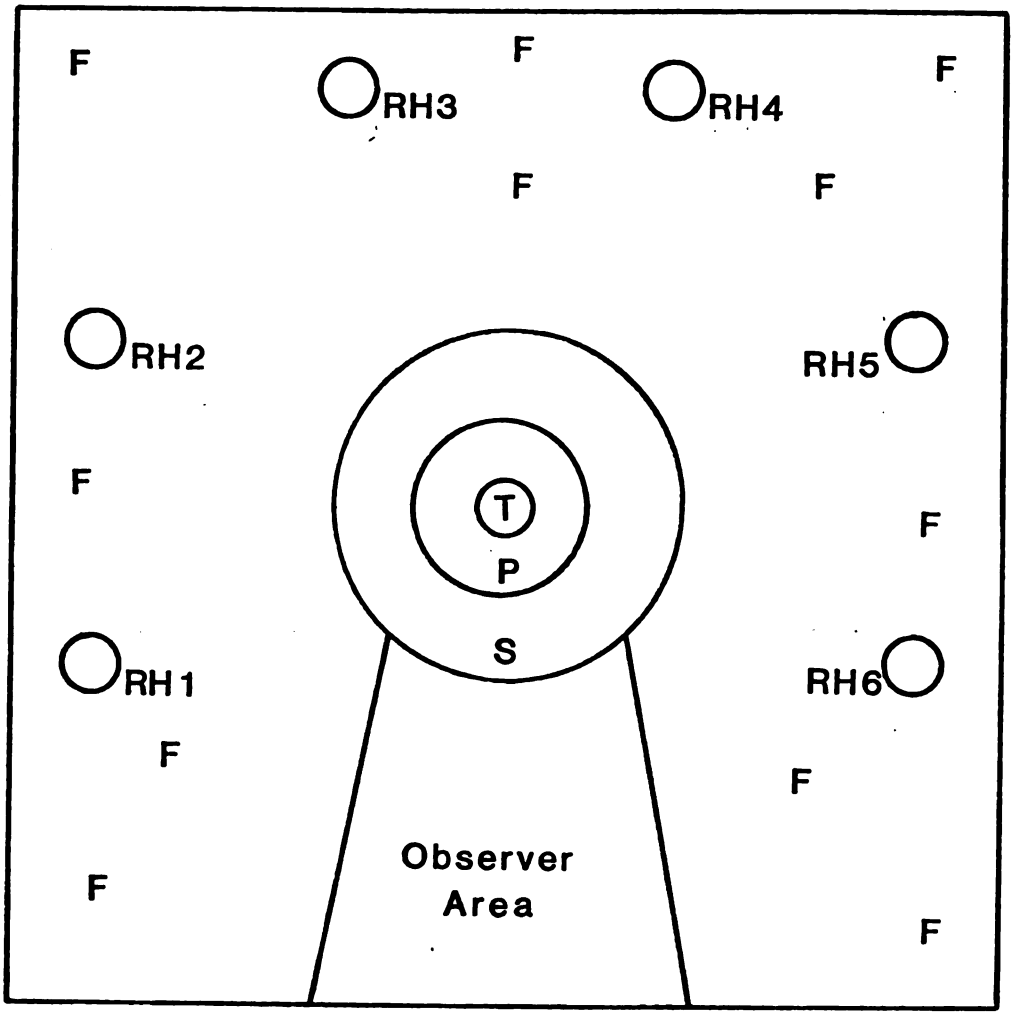


Figure 3. Map of the field cage interior. T=target plant, P=plant area, S=soil area, RH=reserve host, F=cut flowers.

Plants used as reserve hosts were randomly selected from greenhouse plants and randomly placed into one of the six positions. The day following their initial placement in the field cage, reserve hosts were removed, the number of eggs laid on each plant was counted, and the plants were placed into new randomly selected positions. Reserve hosts were left in the cage for three to five days before being removed and replaced by clean plants.

Three different sets of plants were used as reserve hosts. From June 29 to August 15, the six reserve hosts consisted of one plant each of mustard, broccoli, brussel sprouts, cabbage, cauliflower, and collards. Ten replicates of this set were used. During this time the plants were from 74 to 120 days old.

The second set of reserve hosts included one plant each of mustard, turnip, broccoli, brussel sprouts, cauliflower, and collards. Five replicates of this set were used from August 15 to September 6. Plants were from 93 to 114 days old.

The third set, which was comprised of two 87 to 127 day old plants each of collards, cauliflower, and broccoli, served as reserve hosts for the remainder of the study period--from September 6 to October 17.

In addition to reserve hosts, flowers and artificial nectar sources were placed amid the wild vegetation. Cut flowers were collected from nearby weedy fields and placed in plastic half liter soda pop bottles which were kept in

ho

th

wa

Ta

sp

cu

in

us

mo

art

flo

cm

flo

wir

arc

wit

gro

sol

fad

day

"fl

cage

obse

area

holes in the ground. Eleven buried bottles were located amid the wild vegetation (Figure 3). These were kept full of water and the flowers changed every three to five days.

The flower species used during the study are given in Table 2. Pieris rapae feeds on a great diversity of flower species (Opler and Krizek 1984). The species composition of cut flowers changed during the study, reflecting differences in blooming times. Early in the summer the most commonly used species were alfalfa and red clover. Goldenrod was the most commonly used flower during late summer and early fall.

To support the relatively high butterfly population, artifical nectar sources were provided in addition to cut flowers. Cubes of yellow cellulose sponge (approximately 3 cm^3) were placed on the ends of green wire (artificial flower stems). To prevent the sponge from slipping down the wire, and to delay dessication, aluminum foil was wrapped around the base of the sponge. The sponge was saturated with a 20% honey water solution and the wires placed in the ground among the wild vegetation. Extra honey water solution was added daily. When the sponges became soiled or faded, they were replaced (approximately every week to ten days). Butterflies were observed to feed readily on these "flowers."

The wild vegetation was cleared from the center of the cage to provide an area in which butterfly behavior could be observed and recorded during experiments. This area (target area) consisted of a cylinder of space 68 cm in diameter and

Tab

Cor

Rec

Alf

Bul

Sow

Gol

Ast

Wil

Cic

Cir

Yel

Tre

Table 2. Cut flowers used to feed *Pieris rapae* in the field cage.

Common Name	Scientific Name
Red Clover	*Trifolium pratense*
Alfalfa	*Medicago sativa*
Bull thistle	*Cirsium vulgare*
Sow thistle	*Sonchus oleraceus*
Goldenrod	*Solidago nemoralis*
Aster	*Aster pilosus*
Wild mustard	*Brassica* spp
Cichory	*Cichorium intybus*
Cinquefoil	*Potentilla recta*
Yellowrocket	*Barbarea vulgaris*
Trefoil	*Lotus corniculatus*

30 cm
area
point
buried
by 6
ground
the ta
with d
occupy
termed
cylind
(plant
buried
closes
pots t
space
space
soil s
string
respons
target
during
growing
vegetat

30 cm in height (Figure 3). The outer boundary of the target area was 92 cm from the cage corners, 54 cm, at the nearest point, from the sides, and was marked with a partially buried brown string. The height of the cylinder was marked by 6 green wires (artificial flower stems) placed in the ground extending upward 30 cm.

A 15 cm clay pot, buried in the center of the floor of the target area, was removed during experiments and replaced with different test species of potted plants. The plant occupying this central position during experiments was termed the target plant.

The target area was divided into two concentric cylinders: an outer (soil) space (16 cm wide) and an inner (plant) space (36 cm in diameter). Four 15 cm pots were buried in the ground at the base of the soil space, one pot closest to each of the four cage corners. The buried flower pots touched both the inner and outer boundaries of the soil space and served only to mark the boundaries of the soil space and the plant space. The inner boundary (between the soil space and the plant space) was also marked by a brown string partially buried in the ground.

To prevent butterflies from entering the target area in response to objects other than the target plant, the entire target area was maintained free of vegetation and debris during the experiments. In addition, any plant parts growing into the target area from the surrounding wild vegetation were removed.

The area inside the cage in which I sat and recorded behavioral sequences is termed the observer area. The observer area was located in the middle of the east side of the cage, next to the zipper (Figure 3, p 43). This area was also used to gain access to other parts of the cage, e.g., reserve hosts and flowers. To limit the damage done to wild vegetation, walking was confined to the observer area and the target area. As a result of being repeatedly walked and sat upon, the vegetation in the observer area died.

Sequence Description

During the interval of June 21 to July 11, preliminary observations of *P. rapae* behavior in the field cage were made. Because the target area inside the cage was not constructed until June 26, some of these observations were of butterflies flying around the wild vegetation. Particular notice was taken of behaviors exhibited in the vicinity of host plants.

Table 3 gives a list and description of the behavior patterns identified during the preliminary observation period. Behavior patterns were identified using the generalized criteria of Blurton-Jones (1968), i.e., they were fairly common, readily recognizable, and distinguishable.

An individual sequence was defined as consisting of the temporal order of specific behavior patterns performed by an

T

—
—

Na
to

—

So

Pl

Ai

Vi

Fl

Co

La

Lar

Cur

End

Flu

Flu

Flu

Cont

Table 3. Description of Pieris rapae behavior patterns recorded in the target area.

Name Given to Behavior	Symbol	Description
Soil	s	Flying into the soil space.
Plant	p	Flying into the plant space.
Air-to-Plant	Ap	Flying into the plant space directly, by descending from above.
Visit	V	An observable response to the target plant.
Flutter	f	Slowing of flight around an object.
Contact	c	Making tarsal contact with an object which lasts less than .5 seconds. The wings remain moving.
Land	l	Making tarsal contact with an object which lasts longer than .5 seconds.
Land-rest	lr	A land lasting more than five seconds during which no curling, drumming or wing movement occurs.
Curl	c	Curling the abdomen downward so that the abdomen tip touches the substrate.
Ending Behaviors:		
Flutter-host	fh	Fluttering around a host.
Flutter-vegetation	fv	Fluttering around a non-host.
Flutter-flower	ff	Fluttering around a flower.
Contact-host	ch	Contacting a host.

Ta

Na
to

Co

Co

La

La

La

La

Soc

Air

Beh
are

Flu

Con

Lan

Beh
are

Dru

Win

Beha
they

Prob

Table 3 cont.

Name Given to Behavior	Symbol	Description
Contact-vegetation	cv	Contacting a non-host.
Contact-flower	cf	Contacting a flower.
Land-host	lh	Landing on a host.
Land-vegetation	lv	Landing on a non-host.
Land-flower	lf	Landing on a flower.
Land-host-oviposit	lh-ov	Landing on a host and exhibiting behavior associated with oviposition, such as drumming or curling.
Social	S	Fly toward and into another butterfly.
Air	A	Fly upward in cage.
Behaviors Excluded from Hypothetical Sequence because they are Irrelevent to Oviposition:		
Flutter-soil	fs	Fluttering above bare ground.
Contact-soil	cs	Contacting bare ground.
Land-soil	ls	Landing on bare ground.
Behaviors Excluded from Hypothetical Sequence because they are Difficult to Observe Objectively:		
Drumming	dr	Scraping the foretarsi across the plant with a rapid, alternating motion.
Wings	w	Extended wing movement after landing.
Behaviors Excluded from the Hypothetical Sequence Because they are Rare During Oviposition:		
Proboscis Extension	prob	Extending the proboscis.

ind

dur

rec

the

(se

co

hy

cn

fo

in

be

pe

th

re

ty

se

ov

se

ob

an

se

a

se

individual butterfly while in the target area. Because the duration of the individual behaviors was shorter than the recording capabilities of any timing device available to me, the recorded sequences lack a time base.

A hypothetical sequence was constructed for analysis (see Figure 4). This consisted of a series of steps, each corresponding to an individual behavior pattern. The hypothetical sequence included all possible transitions from one type of behavior to another (certain transitions were forbidden by definition). Most of the data analysis involved comparing the transitional frequencies from a given behavior to all possible succeeding behaviors for sequences performed in response to different plant species.

Several identified behavior patterns were excluded from the hypothetical sequence (these are listed, along with the reason for their exclusion, at the end of Table 3). Three types of behaviors were eliminated from the hypothetical sequence: 1) behaviors judged to be irrelevent to oviposition, 2) behaviors not equally observable during all sequences; the position of the butterfly relative to the observer determined whether the behavior could be observed, and 3) behaviors rare during the ovipositional sequence.

The following is an explanation of the hypothetical sequence, including a list of all possible transitions, and a description of the behaviors involved. The hypothetical sequence is presented in Figure 4.

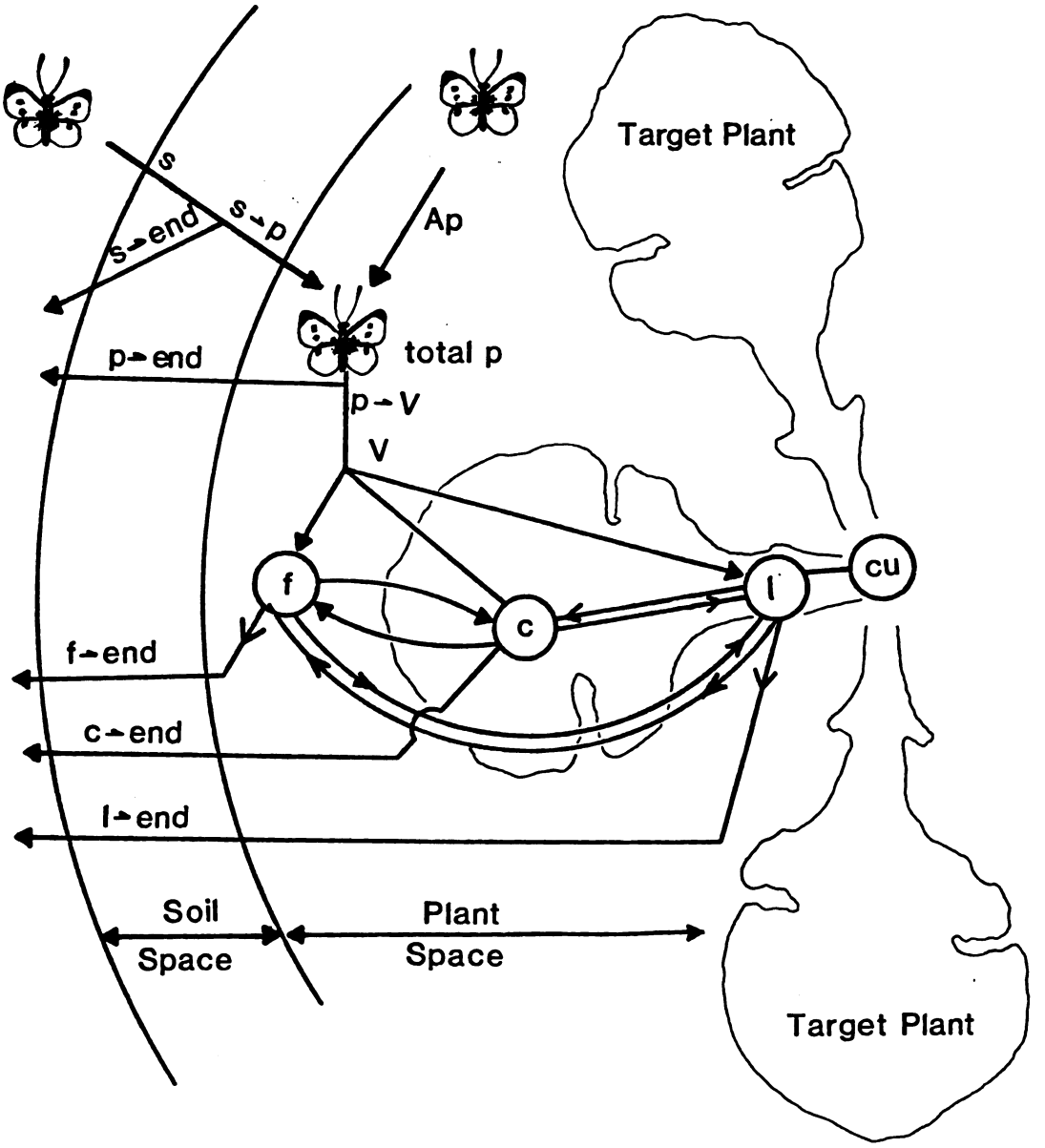


Figure 4A. Spatial representation of hypothetical sequence of behaviors of Pieris rapae in target area. S=soil space, p=plant space, A=enter target area from above, V=visit, f=flutter, l=land, c=contact, cu=curl, end=leave target area.

Figu

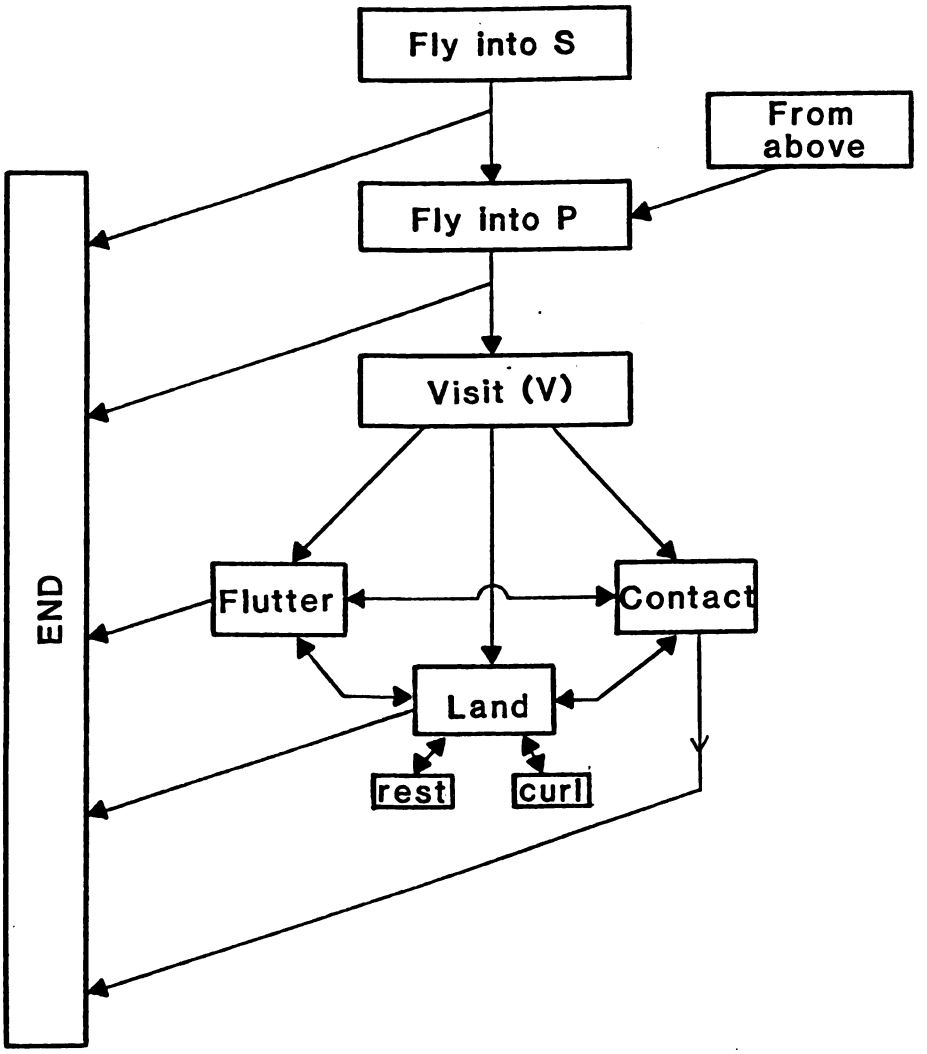


Figure 4B. Diagramatical representation of hypothetical sequence of behavior of Pieris rapae in target area. S= soil space, p=plant space, A=enter target area from above, V=visit, f=flutter, l=land, c=contact, cu=curl, end=leave target area.

Observation of a sequence began when a butterfly flew into the target area and ended when the butterfly either left the target area or curled (see below). Since the target area was divided into a soil space (s) and a plant space (p), butterflies could begin a sequence by flying more or less horizontally from the surrounding vegetation into the soil space (s) or descending more or less vertically from above (A) into the plant space directly (Ap).

Sequences initiated by butterflies which flew downwards and cut across the outer edge of the soil space while flying toward the wild vegetation were not recorded.

Once a butterfly entered the target area, it could end a sequence by flying out of the target area or by curling (see below). Flying out of the target area is designated as "end" and could occur at any step in the sequence.

The following is an explanation of the sequence steps, and the transitions between steps, that were possible after sequence initiation:

1. Soil space to plant space (s-->p). A butterfly flying into the soil space would ultimately either fly into the plant space (s-->p) or leave the target area (s-->end).

2. Plant space to Visit (p-->V). Once a butterfly had entered the plant space (p), either by flying into it from the soil space (s-->p) or by entering it directly (Ap), it would either leave the target area (p-->end) or visit the target plant (p-->V). A "visit" was a category of behaviors, not a single act. Included in the "visit"

category were the behaviors "flutter," "contact," and "land." These behaviors were lumped into one category because they constituted an observable response to the target plant. Behaviors included in the visit category are described below.

3. Flutter (f): This behavior consisted of an observed slowing of flight, and/or stopping in the vicinity of the target plant, i.e., the butterfly appeared to hover around the plant. A flutter could last between approximately .5 and 10 seconds. No tarsal contact occurred during fluttering, although butterflies sometimes appeared to make contact with the plant with their wings and/or antennae. Fluttering butterflies were often observed to fly into the underside of target plant leaves.

4. Contact (c): The butterfly made brief tarsal contact with the plant (usually with the leaves). Contact lasted for less than .5 seconds. A butterfly's wings remained moving during a contact.

5. Land (l): The butterfly landed on the plant surface (usually the leaves). Tarsal contact lasted for more than .5 seconds. Typically, some wing movement occurred after landing, but it usually did not last for the duration of the land.

The first behavior performed during a visit could be a land, a contact, or a flutter. Thereafter, a butterfly could end the visit by leaving the target area, or continue the visit by performing additional behaviors. For

bu
de
tr
tr
th
It
wa
pe
ar
co
ta
re
al

la
ob
a r

do
su

ta
co
Wa
Un
lo
ac

butterflies continuing the visit, the type of act performed depended, to some extent, on the preceding act. Some transitions were forbidden by definition. Possible transitions included: 1) a fluttering butterfly could leave the target area (f-->end), land (f-->l), or contact (f-->c). It could not immediately repeat the flutter since a flutter was defined as continuing until another behavior was performed, 2) contacting butterflies could leave the target area (c-->end), flutter (c-->f), land (c-->l), or repeat the contact(c-->c), and 3) Landing butterflies could leave the target area (l-->end), flutter (l-->f), contact (l-->c), or re-land (l-->l). In addition, landing butterflies could also rest (lr) or curl (lcu).

A rest (lr) was defined as a land on a plant which lasted longer than five seconds. The butterfly performed no obvious movement such as wing fluttering or drumming during a rest.

During a curl (cu) a butterfly curled her abdomen downward so that the ovipositor tip pointed toward the leaf surface.

After a butterfly had curled, it could either leave the target area or continue the visit (by performing a land, contact, or flutter). When recording sequences, an attempt was made to record the behavior of individual butterflies until they left the target area. However, during especially long sequences involving numerous curls, it was difficult to accurately record data. Therefore, a sequence was

con

cur

sam

in

spe

seg

sam

per

dat

emp

rep

spe

are

det

the

the

the

the

pla

was

unt

spe

considered complete when a butterfly performed the first curl.

Sampling Procedure

A day during which data were recorded is termed a sampling date. On each sampling date, behavioral sequences in response to from three to six different target plant species were recorded. The period of time during which the sequences toward one target plant were recorded is termed a sampling interval. No more than one sampling interval was performed for any target plant species on any one sampling date.

The procedure for recording data was as follows: the empty pot in the center of the target area was removed and replaced with a target plant randomly selected from the species to be sampled on that day. I sat in the observer area (Figure 3, p 43) of the cage and recorded a pre-determined number of sequences, as outlined below. After the required number of sequence observations had been taken, the target plant was removed and taken out of the cage. If the plant had received eggs during the sampling interval, these were counted, recorded, and gently brushed off of the plant. After at least three minutes, another target plant was placed in the target area. This procedure was repeated until observations had been made on all the target plant species to be tested on that particular sampling date.

of

int

rec

int

ani

per

and

of

im

al

in

en

se

ir

sa

ta

se

m

w

c

w

c

n

In addition to recording sequences and eggs, the times of day (at both the beginning and end of the sampling interval) and the total length of the sampling interval were recorded. Data were replicated by repeating sampling intervals on different days.

The sampling procedure was a combination of focal animal and sequence sampling (Lehner 1979). All behaviors performed by an individual butterfly between the initiation and termination of the sequence were recorded in the order of performance. In addition, any behaviors performed immediately after an individual left the target area were also recorded. While observation and recording of an individual sequence was occurring, all other individuals entering the target area were ignored. Sampling of sequences was randomized in the sense that the first individual to enter the target area after the previously sampled individual had left became the next subject.

An equal number of sequences was recorded for each target plant used on the same sampling date. The number of sequences sampled per target plant varied from day to day, mostly ranging from 30 to 39 sequences per day. This number was decided on prior to initiation of sampling. The criteria for deciding the number of sequences to be sampled were: the number of target plants to be used, the weather conditions, and an intuitive assessment of the responsiveness of the butterflies.

seque

influ

inter

elimi

seque

sampl

these

recor

sequ

equa

comp

pres

of

typ

acc

4)

fol

1)

mea

Th

ac

re

ad

In cases where the behavior of a butterfly during a sequence was ambiguous or where other factors appeared to influence its behavior (for example, a male seeming to interfere with a female's behavior) it was necessary to eliminate recorded sequences from the data. When problem sequences were identified while recording data, additional samples were taken to compensate. Occasionally, however, these problem sequences were identified only after data recording was complete. As a result, the total number of sequences taken on each plant in a comparison is not always equal (less than 1% of the sequences for any plant in any comparison were eliminated).

Experiments

A major objective of this study was to establish the presence or absence of discrimination occurring at each step of the ovipositional sequence between the following plant types: 1) hosts vs non-hosts, 2) hosts of different acceptabilities, 3) different species of non-hosts, and 4) repellent and non-repellent plants. To that end, the following plants were selected as target plants:
1) Broccoli. As a reserve host, broccoli received a greater mean number of eggs than other host species or variety. Therefore, as a target plant, broccoli was used as a highly acceptable host. 2) Mustard. As a reserve host, mustard received a lower mean number of eggs than broccoli. In addition, mustard, being a different species, is

morpho

was us

in out

repute

studie

ovipos

1983b)

tansy

larvae

repell

"repel

(and

these

plant

potti

a non

Addit

host

repel

Soybe

repel

simil

as a

8) Ra

potte

soil

host

morphologically different from broccoli. Therefore, mustard was used both as a less acceptable host and a host differing in outward appearance from broccoli. 3) Tansy. Tansy is a reputed "repellent" plant which has been used in several studies on the effects of companion plants on P. rapae oviposition (Mathews et al. 1984, Latheef and Ortiz 1983a, 1983b). In addition, Brewer and Ball (1981) found that tansy extract acts as a feeding deterrent to P. rapae larvae. Therefore, tansy was used in this study as a repellent plant. 4) Sage. Sage is another purported "repellent" plant (McKillip 1973) which is morphologically (and presumably, chemically) quite different from tansy. In these experiments it was used as as a second "repellent" plant species. 5) Pot. A 15 cm clay pot filled with potting soil was used as a control. 6) Lettuce. Lettuce is a non-host species not reported to be repellent to P. rapae. Additionally, lettuce is, to humans, visually similar to the host species, mustard. Lettuce was used here as a non-repellent, "host-like" non-host plant. 7) Soybean. Soybean is also a non-host species not reported to be repellent to P. rapae. Unlike lettuce, it is not visually similar to hosts. Therefore, in this study soybean was used as a non-repellent, non-host unlike a host in appearance. 8) Host-Repellent Combination: Broccoli-tansy . This was a potted broccoli plant with a tansy cutting placed in the soil next to it. Broccoli-tansy presumably possessed both host and repellent properties, and was used in the study to

assess the butterflies' responses toward a host-repellent combination.

In all, five experiments were done, each involving the same proceedure but using a different combination of target plants. The particular combination of target plant species used in each experiment is referred to as a comparison. Data were taken on the plants within a comparison on the same set of sampling dates.

The reason for conducting five separate experiments, rather than using all the target plants in a single experiment is as follows: First, there was wide day-to-day variation in the behavior of the butterflies, mostly in their level of activity and in their responsiveness toward target plants. Therefore, data for different target plant species could only be compared if it were taken on the same dates. Second, the activity and responsivness of the butterflies also varied during the course of a single day. Butterflies were usually most active between the hours of 11:00 and 15:00. Outside of this period, there was minimal activity in the cage. The length of the period of maximum responsiveness varied from day to day and changed over the course of the study. To minimize the possible effects of this natural "waxing and waning" of response on between treatment comparisons, only 3 to 6 different target plants could be used each day.

The plant comparisons are designated as Comparison I - Comparison V, and are given, along with the number of

samp

Tabl

the

a no

obse

The

ovip

comp

poin

diff

the

diff

inat

the

targ

diff

disc

duri

disc

ovip

whic

divi

secu

sampling intervals and the purpose of each comparison, in Table 4.

Methods of Analysis

The first objective of this study, that of determining the sequence of behaviors leading to P. rapae oviposition on a normal host, was accomplished during preliminary observations and has been described previously (see p 48). The second objective of determining where in the ovipositional sequence discrimination occurs, involved comparing the behavior exhibited by butterflies at the same point of ovipositional sequences performed in response to different plant types. If butterflies, at a given point in the ovipositional sequence, behaved significantly differently toward different plant types, then discrimination was said to exist at that point. For example, if the proportions of butterflies curling and leaving the target area (ending) after having landed on the target plant differed significantly between hosts and non-hosts, then discrimination between hosts and non-hosts was said to occur during the land.

An implicit assumption of this study was that discrimination could be shown at several points in the ovipositional sequence. The points in the sequence during which discrimination was to be assessed were determined by dividing the total sequence, first into a series of consecutive stages, and then dividing each stage into a series

Table 4: Plant Comparisons--The plant types between which discrimination was assessed in the 5 experiments.

Table 4: Plant Comparisons--The plant types between which discrimination was assessed in the 5 experiments.

PLANT COMPARISON NUMBER	PLANTS INCLUDED IN COMPARISON	NUMBER OF SAMPLING DATES	HOSTS VS NON-HOSTS	HOSTS OF DIFFERENT ACCEPT-ABILITIES	DIFFERENT SPECIES OF NON-HOST	REPELLENT VS NON-REPELLENT PLANTS	COMMENTS
I	Broccoli, Tansy	42	X				
II	Broccoli, Tansy, Sage "Pot"	18	X		X	X	The use of "pot" as a control allowed for determination of behaviors performed in response to the plant.
III	Broccoli Tansy, Lettuce, Mustard	19	X	X	X	X	
IV	Tansy Lettuce Soybean	10			X	X	
V	Broccoli, Tansy, Broccoli-Tansy	14	X			X	Differences between broccoli and the combined broccoli-tansy could be attributed to the effect of tansy.

of co

each

4 suc

divis

behav

both

part

ment

(Leh

the

spec

rece

anal

degr

duri

each

II).

obse

vis

sta

the

The

fir

of consecutive steps. Discrimination was determined for each stage and step of the ovipositional sequence.

The reporting of results of analysis are organized into 4 successive "levels"; each level involves finer subdivisions of the sequence (i.e., less "lumping" of behaviors). Analysis of data at different "levels" allowed both a more detailed assessment of discrimination during a particular sequence step as well as a more general assessment of discrimination relative to the total sequence (Lehner 1979).

In Level I, discrimination was assessed by comparing the mean number of eggs received by different target plant species (see Figure 5). Since the number of eggs a plant receives was the net result of behavioral sequences, the analysis of data at this level established the minimal degree of discrimination which must have been occurring during the sequence.

The sequence was then divided into a series of stages, each stage including a group of behaviors (Figure 5, Level II). The movement stage included behaviors up to the first observable response (visit). The response stage included visit behaviors up to the first land or contact. The alight stage included behaviors from the first tarsal contact with the plant (land or contact) up to the first abdominal curl. The curl stage included those behaviors performed after the first abdominal curl.


LEVEL
Mean Number of Eggs Received Per Sampling Interval
ANOVA

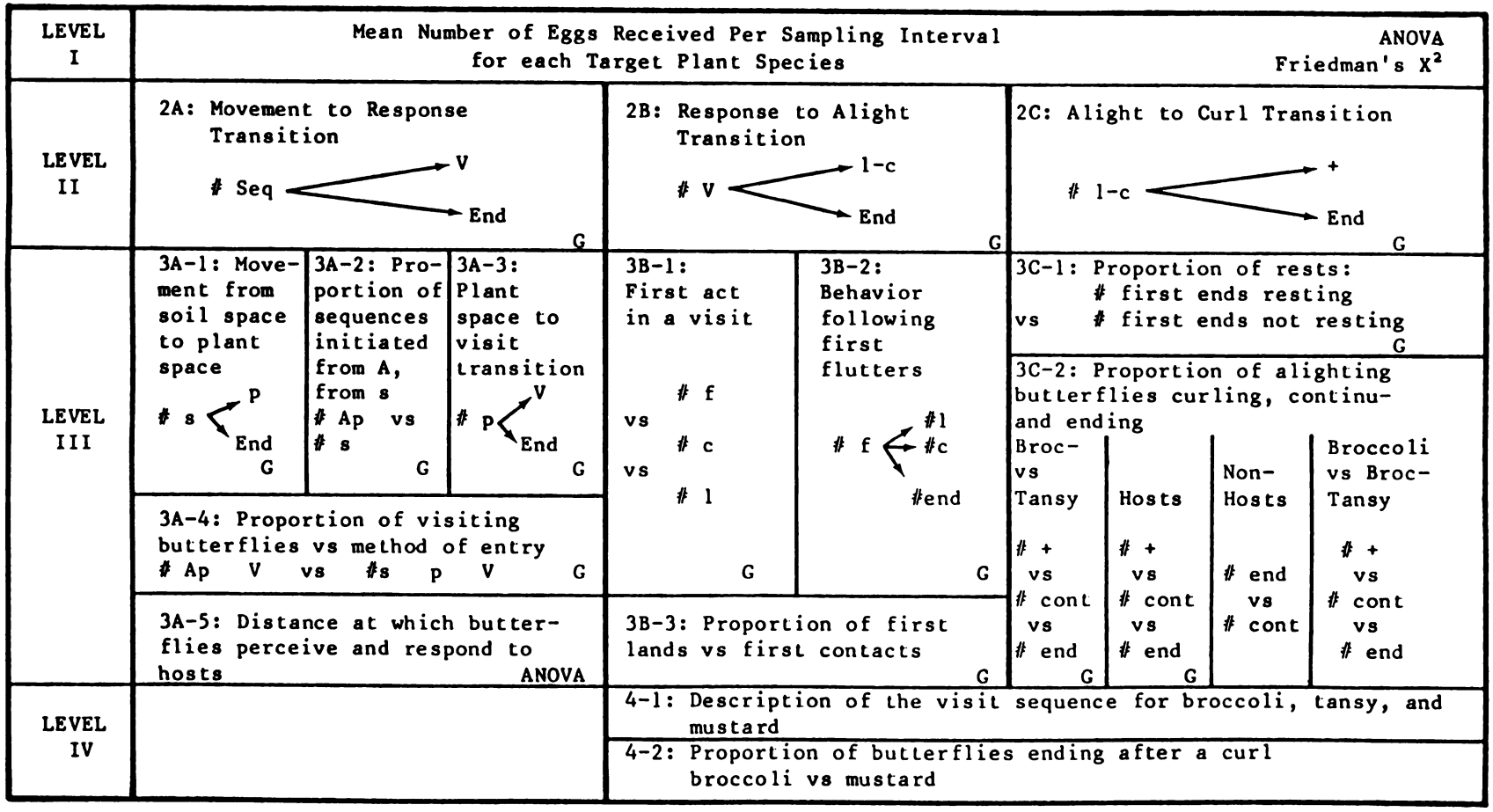


Figure 5. Organization of the analysis in first part of the results. Data is analyzed on successive Levels (I through IV). Each subdivision of a level represents one test. Statistical test used is given in lower right corner of box (G = G test, ANOVA = Analysis of Variance). Seq = sequence, V = visit, end = leave target area, l = land, c = contact, f = flutter, cu = curl, Ap = enter target area from above, s = soil space, p = plant space, cont = continue (no curl, but reland).

ovip

stag

ente

This

ovip

visi

the

beha

were

alig

butt

ovip

cons

was

beer

incl

butt

the

fron

terr

the

invo

stag

that

These stages appear to be natural subdivisions of the ovipositional sequence. Prior to the response (visit) stage, an observer could not be sure if butterflies were entering the target area in response to the target plant. This stage necessarily included many sequences irrelevant to oviposition. Once a butterfly exhibited a behavior in the visit category, an observer could be fairly confident that the butterfly was responding to the target plant. The behaviors in a visit, up to and including the first alight, were elicited by non-contact plant stimuli. After the first alight, contact stimuli also potentially also influenced the butterflies' subsequent response.

The abdominal curl was correlated highly enough with oviposition to be considered synonymous with the consummatory act of the ovipositional sequence. However, it was not possible to record consistently whether an egg had been deposited after curling, so egg deposition was not included as a behavior in the sequence. After curling, butterflies would either leave the target area or continue the visit.

In order to lay an egg, a butterfly had to progress from one stage to the next. However, a butterfly could also terminate the sequence after reaching any stage by leaving the target area (end). The analysis of data in this section involved comparing the proportion of butterflies at a given stage that advanced to the next stage, vs the proportion that ended the sequence, for sequences performed in response

to different plant types. The purpose of the analysis of Level II was to establish and compare the amount of discrimination occurring between different plant types at each sequence stage.

The stages identified in Level II, above, were then subdivided into their behavioral components. Each discrete behavior performed during the sequence is referred to as a step. Most of the analysis of data at this level (Level III) involved comparing the proportions of butterflies, that had performed a given behavior, that subsequently performed the possible following behaviors, for sequences performed in response to different plant types. The purpose of the analysis of Level III was to determine exactly which of the behaviors in the sequence involved discrimination.

Finally, the visit sequences to 3 different target plant species--broccoli, mustard and tansy--were analyzed as a Markov chain in Level IV. A summary of the tests performed on each of the 4 levels is shown in Figure 5.

It was hypothesized that discrimination would occur at the various sequence stages and steps because the nature of the plant stimuli perceived by the butterflies during any given stage or step would affect butterfly response. Specifically, it was hypothesized that:

1. Host plants possess host-specific stimuli that cause butterflies to respond to the plant. Therefore, it was predicted that a higher proportion of butterflies at any given stage or step of the ovipositional sequence would

respond to the plant (and thus continue the sequence) for sequences performed in response to hosts than for sequences performed in response to non-hosts.

2. Host plants differ quantitatively and/or qualitatively in host-specific stimuli perceived by butterflies. These differences in stimuli result in differences in the degree of response exhibited by butterflies which, in turn, result in differences in acceptability. Therefore, it was predicted that a higher proportion of butterflies at any given step or stage in the ovipositional sequence would respond to a host of higher acceptability (broccoli) than to a host of lesser acceptability (mustard).

3. General plant stimuli (i.e., stimuli that are not host-specific) affect the responses of butterflies. Lettuce is somewhat visually similar (to humans) to the host mustard. Visually perceived aspects of plants influence the degree of response exhibited toward plants. Therefore, it was predicted that the proportion of butterflies at any given step or stage in the sequence responding to the plant would be higher for sequences performed in response to lettuce than for sequences performed in response to other non-host species.

4. Tansy and sage generate repellent plant stimuli that butterflies are able to perceive and which deter response to the plant. Therefore, it was predicted that a lower proportion of butterflies at any given step or stage of the sequence would respond to tansy than to other

non-host species. In addition, it was predicted that, as the result of the presence of tansy, a lower proportion of butterflies would respond to broccoli-tansy than to broccoli alone.

Hypotheses and predictions concerning transitions between specific stages and steps are given in Table 5.

The final objective of this study was to compare the relative degree of discrimination occurring: 1) between hosts and non-hosts during different steps and stages of the ovipositional sequence, and 2) among different plant types during the same sequence step or stage. Assessing the relative degree of discrimination between hosts and non-hosts at different stages and steps was accomplished by calculating and comparing the normalized transmission for each stage and step of the ovipositional sequence. To determine the relative degree of discrimination occurring among different plant types during the same sequence stage or step, an index, the percent relative discrimination, was developed. The percent relative discrimination was calculated and compared for: hosts vs non-hosts, hosts of different acceptabilities, and different species of non-hosts, for each of the stages and steps in the ovipositonal sequence.

Table 5: Hypotheses and predictions tested in determining where in the ovipositional sequence discrimination occurs.

Table 5: Hypotheses and predictions tested in determining where in the ovipositional sequence discrimination occurs.

LEVEL II: TRANSITIONS BETWEEN SUCCESSIVE STAGES.

SECTION	TRANSITION	HYPOTHESIS	PREDICTIONS
2A	Seq --> V/end (Butterflies entering the target area will visit the target plant or leave the target area)	Plant stimuli perceived by butterflies while they are short distances from a plant will determine whether they will visit the plant.	A higher proportion of butterflies entering the target area will visit: A. Hosts rather than non-hosts. B. Lettuce than other non-host species. C. Broccoli than mustard. A lower proportion of butterflies entering the target area will visit: D. Tansy and sage than other non-host species. E. Broccoli-tansy than broccoli.
2B	V --> l-c/end (Butterflies visiting the target plant will land on or contact the plant or leave the target area)	Plant stimuli perceived by visiting butterflies will determine whether they will respond by alighting.	A higher proportion of visiting butterflies will land on or contact: A. Hosts than non-hosts. B. Broccoli than mustard. C. Lettuce than other non-host species. A lower proportion of visiting butterflies will land on or contact: D. Tansy and sage than other non-host species. E. Broccoli-tansy than broccoli.

Table 5 cont.

Table 5 cont.

SECTION	TRANSITION	HYPOTHESIS	PREDICTIONS
2C	1-c -->cu/end (Alighting butterflies will curl or leave the target area)	Host-specific stimuli (contact chemicals) perceived by butterflies after alighting are the releasers of the curl response.	A higher proportion of visiting butterflies will curl on: A. Hosts than non-hosts. B. Broccoli than mustard. No difference in the proportion of alighting butterflies that curled will be found among different species of non-hosts.
LEVEL III: TRANSITIONS BETWEEN SUCCESSIVE STEPS.			
3A-1	s -->p/end (Butterflies entering the soil space or leave the target area)	Plant stimuli, perceived while butterflies are at least short distances from plants influence whether butterflies will respond by approaching.	A higher proportion of butterflies flying into the soil space will subsequently fly into the plant space in response to: A. Hosts than non-hosts. B. Broccoli than mustard. C. Lettuce than other non-host species. A lower proportion of butterflies flying into the soil space will subsequently fly into the plant space in response to: D. Tansy and sage than other non-host species. E. Broccoli-tansy than broccoli.

Table 5 cont.

SECTION	TRANSITION	HYPOTHESIS	PREDICTIONS
3A-2	p --> V/end (Butterflies entering the plant space will visit the plant or leave the target area)	Plant stimuli will influence whether butterflies will visit the plant.	A higher proportion of butterflies in the plant space will visit: A. Hosts than non-hosts. B. Broccoli than mustard. C. Lettuce than other non-host species. A lower proportion of butterflies in the plant space will visit: D. Tansy and sage than other non-host species. E. Broccoli-tansy than broccoli.
3B-1	V --> f/c/l (Butterflies visiting a plant will flutter, contact, or land as their first act in a visit)	Plant stimuli, perceived by butterflies while they are approaching a plant, will influence the first act in a visit.	A higher proportion of butterflies will land as their first act in a visit and a correspondingly lower proportion will flutter or contact in visits to: A. Hosts than non-hosts. B. Broccoli than mustard. C. Lettuce than other non-host species. A higher proportion of butterflies will flutter or contact as their first act in visits to: D. Tansy and sage than other non-host species. E. Broccoli-tansy than broccoli.

Table 5 cont.

SECTION	TRANSITION	HYPOTHESIS	PREDICTIONS
3B-2	f -->l/c/end (Butterflies fluttering as their first act in a visit will land, contact, or leave the target area)	Plant stimuli, perceived by fluttering butterflies, will influence whether a butterfly will alight on a plant.	A higher proportion of butterflies that flutter as their first act in a visit will subsequently alight (land or contact) on: A. Hosts than non-hosts. B. Broccoli than mustard. C. Lettuce than other non-host species. A lower proportion of butterflies that flutter as their first act in a visit will subsequently alight on: D. Tansy and sage than other non-host species. E. Broccoli-tansy than broccoli.
3C-1	l-c -->cu/cont./end (Butterflies, after any given alight will either curl, not curl but continue the visit by making additional lands or contacts, or leave the target area)	Host-specific contact stimuli perceived after alighting are the primary releasers of the curl response. The absence of host-specific contact stimuli induces an alighting butterfly to terminate the visit.	A higher proportion of butterflies will curl or continue after any given alight on: A. Hosts than non-hosts. B. Broccoli than mustard. C. Broccoli than broccoli-tansy. No difference in the proportion of butterflies that, on any given alight, curl, continue, or end, will be found among different species of non-hosts.

RESULTS AND DISCUSSION

Establishing where Discrimination Occurs

Level I: Acceptability of Plants for Oviposition

Results: Broccoli

Eggs laid on broccoli were counted in 37 of the 42 sampling dates during which broccoli served as the target plant. A total of 364 eggs was laid. The mean number of eggs laid per sampling interval was 9.73 (+/- 1.59 S.E.).

The distribution of the number of eggs laid on broccoli per sampling interval is shown in Figure 6. This distribution fits a negative binomial distribution with a k of .836 (Chi-Square = .326, df=1). Since this is a distribution of eggs laid per sampling interval, it represents a distribution over time. A negative binomial distribution has also been shown to fit spatial distributions of the number of P. rapae eggs laid per plant in the wild (Harcourt 1961) and in a field cage (Kobayashi 1965, 1966). Bliss (1958) points out that there are two reasons for obtaining a contagious distribution such as a negative binomial: contagious interactions between individuals, or unequal exposure of the units to infestation (most likely due to environmental heterogeneity). Over time, many factors may lead to heterogeneity: weather, the number of butterflies in the cage, the age and sex composition of the population, changes in the wild

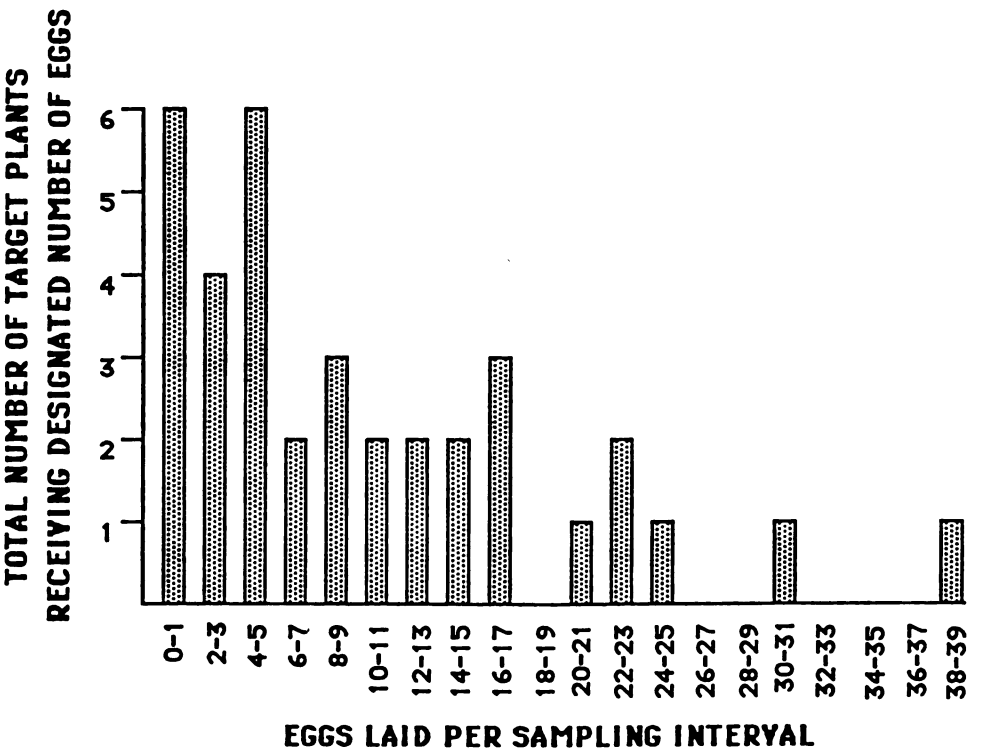


Figure 6. Distribution of the number of eggs laid per sampling interval on the broccoli target plant (comparison I).

vegetation in the cage over time, etc. Of these, weather, age (Gossard and Jones 1977), and parental density (Kobayashi 1965) are known to affect egg laying behavior and/or the spatial distribution of eggs by P. rapae. Kobayashi (1966) found that a negative binomial spatial distribution of eggs on cabbage plants in a field cage was produced by a random distribution of butterflies visiting plants compounded by a logarithmic distribution of the number of eggs laid per visit. Considering this, it seems likely that the negative binomial temporal distribution of eggs was produced by heterogeneity factors rather than an interaction of butterflies visiting plants, such as a visiting butterfly inducing other butterflies to visit. Still, it intuitively appeared to this observer that butterflies might be inducing each other to visit plants. To check for this possibility, a runs test (Schefler 1980) was performed using the broccoli data. Separate runs tests were performed for each sampling interval. Each butterfly entering the plant space was classified as (V) visiting or (N) not visiting the target plant. The runs test checks whether the number of runs obtained (a run, in this example, is defined as a list of consecutive V's or N's) is significantly different from that expected due to random occurrences of independent events. If the visits were contagiously distributed (i.e., butterflies inducing each other to visit) significantly fewer runs than expected would result.

In none of the sampling intervals were the number of runs significantly different from that expected due to random fluctuations. Thus, the idea that butterflies are inducing each other to visit is not supported.

Results: Comparisons

The mean number of eggs per sampling interval received by each target plant species is shown in Table 6. It is evident that P. rapae exhibits a great deal of discrimination between hosts and non-hosts. None of the non-host species received eggs. Non-hosts are clearly unacceptable for ovipositing P. rapae.

In comparison III, the host broccoli received a mean of 11.91 eggs per sampling interval (+/- S.E.=2.64) while mustard received a mean of 5.21 eggs per sampling interval (+/-S.E.=1.18). These means are significantly different ($F=6.01$, $P=.0247$, $df=1$). Therefore, broccoli is more acceptable as a target plant than mustard and some degree of discrimination occurs during the ovipositional sequence between these two host species.

In comparison V the broccoli-tansy combination target received a mean of 11.91 eggs per sampling interval (+/- S.E.=3.60) while the broccoli target received a mean of 12.07 eggs per sampling interval (+/- S.E.=2.28). Performance of a Friedman's Chi-Square test for randomized blocks resulted in a Chi-Square value of 1.23 which is not significantly different at the .05 level ($df=1$, $P=.267$). Thus, from these data, the broccoli-tansy combination target

Table 6. Mean number of eggs received per sampling interval by each plant species in the five comparisons.

Comparison	Plant Species	Mean Number of Eggs	
I	Broccoli	9.8	
	Tansy	0.0	
II	Broccoli	7.1	
	Tansy	0.0	
	Pot	0.0	
	Sage	0.0	
III	Broccoli	11.9	1
	Tansy	0.0	
	Mustard	5.2	1
	Lettuce	0.0	
IV	Tansy	0.0	
	Lettuce	0.0	
	Soybean	0.0	
V	Broccoli	12.1	2
	Tansy	0.0	
	Broccoli-Tansy	11.9	2

1. Data significantly different (P=.025) by a 2-way ANOVA (randomized block design with days as blocks). The log (x + 1) transform was used to stabilize the variance (Harcourt 1961).

2. Data not significantly different (P=.267) by a Friedman's Chi-Square test for randomized blocks (Sokal and Rholf 1969) with days as blocks.

does not appear to be less acceptable to ovipositing P. rapae than the broccoli target alone.

Level II: Transitions between Successive Stages of Oviposition

As discussed previously, on Level II the total ovipositional sequence was divided into four consecutive stages: movement, response, alight, and curl. In order to lay an egg a butterfly necessarily had to advance through each of these stages. However, a butterfly could also end the sequence at any stage by leaving the target area (end). Analysis of data on this level consisted of comparing the proportion of butterflies at each stage that advanced to the next stage vs the proportion that ended the sequence by leaving the target area, for sequences performed in response to different plant species.

The number of butterflies entering each stage of the ovipositional sequence and the transitional probabilities (the probability of entering the next stage given that the butterfly is in the previous stage) for the plants in each comparison are given in Appendix B.

For the movement to response transition (Seq-->V), a small proportion of butterflies flying into the target area visited the plant (Table 7). Percentages ranged from 25.5% (broccoli, comparison V) to 2.6% (pot, comparison II). Thus, it can be assumed that most butterflies entering the target area did so for reasons other than response to the target plant.

Table 7. Number of butterflies entering the target area ending (seq-->end) and visiting seq-->V) for different plant species.

Comparison	Plant Species	Number Ending	Number Visiting	Percent Visiting	
I	Broccoli	1137	260	18.6	a
	Tansy	1345	49	3.5	b
		***G=175.56, df=1, P <.001			
II	Broccoli	518	92	15.1	a
	Tansy	582	30	4.9	b
	Pot	594	16	2.6	b
	Sage	577	34	5.6	b
		***G=76.93, df=3, P <.001			
III	Broccoli	505	118	18.9	a
	Tansy	608	13	2.1	c
	Mustard	544	79	12.7	c
	Lettuce	599	23	3.7	c
		***G=145.59, df=3, P <.001			
IV	Tansy	324	7	2.1	a
	Lettuce	318	15	4.5	a
	Soybean	330	9	2.3	a
		G=3.28, df=2, P=.194			
V	Broccoli	345	118	25.5	a
	Tansy	447	13	2.8	b
	Broccoli-Tansy	350	110	23.9	a
		***G=129.45, df=2, P <.001			

a,b,c, = Data were analyzed by a G-test (Sokal and Rholf 1969). Percentages followed by the same letter are not significantly different at the .05 level by an STP test.
* = $P \leq .05$
** = $P \leq .01$
*** = $P \leq .001$

There are several reasons for butterflies to fly into the target area without visiting the plant: 1) a butterfly may respond to an object outside of the target area (i.e., a flower or another butterfly), and fly through the target area in approaching it, 2) a butterfly may not respond to any particular object, but fly through the target area as a result of random (non-directed) movement, 3) a butterfly may respond to the target plant by approaching, but not make an observable response, or make a response so brief and so subtle that the observer fails to notice.

Because many butterflies presumably entered the target area for reasons other than oviposition, it is a slight misnomer to state that all butterflies entering the target area are in the "movement" stage of oviposition. However, it was not possible to determine the motivation of butterflies prior to the response stage.

The "pot" target in comparison II received fewer visits than any plant species in that comparison. The proportion of butterflies visiting the pot was significantly different from the proportion of butterflies visiting the broccoli, tansy, and sage targets. This result supports the assumption presented earlier: that visit behaviors represent a behavioral response to the plant. In addition, the number of butterflies visiting the pot target is overinflated due to the wish to be conservative. Butterflies often "fluttered" above the bare soil in the target area and occasionally landed on the soil of the pot target. When an

actual plant served as the target it was relatively easy to distinguish these behaviors from the behaviors involved in a visit response (e.g., those directed toward the plant), and they were not recorded as a "visit". However, when the target was the pot, the plant itself was lacking as a point of reference. To correct for any bias toward obtaining expected results, I was intentionally biased in the opposite direction: All flutters above the soil in the plant space and all landings on the soil in the pot were recorded as visits. Thus, the actual unbiased number of visits to the pot target was most likely considerably lower.

The proportion of butterflies visiting hosts was significantly higher than the proportion visiting non-hosts in all comparisons involving both hosts and non-hosts. Host plants received between 3 and 9 times as many visits as non-hosts. Therefore, discrimination between hosts and non-hosts occurs during the movement stage of oviposition.

Broccoli (a highly acceptable host) received a significantly higher proportion of visits than did mustard (a host of lower acceptability) (comparison III). Thus, discrimination also occurs between hosts of different acceptabilities during the movement stage.

The proportion of butterflies visiting target non-hosts did not differ significantly for any of the non-host species in comparisons involving two or more non-hosts (comparisons II, III and IV). Although the trend obtained in comparison number IV is consistent with the hypothesis (repellent tansy

with the lowest proportion of visits, lettuce with the highest proportion), these proportions are not very different. Thus, these data do not support the idea that discrimination between non-hosts occurs during the movement stage of oviposition.

The presence of tansy near the broccoli host did not have the hypothesized "repellent" effect during the movement stage. The proportion of butterflies visiting the broccoli-tansy combination target, although lower, was not significantly different from the proportion visiting broccoli alone.

In summary, discrimination was observed between hosts and non-hosts and between hosts of different acceptabilities during the movement stage of oviposition. Thus, the following two ideas are supported by these data: 1) host-specific stimuli are responsible for eliciting visit behaviors, and 2) quantitative and qualitative variations in host-specific stimuli result in hosts of higher acceptability being recognized sooner and/or by a higher proportion of butterflies than hosts of lower acceptability.

Analysis of the response to alight stage (V-->1-c) revealed that, in most cases, a large proportion of the butterflies visiting a target plant ultimately landed on and/or contacted that plant (Table 8). The percentage of responding butterflies alighting ranged from 100% (lettuce, comparison III) to 33% (tansy, comparison II).

Table 8. Number of visiting butterflies alighting (V-->l-c) and ending (V-->end) for different plant species.

Comparison	Plant Species	Number Ending	Number Alighting	Percent Alighting	
I	Broccoli	38	222	85.4	a
	Tansy	27	22	44.9	b
		***G=31.52, df=1, P <.001			
II	Broccoli	19	73	79.4	a
	Tansy	20	10	33.3	b
	Sage	18	16	47.1	b
		***G=25.89, df=3, P <.001			
III	Broccoli	13	105	89.0	a
	Tansy	7	6	46.0	b
	Mustard	10	69	87.3	a
	Lettuce	0	23	100.0	a
		***G=19.13, df=3, P <.001			
IV	Tansy	2	5	71.4	a
	Lettuce	0	15	100.0	b
	Soybean	3	6	66.7	a
		*G=7.56, df=2, P=.0228			
V	Broccoli	13	105	90.0	a
	Tansy	5	8	61.5	b
	Broccoli-Tansy	21	89	80.9	a
		*G=6.93, df=2, P=.0312			

a,b,c = Data were analyzed by a G test (Sokal and Rholf 1969). Percentages followed by the same letter are not significantly different at the .05 level by an STP test.
* = $P \leq .05$
** = $P \leq .01$
*** = $P \leq .001$

In most comparisons, a much higher proportion of butterflies visiting hosts alighted than butterflies visiting non-hosts. For example: in comparison I, over 85% of the butterflies visiting broccoli alighted while less than 45% of visiting butterflies alighted on tansy. The sole exception to this trend involved visits to the lettuce target plant (comparison III). A higher proportion of visiting butterflies ultimately alighted on the non-host lettuce than on either host (broccoli or mustard) in that comparison (100%, 87% and 89% respectively). Thus, some degree of discrimination between hosts and non-hosts occurs during the response stage of the ovipositional sequence, although there are exceptions.

A slightly lower proportion of visiting butterflies alighted on mustard (a less acceptable host) than on broccoli (a more acceptable host). This difference though, was not statistically significant (P=.989). Therefore, the idea that discrimination between hosts of different acceptabilities occurs during the response stage of oviposition is not supported by these data.

The only significant difference among non-hosts in the proportion of visiting butterflies alighting is the aforementioned case of the lettuce target. In comparison IV, the proportion of visiting butterflies that alighted on lettuce was 100%. The proportions for tansy and soybean were 71% and 67% respectively. Thus, some degree of

discrimination between different non-host species appears to occur during the response stage of oviposition.

The data do not support the hypothesis that tansy has a repellent effect on visiting butterflies. In comparison IV, the proportion of visiting butterflies alighting on the tansy target was only slightly lower than the proportion alighting on the soybean target. In comparison V, the proportion of visiting butterflies alighting on the broccoli-tansy combination target was also only slightly lower than the proportion alighting on the broccoli target. In both cases, this difference was not statistically significant.

In summary, the analysis of the response to alight transition shows that discrimination occurs between hosts and non-hosts and among different species of non-host during the alight stage of the ovipositional sequence. Thus, the ideas that host-specific stimuli elicit alighting and that visual stimuli influence the nature of the visit are supported by these data.

The analysis of the alight to curl transition (l-c-->cu) showed that, in all comparisons, a large proportion of butterflies alighting on host plants curled their abdomens (Table 9). With a single exception, none of the butterflies alighting on non-hosts did so. Thus, strong discrimination occurs between hosts and non-hosts during the alight stage of the ovipositional sequence.

Table 9. Number of alighting butterflies curling (1-c-->cu) and ending (1-c-->end) for different plant species.

Comparison	Plant Species	Number Ending	Number Curling	Percent Curling	
I	Broccoli	31	191	86.0	a
	Tansy	22	0	0.0	b
		***G=66.11, df=1, P <.001			
II	Broccoli	13	60	82.2	a
	Tansy	10	0	0.0	b
	Sage	16	0	0.0	b
		***G=64.36, df=3, P <.001			
III	Broccoli	12	93	89.0	a
	Tansy	6	0	0.0	b
	Mustard	16	53	76.8	a
	Lettuce	22	1	4.4	b
		***G=81.54, df=3, P <.001			
IV	Tansy	5	0	0.0	a
	Lettuce	15	0	0.0	a
	Soybean	6	0	0.0	a
V	Broccoli	12	93	88.6	a
	Tansy	8	0	0.0	b
	Broccoli-Tansy	18	71	79.8	a
		***G=31.07, df=2, P <.001			

a,b,c = Data were analyzed by a G test (Sokal and Rholf 1969). Percentages followed by the same letter are not significantly different at the .05 level by an STP test.
* = $P \leq .05$
** = $P \leq .01$
*** = $P \leq .001$

In comparison III, 89% of the butterflies alighting on the broccoli target curled their abdomen while 76.8% of the butterflies alighting on mustard curled. Although the results conformed to the prediction (a lower proportion of alighting butterflies curling on a less acceptable host), the difference is not statistically significant (P=.244).

As expected, the proportion of alighting butterflies that curled did not differ for different species of target non-hosts. In almost all cases, butterflies alighting on non-hosts did not curl. The only exception involved lettuce (comparison III). One of the 23 individuals alighting on lettuce curled her abdomen (4%), but did not lay an egg. Therefore, the data support the idea that discrimination does not occur between different non-host species during the alight stage.

As expected, a lower proportion of butterflies alighting on the combined broccoli-tansy target curled their abdomen than those alighting on broccoli alone (80%, broccoli-tansy; 89%, broccoli). The difference, however, was not statistically significant. Therefore, these data do not support the idea that the presence of tansy has a significant repellent effect on alighting butterflies.

In summary, these results show that discrimination occurs only between hosts and non-hosts during the alight stage of oviposition. Thus, the idea that host-specific contact chemicals release the curl response is supported by these data.

Level III: Transitions between Successive Steps of Oviposition

On this level, the component behaviors involved in each of the stages examined in Level II are analyzed. Whereas the analysis of Level II established the presence or absence of discrimination at each stage, the present analysis determines precisely how this discrimination is manifested behaviorally.

IIIA: Movement to Response Transition

In the analysis of Level IIA (movement to response transition), discrimination was assessed by comparing the proportion of butterflies entering the target area that exhibited an observable response (visit) toward the target plant for different target plant species. In order to exhibit a response (visit) toward the target plant a butterfly flying into the target area had to either: 1) fly into the plant space directly via the air (i.e., descend from above) and visit the plant (Ap-->V), or 2) fly into the soil space, fly into the plant space, and then visit the plant (s-->p-->V). In this section these individual steps of the movement stage are examined.

The numbers of butterflies making each specific behavioral transition, and the transitional probabilities between behaviors are given in Appendix C. Approximately half of all butterflies flying into the soil space also flew into the plant space (Table 10). Percentages ranged from

Table 10. Number of butterflies entering the soil space that entered the plant space (s-->p) and that ended (s-->p) for different plant species.

Comparison	Plant Species	Number Ending	Number Entering Plant Space	Percent Entering Plant Space	
I	Broccoli	680	682	51.1	a
	Tansy	837	539	39.2	b
		***G=32.99,	df=1,	P <.001	
II	Broccoli	324	274	45.8	a
	Tansy	393	212	35.0	b
	Pot	369	239	39.3	ab
	Sage	382	218	36.3	b
		***G=17.34,	df=3,	P <.001	
III	Broccoli	298	315	51.4	a
	Tansy	362	252	40.1	b
	Mustard	323	289	47.2	a
	Lettuce	378	238	38.6	b
		***G=25.18,	df=3,	P <.001	
IV	Tansy	186	144	43.6	a
	Lettuce	193	136	41.3	a
	Soybean	178	148	45.4	a
		G=1.11,	df=2,	P=.574	
V	Broccoli	183	264	59.1	a
	Tansy	229	225	49.6	b
	Broccoli-Tansy	181	265	59.4	a
		**G=11.42,	df=2,	P=.0033	

a,b,c = Data were analyzed by a G test (Sokal and Rholf 1969). Percentages followed by the same letter are not significantly different at the .05 level by an STP test.
* = $P \leq .05$
** = $P \leq .01$
*** = $P \leq .001$

59.4% (broccoli-tansy, comparison V) to 35.0 % (tansy, comparison II).

Without exception, the percentage of butterflies flying into the plant space was higher for target hosts than for target non-hosts. In most cases, these differences were significant. Therefore, these results support the idea that host-specific stimuli stimulate the approach to plants.

As expected, a lower proportion of butterflies flew from the soil space to the plant space when the less acceptable host, mustard, was the target plant rather than the more acceptable host, broccoli (comparison III). This difference, however, was not statistically significant (P=.546).

Contrary to expectation, the proportion of butterflies flying from the soil space to the plant space was lower for lettuce than for other non-host species in comparisons III and IV. Therefore, these data do not support the idea that general plant appearance influences the approach to the plant.

The proportion of butterflies flying into the plant space from the soil space was lower for the tansy and sage targets than for the pot target in comparison II. Initially, this may appear to confirm the repellent effect of tansy and sage. However, butterflies may have simply perceived tansy and sage as a obstacle in their flight path to be avoided. The target plant took up considerable area within the plant space. This fact alone may explain the

lower proportion of butterflies flying into the plant space with the tansy and sage targets as compared with the pot target. There were no non-repellent non-hosts in comparison II to test this idea.

In agreement with the idea that the lower proportion of butterflies flying from the soil space to the plant space is not due to a repellent effect of tansy or sage, the proportion was not lower for the tansy target than for other non-host targets in comparisons III and IV. In fact, this proportion was higher for tansy than for lettuce. In addition, the proportion of butterflies flying from the soil space to the plant space was not different for the broccoli-tansy combination target than for the broccoli target alone (59.1% and 59.4% respectively).

The proportion of butterflies in the plant space that visited the plant (p-->V) ranged from 42.1% (broccoli, comparison V) to 7% (pot, comparison II) (Table 11). The trends are the same as those discussed in the analysis of the response to alight transition (Level II). The advantage to the present analysis is that certain differences (in the proportion of butterflies visiting) between plant species within a comparison may become significant due to the elimination of superfluous data (i.e., many of the butterflies entering the target area for reasons other than response to the target plant left the target area without entering the plant space and are, thus, not considered in this analysis).

Table 11. Number of butterflies entering the plant space visiting (p-->V) and ending (p-->end) for different plant species.

Comparison	Plant Species	Number Ending	Number Visiting	Percent Visiting	
I	Broccoli	457	260	36.3	a
	Tansy	508	49	8.8	b
		***G=140.66, df=1, P <.001			
II	Broccoli	194	92	32.2	c
	Tansy	189	30	13.7	ab
	Pot	225	16	7.3	a
	Sage	195	34	14.8	b
		***G=140.66, df=3, P <.001			
III	Broccoli	207	118	36.3	a
	Tansy	246	13	5.0	b
	Mustard	221	79	26.3	a
	Lettuce	221	23	9.4	b
		***G=121.83 df=3, P <.001			
IV	Tansy	138	7	4.8	a
	Lettuce	125	15	10.7	a
	Soybean	143	9	5.9	a
		G=4.03, df=2, P=.258			
V	Broccoli	162	118	42.1	a
	Tansy	218	13	5.6	b
	Broccoli-Tansy	169	110	39.4	a
		***G=218.58, df=2, P <.001			

a,b,c = Data were analyzed by a G test (Sokal and Rholf 1969). Percentages followed by the same letter are not significantly different at the .05 level by an STP test.
* = $P \leq .05$
** = $P \leq .01$
*** = $P \leq .001$

In comparison II the proportion of butterflies entering the plant space that visited the plant is significantly lower for the "pot" than for the other targets. This supports the idea presented earlier; that visit behaviors represent a response to the plant itself.

However, in comparison III the difference in the proportion of butterflies visiting broccoli and mustard falls short of significance at the .05 level ($G=7.23$, $df=3$, $P=.065$).

In summary, analysis of the soil space to plant space (s-->p) and plant space to visit (p-->V) transitions support the idea that butterflies are able to perceive host-specific stimuli while at least short distances from the plant and respond to these stimuli by approaching and by visiting. The data do not support the idea that visually perceived characteristics that lettuces shares with the host mustard play a role in the approach or visit response. Neither do the data support the idea that tansy and sage possess repellent stimuli that deter the approach and visit response.

Proportion of butterflies entering the target area from above vs the proportion entering via the soil space (Ap vs s). As explained previously, there were two ways for butterflies to enter the target area and, thus, initiate sequences: by flying into the soil space (s) or by flying into the plant space directly (Ap). It was predicted that the proportion of butterflies entering the target area via

the air would be higher for host targets than for non-host targets. This prediction rests on two ideas: 1) butterflies entering the target area from above (Ap) were less likely to be entering for reasons other than response to the target plant, than those entering via the soil space (see next section), and 2) butterflies are able to perceive and respond to plant stimuli from outside of the target area. If these ideas are true, then the effect of a host in the target area would be to draw in responsive butterflies from above. The presence of a host in the target area would also draw responsive butterflies into the soil space. However, since the number entering the target area via the soil space for reasons other than oviposition would not change and because the number of sequences observed per day was fixed, a higher proportion of butterflies would be entering the target area from above (Ap increases more than s because a higher proportion of the latter group of butterflies are responding to the plant).

It was found that a very small proportion of butterflies entering the target area entered the plant space directly (Ap) (Table 12). Percentages ranged from .3% (tansy, comparison IV; pot, comparison II) to 3.5% (broccoli, comparison V). In all comparisons, the proportion of butterflies entering the target space directly from above (Ap) was higher for hosts than for non-hosts. However, in only two of the comparisons (comparisons I and II) were these proportions shown to be significantly

Table 12. Number of butterflies entering the target space via the soil space (s) and from above (Ap) for different plant species.

Comparison	Plant Species	Number Via Soil Space	Number From Above	Percent From Above	
I	Broccoli	1362	35	2.5	a
	Tansy	1376	18	1.3	b
		*G=5.62, df=1, P=.0178			
II	Broccoli	598	12	2.0	a
	Tansy	605	7	1.1	ab
	Pot	608	2	0.3	b
	Sage	600	11	1.8	ab
		*G=9.42, df=3, P=.0242			
III	Broccoli	613	10	1.6	a
	Tansy	614	7	1.1	a
	Mustard	612	11	1.8	a
	Lettuce	616	6	1.0	a
		G=2.03, df=3, P=.566			
IV	Tansy	330	1	0.3	a
	Lettuce	329	4	1.2	a
	Soybean	326	4	1.2	a
		G=2.42, df=2, P=.298			
V	Broccoli	447	16	3.5	a
	Tansy	454	6	1.3	a
	Broccoli-Tansy	446	14	3.0	a
		G=5.27, df=2, P=.0717			

a,b,c = Data were analyzed by a G test (Sokal and Rholf 1969). Percentages followed by the same letter are not significantly different at the .05 level by an STP test.
* = $P \leq .05$
** = $P \leq .01$
*** = $P \leq .001$

different. This may be, in part, due to the low numbers of butterflies entering the plant area directly (Ap).

As expected, the proportion of butterflies entering the target area from above was less for the "pot" target than for any target plant species in comparison II. This agrees with the idea that a certain proportion of butterflies entered the target area in response to the target plant. The proportion entering from above was significantly different between pot and broccoli. There is no significant difference among the proportions entering from above between pot, sage, and tansy. Therefore, these data support the ideas that: 1) host-specific stimuli elicit the approach to the plant, 2) butterflies are able to perceive these host-specific stimuli from outside the target area, and 3) butterflies entering the target area from above are less likely to be entering for reasons other than in response to the target plant than butterflies entering the target area via the soil space.

Proportion of visiting butterflies vs method of entry. The idea that a higher proportion of butterflies entering the plant space from above (Ap) do so in response to the target plant than butterflies entering the target area via the outer (soil) space (s) was further tested by comparing the proportion of butterflies visiting the plant for these two methods of entry. It was predicted that a higher proportion of those butterflies entering the plant space from above would visit the plant (Ap-->V) than those

entering the plant space via the soil space (s-->p-->V). A significantly higher proportion of butterflies entering the target area from above visited the broccoli target (comparison I) (Figure 7). Although the proportion of butterflies entering from above that visited was higher for both the tansy and sage targets (comparison II), the differences were not significant. It is, perhaps, not surprising that the proportion of butterflies visiting from above was not significantly greater for the non-host plant species. As discussed previously, there is good evidence that butterflies perceive host-specific plant stimuli and respond preferentially to host plants while they are at least short distances from plants. A non-host plant, lacking host-specific releasers, would not have the effect, expected with hosts, i.e., of "drawing" in responsive butterflies from above.

The surprise result was the mustard target. A higher proportion of butterflies visited mustard from the soil space than from above (35% from soil space, 18% from above). The number of butterflies entering the plant space from above was low, (11 sequences), and this may in part account for the unexpected result. However, it may be that mustard, being a less acceptable host, is not recognized from the same distances as is broccoli.

In summary, the data support the idea that butterflies entering the plant space from above are more likely to visit than those entering from the soil space for at least highly

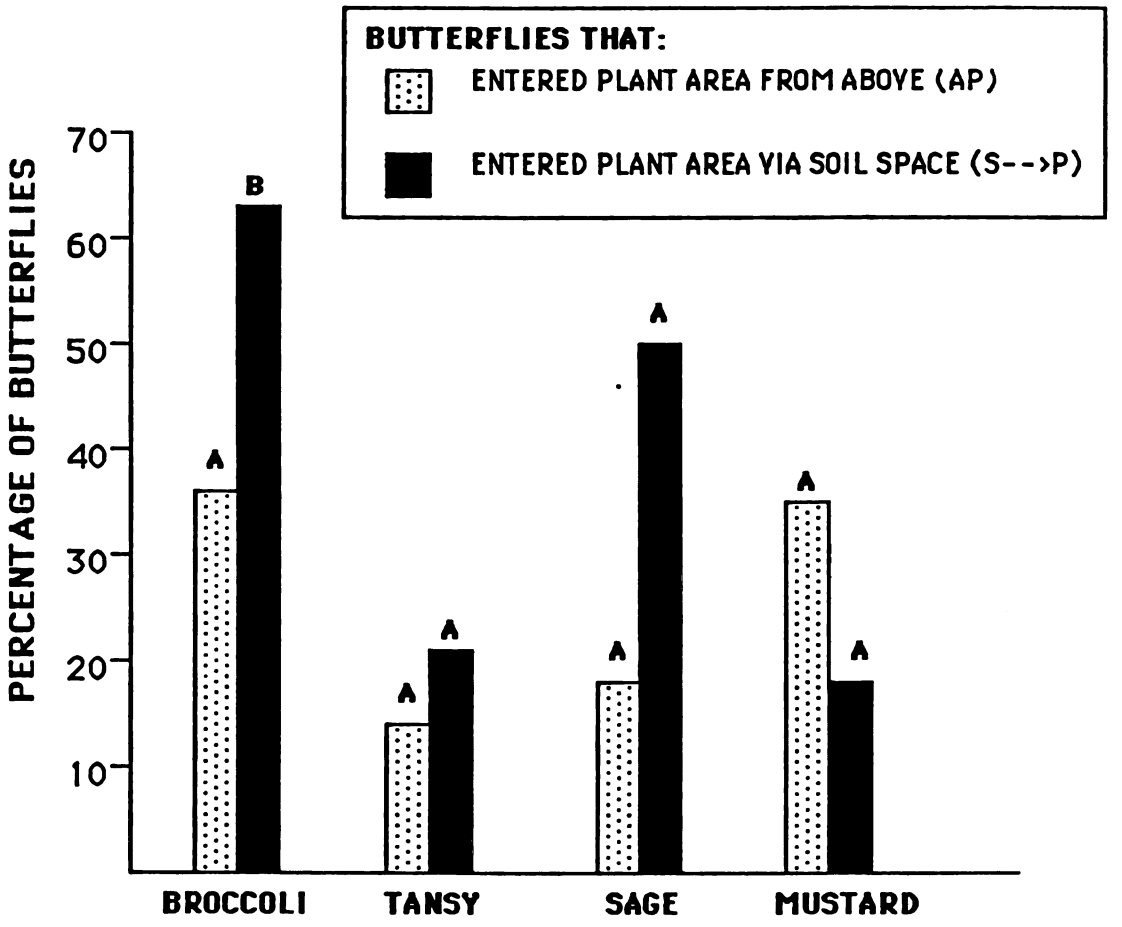


Figure 7. Percentage of butterflies entering the plant area from above (Ap) and via the soil space (s-->p) that visited broccoli, tansy, sage and mustard. Percentages shown under the same letter are not significantly different at the .05 level.

acceptable target plants (broccoli). This result suggests that butterflies are able to recognize and respond to some host species from short distances.

Distance from which butterflies perceive and respond to hosts. Analyses in previous sections have suggested that butterflies are capable of perceiving host-specific plant stimuli while some distance from hosts and that they respond to these stimuli by approaching the plant. With these data there is no way of determining the exact distance from which host-specific stimuli are perceived. However, it is possible to determine indirectly whether most perception and response takes place at distances shorter than, or longer than, the soil space/plant space boundary. Butterflies entering the soil space can be divided into three groups according to their ultimate fate: 1) those that leave the soil area without entering the plant space (s-->end), 2) those that enter the plant space and leave the target area without visiting the plant (s-->p-->end), and 3) those that visit the target plant (s-->p-->V).

Since the total number of sequences observed each day was equal for each target plant species, if one assumes that a greater proportion of butterflies respond to (visit) broccoli than tansy (established previously), then the proportion of butterflies in group 3 (s-->p-->V) was greater for broccoli than for tansy, and the proportion of group 1 and/or group 2 MUST be less for broccoli than for tansy.

If the majority of butterflies first perceive and respond to the plant at distances greater than the soil space/plant space border, then the proportion of group 1 (s-->end) will be lower for broccoli than for tansy. If butterflies perceive and respond to plants only after entering the inner space, then the proportion of group 2 (s-->p-->end) will be lower for broccoli than for tansy. If perception and response occurs at both distances, then the proportions in both groups 1 and 2 will be lower for broccoli than for tansy.

Results discussed previously (see p 94) suggest that most recognition of hosts occurs prior to butterflies crossing the soil space/plant space border. This hypothesis was tested in this section. Two 2-way ANOVA's were performed on the percentage of butterflies entering the target area each day that left the target area without entering the inner plant space (s-->end), and that entered the inner plant space, but left the target area without visiting the target plant (s-->p-->end), for broccoli and tansy in comparison I (randomized block design, days as blocks).

The mean percentage of butterflies that entered the soil space, but left the target area without entering the plant space (s-->end) was 49.3% for broccoli and 60.0% for tansy (Figure 8). The analysis of variance yielded a highly significant F value (F=2.97, df=41, P=.0003)

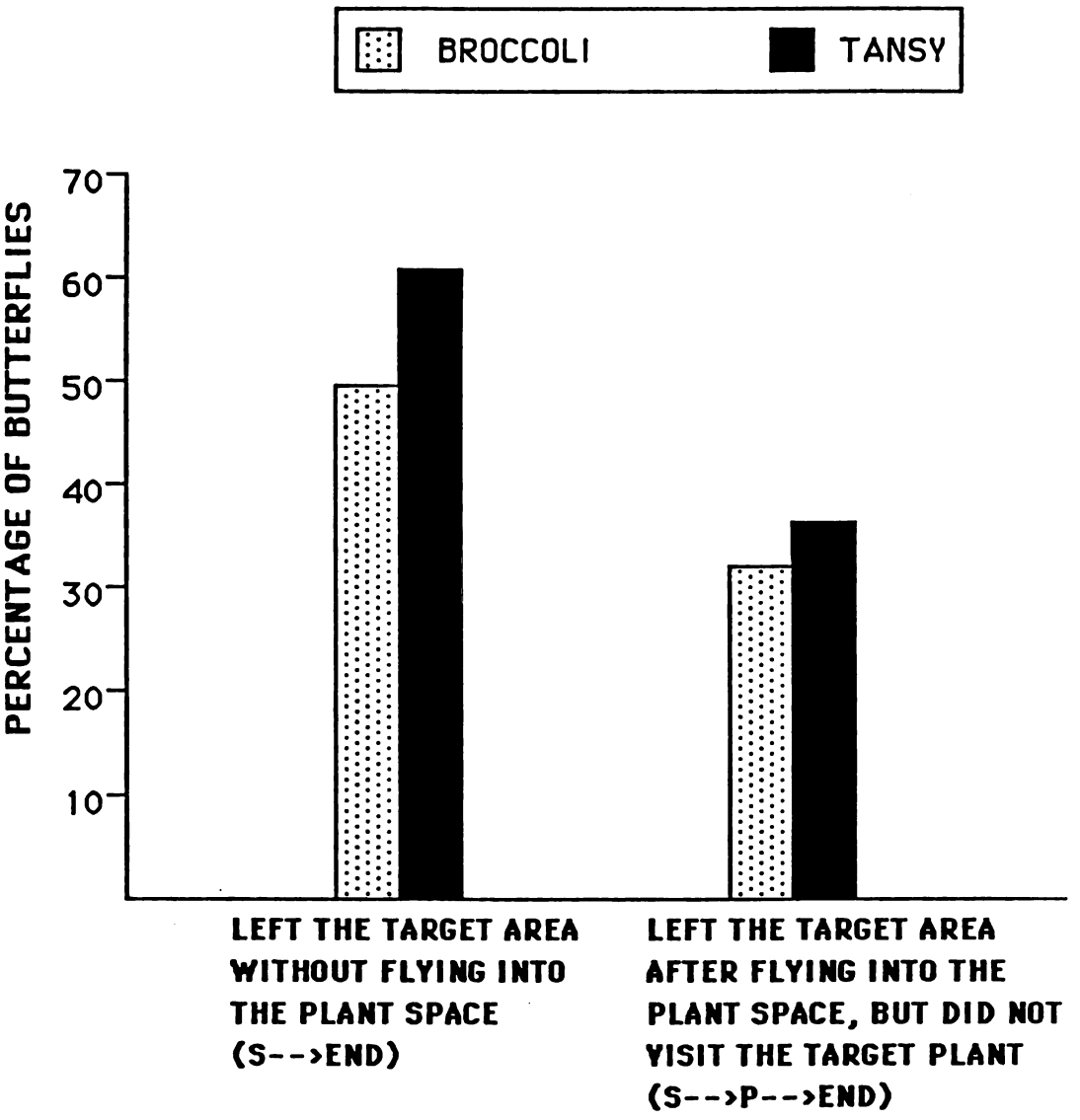


Figure 8. Percentage of butterflies entering the soil space that left the target area without visiting the plant for the broccoli and tansy target plants (comparison 1).

The mean percentage of butterflies flying into the soil area that subsequently flew into the plant area, but left without visiting the plant (s-->p-->end) was 32.1% for broccoli and 36.2% for tansy. These means are significantly different at the .052 level (F=1.67, df=41, P=.0518).

Thus, the data support the hypothesis that most visiting butterflies recognize host plants prior to crossing the soil space/plant space boundary. The analysis also suggests that a smaller proportion of visiting butterflies are induced to visit hosts only after crossing the soil space/plant space boundary. The exact distances at which butterflies are able to perceive host-specific stimuli cannot, however, be determined from these data.

IIIB: Response to Alight Transition

In the analysis in Level IIB (response to alight transition) discrimination was assessed by comparing the proportion of responding (visiting) butterflies that ultimately performed at least one land or contact on the target plant (as opposed to the proportion that fluttered and then left the target area) for the target plant species in each comparison. There were two ways for visiting butterflies to land on or contact target plants. First, a butterfly could perform a land or contact as the first act in a visit. Second, a butterfly could perform a flutter followed by a land or a contact (f-->l-c). Analysis of data in the present section consisted of 1) comparing the proportion of visiting butterflies that performed each of

the three possible acts (flutter, contact, or land) as the initial act in a visit for different target plant species, 2) comparing the transitional frequencies between an initial flutter and the three possible succeeding acts (land, contact, or end) for different target plant species, and 3) comparing the relative proportions of first contacts and first lands. Because very few visits were made to the target plants in comparison IV, this comparison was not included in the analyses. It was assumed that flutters and contacts were more exploratory behaviors than lands. Therefore, a land was likely to be performed only when the plant stimuli the butterfly perceived indicated with a fair degree of certainty that the plant was a host.

The numbers of butterflies performing each behavior during the response stage to alight stage transition, and the transitional probabilities between behaviors are given in Appendix D. The highest proportion of butterflies fluttered as their first act in a visit (Table 13). This was true for all target plant species in all comparisons. The proportions fluttering ranged from 90% (tansy, comparison II) to 48% (mustard, comparison III) . A relatively low proportion of butterflies performed a contact as their first act in a visit (ranging from 17%, lettuce, comparison III; to 4%, tansy, comparison II). The proportion of butterflies initially landing ranged from 39% (mustard, comparison III) to 7% (tansy, comparison II).

Table 13. Number of butterflies fluttering, contacting, and landing as the first act in a visit to different plant species.

Comparison	Plant Species	Number Fluttering	Number Contacting	Number Landing	
I	Broccoli	162	24	74	a
	Tansy	42	4	3	b
		***G=14.49, df=1, P <.001			
II	Broccoli	56	11	25	a
	Tansy	27	1	2	b
	Sage	27	3	4	ab
		*G=12.37, df=3, P=.015			
III	Broccoli	66	11	41	a
	Tansy	11	1	1	b
	Mustard	38	10	31	ab
	Lettuce	16	4	3	a
		*G=12.89, df=3, P=.045			
V	Broccoli	73	10	35	a
	Tansy	11	1	1	a
	Broccoli-tansy	80	6	24	a
		G=5.85, df=2, P=.211			

a,b,c = Data were analyzed by a G test (Sokal and Rholf 1969). Percentages followed by the same letter are not significantly different at the .05 level by an STP test.
* = $P \leq .05$
** = $P \leq .01$
*** = $P \leq .001$

In most cases, the first behavior performed in visits to hosts differed significantly from the first behavior performed in visits to non-hosts. In comparison I the behavior of butterflies visiting broccoli differed significantly from the behavior of butterflies visiting tansy. A higher proportion of the butterflies visiting broccoli immediately landed (29%) than butterflies visiting tansy (6%). Butterflies initiallty fluttering constituted 86% of the butterflies visiting tansy and 62% of the butterflies visiting broccoli.

In comparison II the proportions of butterflies performing each of the three types of initial acts differed significantly between broccoli and tansy. There was no significant difference between broccoli and sage. Even so, the trends were consistent with the predictions: a higher proportion of visiting butterflies immediately landed on broccoli (27%) than on tansy or sage (7% and 12% respectively). Correspondingly, the proportion of fluttering butterflies was higher for sage (79%) and tansy (90%) than for broccoli (61%).

In comparison III initial behavior toward hosts was not significantly different from that toward the lettuce target. Additionally, the initial behavior toward mustard did not differ significantly from that toward tansy (although the behavior toward broccoli and tansy did differ significantly). Even so, a much higher proportion of butterflies visiting hosts immediately landed (35% broccoli

and 39% mustard) than those visiting non-hosts (8% tansy, 13% romaine lettuce).

There was no major difference between the initial behavior of butterflies visiting a highly acceptable host (broccoli) and a less acceptable host (mustard). In fact, the proportion of visiting butterflies that landed was slightly higher for the less acceptable host, mustard, (39%) than for the highly acceptable host, broccoli (35%). More butterflies visiting broccoli initially fluttered (56%) than those visiting mustard (48%). The proportion of contacts was slightly higher for mustard than for broccoli (13% and 9% respectively).

The proportion of the butterflies visiting lettuce (comparison III) that immediately landed (13%) was not significantly different than the proportion visiting tansy (8%). Also, the initial behavior of butterflies visiting broccoli-tansy was not significantly different than the initial behaviors of butterflies visiting broccoli (comparison V).

It is my contention that the three visit behaviors have different functions. Flutters and contacts are more tentative, exploratory behaviors. A butterfly may perform a flutter or a contact if the signal it receives from the plant (i.e., the stimuli it perceives) during the movement stage of the ovipositional sequence conveys ambiguous information about the nature of the plant. During a flutter or a contact, a butterfly examines the plant further to

obtain more precise information. Even though additional information is gathered after landing it is probable that a land is performed by butterflies already quite "knowledgeable" about the nature of the plant.

Analysis of the first behavior performed in visits to different target plant species supports the idea that the signal perceived by butterflies (i.e., plant stimuli) before they visit the plant is fundamentally different between hosts and non-hosts. The data do not support the ideas that the signal perceived is different between two hosts of different acceptabilities or between different species of non-host. The idea that broccoli-tansy transmits a more ambiguous (i.e., less "host-like) signal than broccoli alone is also not supported by these data.

The proportion of butterflies landing, contacting, and ending following an initial flutter around the target plant was strongly influenced by the target plant species (Table 14). Behavior following an initial flutter around a host was significantly different from behavior following an initial flutter around non-hosts for all plant species in all comparisons. With one exception (to be discussed later), the proportion of butterflies that left the target area following an initial flutter (f-->end) was higher for non-hosts than for hosts. Percentages of butterflies leaving the target area after an initial flutter ranged from 34% (broccoli, comparison II) to 18% (broccoli, comparison V) for hosts and from 74% (tansy, comparison II)

Table 14. Number of butterflies contacting, landing, and ending following an initial flutter above different plant species.

Comparison	Plant Species	Number Contacting	Number Landing	Number Ending	
I	Broccoli	32	93	37	a
	Tansy	9	6	27	b
		***G=31.87,	df=1,	P <.001	
II	Broccoli	12	25	19	a
	Tansy	4	3	20	b
	Sage	7	2	18	b
		***G=22.15,	df=3,	P <.001	
III	Broccoli	13	40	13	a
	Tansy	3	1	7	b
	Mustard	10	18	10	a
	Lettuce	14	2	0	c
		***G=40.77,	df=3,	P <.001	
V	Broccoli	11	49	13	a
	Tansy	4	2	5	c
	Broccoli-Tansy	27	32	21	b
		**G=17.67,	df=2,	P=.00143	

a,b,c = Data were analyzed by a G test (Sokal and Rholf 1969). Percentages followed by the same letter are not significantly different at the .05 level by an STP test.
* = $P \leq .05$
** = $P \leq .01$
*** = $P \leq .001$

to 45% (tansy, comparison V) for non-hosts (excluding the exception to be discussed later). There was no significant difference between the proportion of fluttering butterflies that landed, contacted, and ended between the more acceptable host, broccoli, and the less acceptable host, mustard (G=1.71, df=3, P=.0635).

None of the butterflies fluttering around lettuce left the target area (comparison III). The percentages of butterflies continuing (landing or contacting) are actually higher for lettuce than for the two hosts in this comparison. The difference is statistically significant at the .05 level both between lettuce and the two hosts, and between lettuce and the other non-host species, tansy.

The percentage of fluttering butterflies that left the target area was significantly higher for broccoli-tansy (26%) than for broccoli (18%). Therefore, tansy does appear to have a repellent effect on the behavior of fluttering butterflies, although this effect is not great.

In summary, the ideas that host-specific stimuli induce fluttering butterflies to land, and that repellent plant stimuli may inhibit alighting by fluttering butterflies, are supported by these data. In addition, the data support the idea that visually-perceived general plant stimuli may influence whether fluttering butterflies will alight. The idea that variation in host-specific stimuli influences alightment of fluttering butterflies is not supported.

Proportions of lands vs contacts. Previously, it was hypothesized that the act "contact" represents a more exploratory behavior than the act "land." If this were true, then the relative proportions of alighting butterflies that contacted or landed would differ among different target plant species. To examine this idea, the percentages of alighting butterflies that landed or contacted on their first alight were calculated. To obtain these percentages the number of individuals landing (or contacting) as the first act in a visit was added to the number of individuals landing (or contacting) after fluttering first. The sum was then divided by the total number of butterflies alighting.

In general the results support the hypothesis that the act "contact" represents a more tentative, examining type of behavior than the act land. In all cases, the percentage of landing butterflies was higher for hosts than for non-hosts (Table 15). In most cases, this difference was significant. The percentage of alighting butterflies which landed was not significantly different between the more acceptable host and the less acceptable host mustard ($G=.820$, $df=3$, $P=.845$).

These data also support the contention that placing tansy next to a broccoli plant results in a more ambiguous signal. A significantly higher percentage of alighting butterflies landed on broccoli alone (80%) than on the broccoli-tansy combination (63%).

Table 15. Number of butterflies contacting and landing on their initial alight on different plant species.

Comparison	Plant Species	Number Contacting	Number Landing	Percent Landing	
I	Broccoli	56	167	74.9	a
	Tansy	13	9	40.9	b
		**G=10.18, df=1, P=.00142			
II	Broccoli	23	50	68.5	a
	Tansy	5	5	50.0	a
	Sage	10	6	37.5	a
		G=5.84, df=2, P=.0539			
III	Broccoli	24	81	77.1	a
	Tansy	4	2	33.3	b
	Mustard	20	49	71.0	a
	Lettuce	18	5	21.7	b
		***G=28.36, df=3, P <.001			
V	Broccoli	21	84	80.0	a
	Tansy	5	3	37.5	b
	Broccoli-Tansy	33	56	62.9	b
		**G=10.97, df=2, P=.0041			

a,b = Data were analyzed by a G test (Sokal and Rholf 1969). Percentages followed by the same letter are not significantly different at the .05 level by an STP test.
* = $P \leq .05$
** = $P \leq .01$
*** = $P \leq .001$

IIIC: Alight to Curl Transition

In the analysis of level 2C, discrimination was assessed by comparing the proportion of alighting butterflies that ultimately curled their abdomens at least once (as opposed to the proportion that left the target area without curling) for different target plant species. Although the ultimate act of an alighting butterfly was either to curl or not to curl, one to several lands and/or contacts were made before that ultimate act was performed. In this section each successive alight (land or contact) is considered separately. Considered in this way, three different events were possible after alighting: 1) curl: The butterfly curled its abdomen, 2) end: The butterfly did not curl its abdomen and left the target area without making additional lands or contacts, and 3) continue: the butterfly did not curl its abdomen, but continued the visit by making additional lands or contacts.

In this section discrimination between target plants is assessed by comparing the transitional frequencies between any given alight and the three possible succeeding acts (curl, end, or continue) for different target plant species. In addition, this section addresses whether the probabilities of performing these three acts change as the visit progresses.

Results: Broccoli. Alighting butterflies made between one and eight lands and/or contacts on broccoli before either curling or leaving the target area (Figure 9). Six

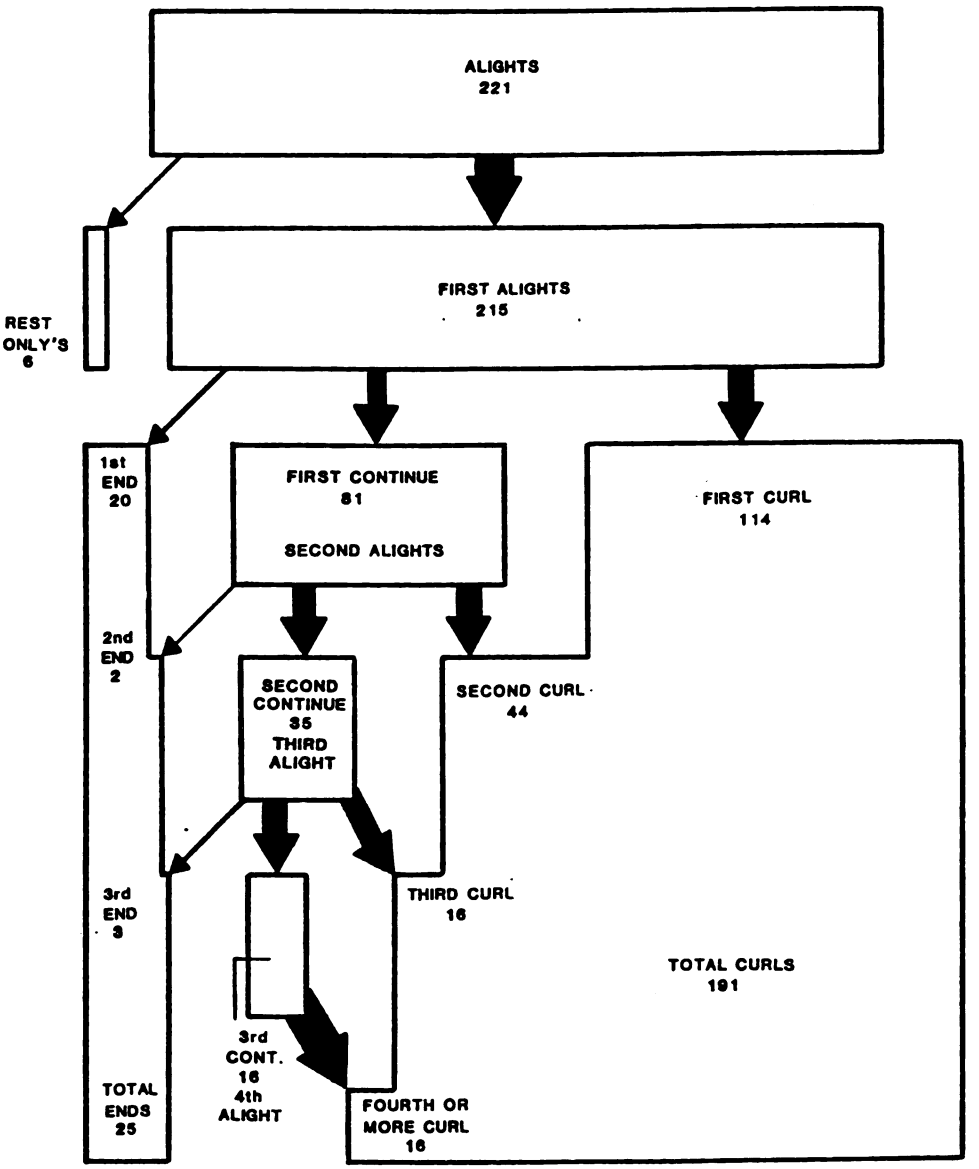


Figure 9. Number of butterflies performing each behavior in the alight stage of oviposition for the broccoli target (comparison I). The width of the boxes is proportional to the number of butterflies performing the designated behavior (this number is given in the box). The width of the arrows is proportional to the transitional probabilities (shown next to the arrow). The total area of the boxes is insignificant.

(2.7%) alighting butterflies "rested" on the plant on their first alight, then left the target area without performing additional visit behaviors. These sequences were eliminated from further analysis.

Figure 10 shows the proportion of alighting butterflies that: 1) curled their abdomens (curl), 2) did not curl but continued the visit by making additional lands and/or contacts (continue), and 3) left the target area without making additional lands and/or contacts (end) for each successive alight. For example, 53% of the butterflies curled on their first land or contact, 37.7% continued the visit, and 9.3% left the target area.

The proportion of butterflies performing each of the three possible events after landing can be used to estimate the probability that an individual butterfly will perform these events after a land or a contact. The probability of a butterfly performing any given event varies slightly between successive alights. For example, the probability of curling steadily decreases from 0.530 on the first alight to 0.438 on the fourth alight. The probability of continuing increases from 0.337 on the first alight to 0.562 on the fourth alight.

A G test was performed to test if these probabilities were independent of the number of alights performed. This was not found to be significant ($G=5.77$, $df=4$, $P=.217$).

The distribution of the first curl performed by a butterfly as a function of the number of alightings made

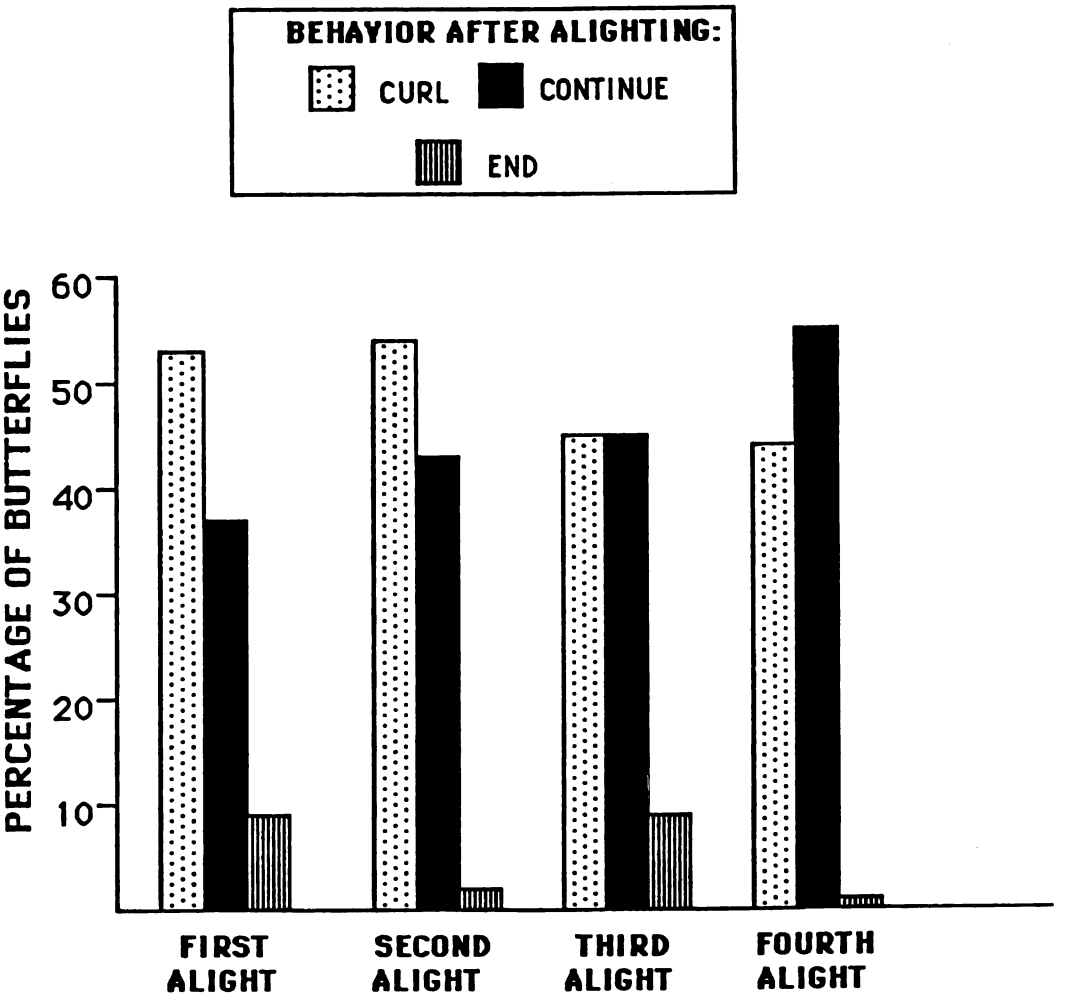


Figure 10. Percentage of butterflies curling, continuing and ending on successive alights on broccoli (comparison I).

before curling is shown in Figure 11. The curve produced is similar to an exponential decay curve. Therefore, it is possible that the probability of curling remains constant on successive alights (provided the butterfly has not curled previously in the visit). This is in agreement with the results discussed previously.

Results: Comparisons. What an observer records as a visit to a plant may, in reality, be a behavior performed in any one of three differents contexts: 1) oviposition: a butterfly is responding to a plant as an ovipositional substrate, 2) social: a butterfly is responding to another butterfly on or near the plant, and 3) resting: a butterfly is responding to the plant as a surface to rest on.

Butterflies responding to the plant in a social context could easily be identified and eliminated from the data. Those responding in a resting context could only be identified after the rest had been performed.

Up to this point, rests have been included as a visit behavior because rests constituted a very small portion of total visits. Because the analysis in this section involves very fine dissection of the post-alight sequence, it is important to identify rests and eliminate them from the data.

Before doing this, the proportion of visiting butterflies resting was examined. It was hypothesized that butterflies do not respond differentially to different plant species when resting. Therefore, it was predicted that the

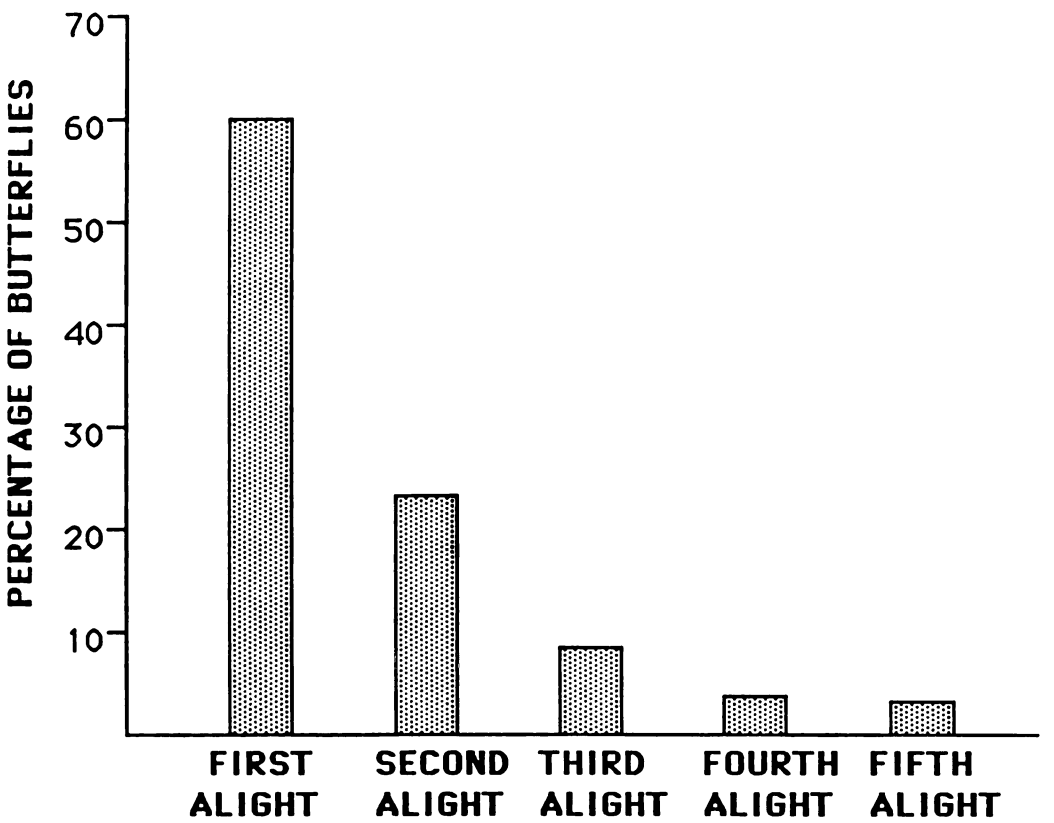


Figure 11. Percentage of butterflies performing their first curl on the first through fifth alight on broccoli (comparison I).

proportion of butterflies resting only (i.e. not exhibiting other visit behaviors) would be independent of target plant species.

The proportion of butterflies "resting only" did not differ significantly for the plants in comparisons I and II (Figure 12). In comparison III a significantly higher proportion of butterflies rested on mustard (93%) than on either broccoli (33%) or lettuce (0%). In comparison IV the proportion of butterflies resting on soybean (83%) was significantly higher than the proportion resting on lettuce (0%). A Fisher's exact test was used to analyze the latter set of data due to the low number of visits.

In comparison V the proportion of butterflies resting on broccoli (40%) was not significantly different (by a Fisher's exact test) from the proportion resting on broccoli-tansy (P=.170).

Therefore, it can be concluded that the probability of a butterfly resting is <u>not</u> independent of target plant species. Some species of plant (i.e., soybean and mustard) elicit proportionally more rests than others. The stimuli affecting resting behavior are not known, but they are not the same stimuli as those responsible for ovipositional behavior, since there were no consistent differences in the proportion of rests on hosts and non-hosts.

The numbers of butterflies ending, continuing, and curling on each land or contact for broccoli and tansy (comparison I) are shown in Figure 13. Percentages are

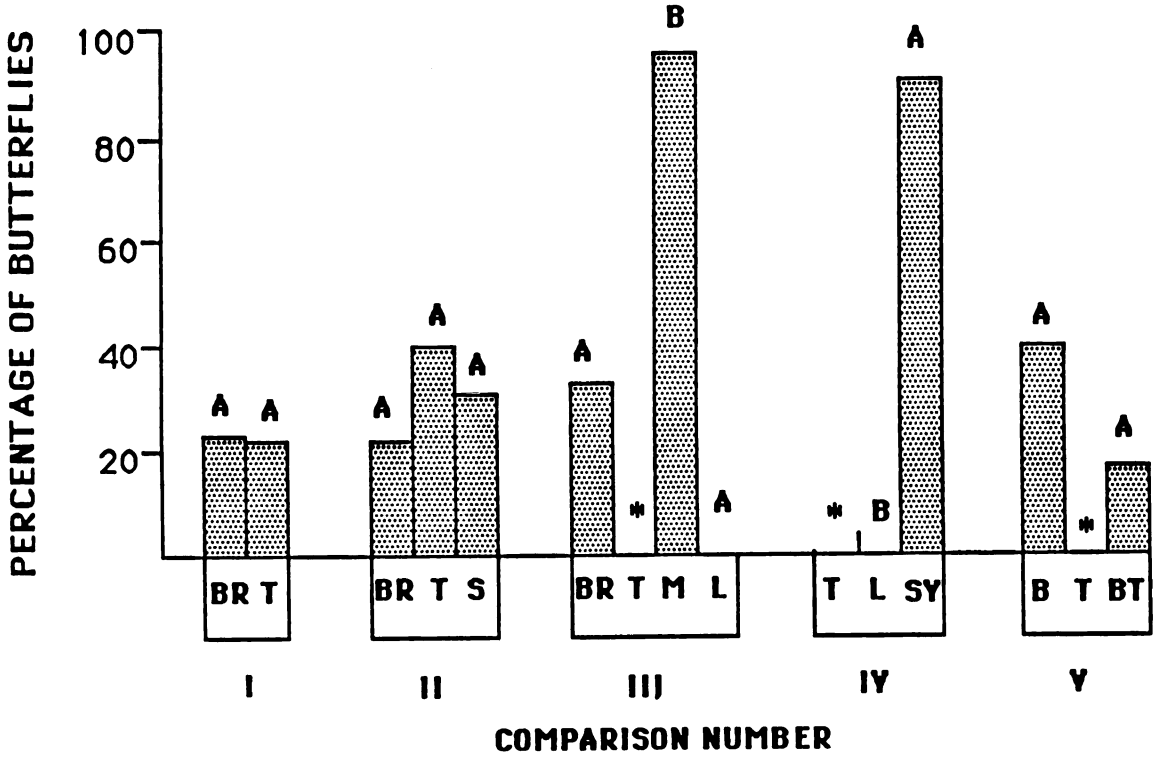


Figure 12. Percentage of alighting butterflies that rested only on different plant species. Percentages shown under the same letter are not significantly different at the .05 level. BR=broccoli, T-tansy, S=sage, M=mustard, L=lettuce, Sy=soybean, BT=broccoli-tansy, *=data not analyzed due to the low number of visits occurring.

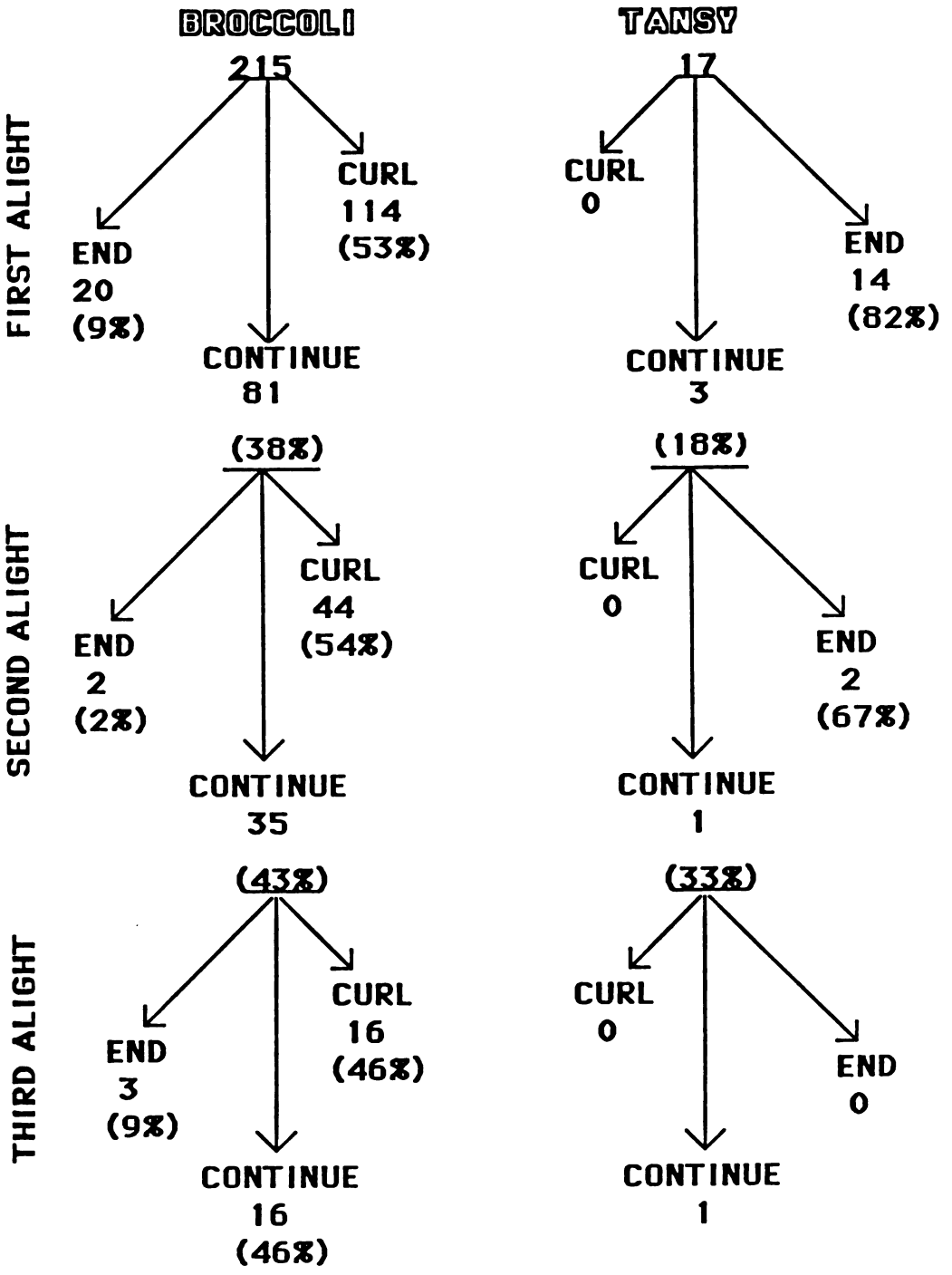


Figure 13. Number of butterflies curling, continuing, and ending after the first three alights on broccoli and tansy (comparison I). The number in parentheses is the percentage of butterflies making that particular alighting that performed the designated behavior.

based on the proportion of butterflies making the particular land/contact that performed each event. The most obvious difference between the two plants lies in the percentage of butterflies curling. Approximately half of the butterflies curled after each alight on broccoli while none of the butterflies curled on tansy.

The second most striking difference is in the percentage ending. A higher proportion of butterflies landing on or contacting tansy ended than those alighting on broccoli. The effect is so striking that only 3 of the 17 butterflies alighting on tansy made more than one land or contact. These results are consistent with the idea that host-specific stimuli, perceived by the butterfly after alighting, are crucial to eliciting post-alight ovipositional behavior (curl or continue).

The proportion of butterflies curling, continuing, and ending after each succesive land and/or contact for broccoli and for mustard (combination III) remains fairly constant for broccoli during the first three alights (Figure 14). The proportion curling on mustard increases with successive alights. The proportion ending after alighting on mustard increases and the proportion continuing decreases.

To test whether the data for mustard were stationary (i.e., whether the frequency of butterflies performing each of the events differed on successive alights) a G-test was performed. The G-statistic was not significant at the .05 level. This indicates that, despite the apparent trend in

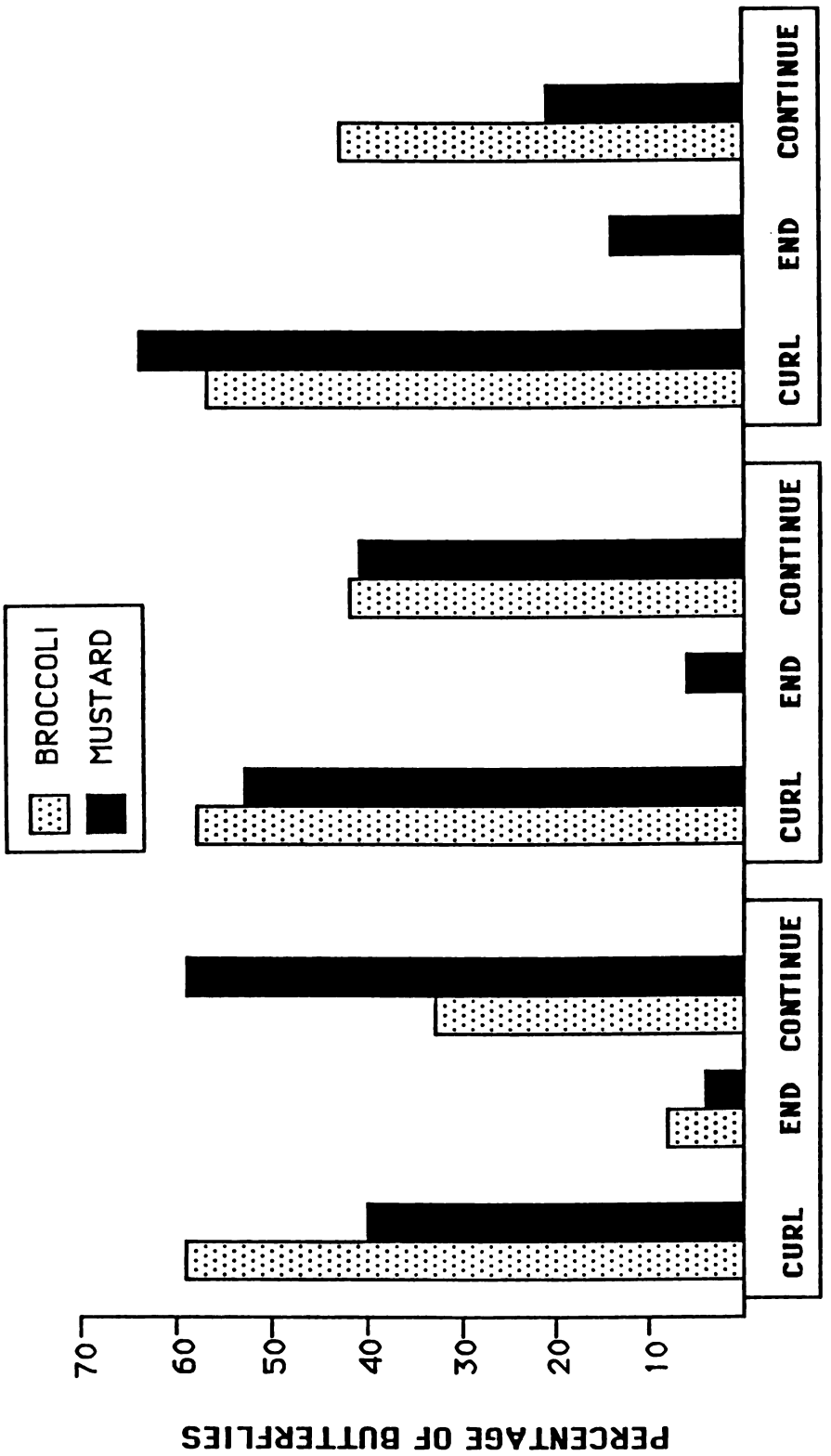


Figure 14. Percentage of butterflies curling, continuing, and ending after the first three alights on broccoli and mustard.

the data, the probability that a butterfly will continue, end, or curl is not significantly influenced by the number of times it has previously alighted on the plant.

Because data for successive alightings were stationary, they were lumped together to test if the probability of ending, continuing, or curling was independent of the target plant species. The G-statistic obtained was 3.88, which is not significant at the .05 level (P=.1437, df=2). Therefore, the hypothesis that post-alighting ovipositional behavior is influenced by variation in host-specific stimuli between these two hosts is not supported by these data.

The numbers of butterflies ending vs continuing after alighting on non-hosts are too low to be analyzed statistically. However, proportions appear not to differ greatly among different non-host species (Table 16). Very few butterflies (a total of eight of the sixty-four butterflies alighting on all non-host species combined) made more than one land or contact. This supports the idea that the absence of host-specific plant stimuli results in termination of the ovipositional sequence. These data also suggest that a single land or contact is sufficient for a butterfly to detect the absence of host-specific chemicals.

Figure 15 gives the proportions of butterflies that curled, continued, or ended after alighting on broccoli and broccoli-tansy (comparison V). Again, these proportions are fairly constant for the first three alightings on broccoli.

Table 16. Number of butterflies ending and continuing after their first alight on different non-host species.

Comparison	Plant Species	Number Continuing	Number Ending	Percent Continuing
II	Tansy	0	6	0
	Sage	1	10	9
III	Tansy	1	5	10
	Lettuce	2	20	20
IV	Tansy	1	4	20
	Lettuce	3	10	23
	Soybean	0	1	0

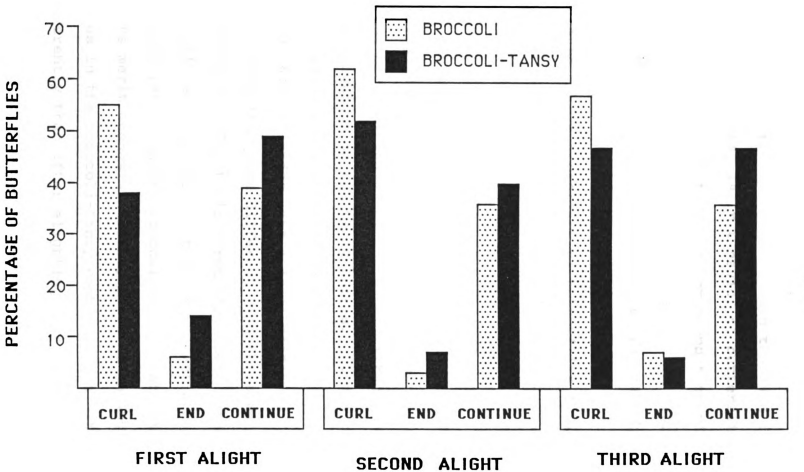


Figure 15. Percentage of butterflies curling, continuing, and ending after the first three alights on broccoli and broccoli-tansy.

The proportions for broccoli-tansy vary with the number of alightings made.

One notable difference between the data for broccoli and broccoli-tansy is in behavior of butterflies after the first land or contact. A higher proportion of butterflies curled after making their first alight on broccoli and a correspondingly lower proportion ended than those alighting on broccoli-tansy. The question arising is whether the increase in the proportion of butterflies ending after alighting on broccoli-tansy results from individual butterflies which made their first alighting on tansy foliage instead of on broccoli foliage.

Figure 16 shows the proportion of butterflies ending, curling, and continuing after making their first alightment on the broccoli leaves of the broccoli-tansy combination vs those alighting on the tansy leaves. Eleven butterflies made their first alightment on tansy. Of these, 1 (9%) curled, 6 (55%) ended, and 4 (36%) continued. These proportions are quite different from the same proportions of butterflies making their first alightment either on the broccoli target alone, on the tansy plant alone, or on broccoli leaves in the broccoli-tansy combination. Two points merit emphasis. First, after alighting on tansy leaves in the broccoli-tansy combination a butterfly behaves differently than after alighting on a host. Therefore, it can be concluded that contact cues are important determinants of butterfly behavior. Secondly, the behavior

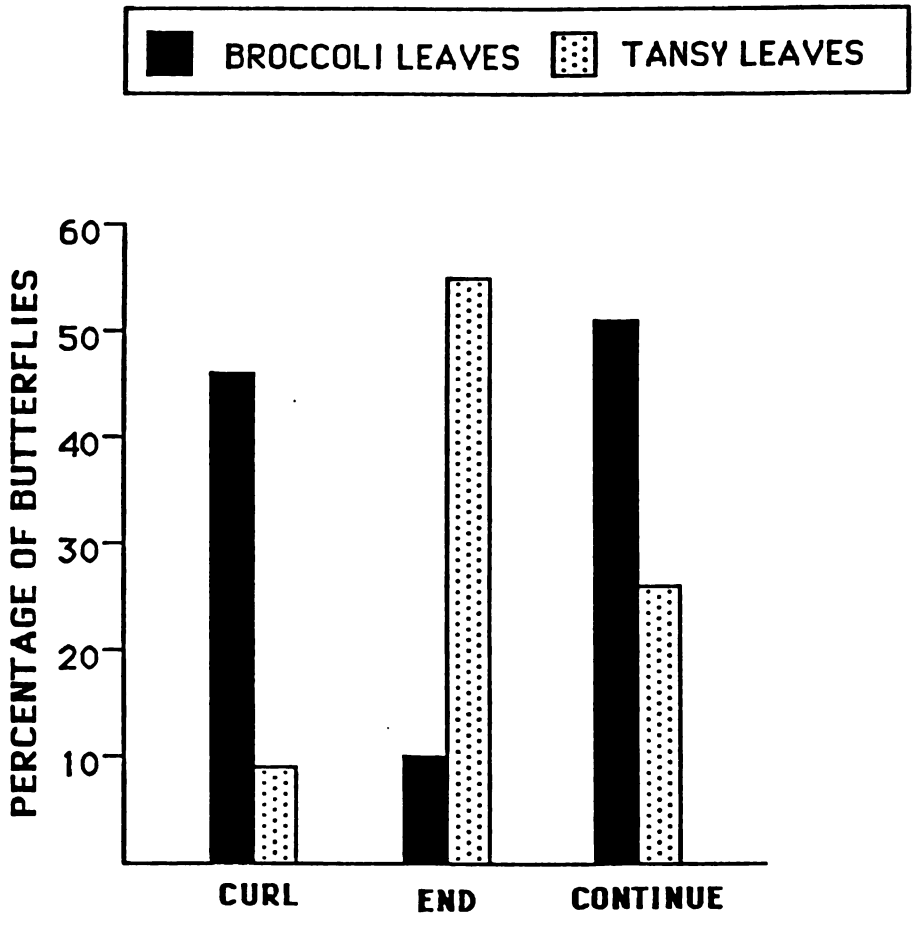


Figure 16. Percentage of butterflies curling, ending, and continuing after making their first alight on the broccoli leaves and the tansy leaves of the broccoli-tansy target.

of butterflies initially alighting on tansy leaves in the broccoli-tansy combination was different from the behavior of butterflies alighting on the tansy target alone. During the entire study, not one alighting butterfly curled on tansy. Yet one of the eleven butterflies making its initial alightment on the tansy leaves of the broccoli-tansy combination curled. The proportion of butterflies ending after the first alight on tansy (comparison V) was 88%. Only 55% of butterflies making their initial alight on the tansy leaves of the broccoli-tansy combination ended. Thus, even though the results suggest that contact stimuli strongly influence post-alighting behavior, they apparently are not the sole determinants. Non-contact plant stimuli perceived either prior to or after alighting seem to also influence post-alighting response.

In summary, analysis of the behaviors involved in the alight stage to curl stage transition support the idea that host-specific contact stimuli are releasers of the curl response. Differences in host-specific contact stimuli between broccoli and mustard do not appear to influence post-alighting behavior. The absence of these host-specific contact stimuli induces a butterfly to terminate the visit. However, data from the broccoli-tansy target indicates that other, non-contact stimuli also influence post-alighting behavior.

Level IV: The Visit Sequence

The purpose of this analysis is to describe visits to a target plant as a sequence of behaviors. Three visit sequence descriptions are produced: one to each of the target plant species broccoli, tansy, and mustard. The visit sequences are analyzed and described as Markov chains. As Cane (1978) states, "The advantage of describing a sequence of observations on the behavior of an animal in terms of a Markov chain is that a summary of the behavior is produced that enables comparisons to be made between different animals and between different conditions for the same animal." Thus, producing descriptions of visit sequences to three different target plant species as Markov chains allows comparisons among sequences and may give some insight into causation of the behaviors.

Two or more behavior patterns are performed by an animal close together in time either because the performance of one act in some way facilitates the performance of the other and/or because the acts have causal factors in common (Slater 1973). Causal factors potentially include the internal state of the animal and/or environmental stimuli (Slater 1973). Sequence analysis enables determination of the degree to which one behavior influences another and, by default, the degree to which the two are determined by common causal factors. It does <u>not</u> allow for separation of internal from external causal factors.

The average internal motivation was assumed to be the same for groups of butterflies visiting different target plant species. This seems a reasonable assumption, although it can neither be proved nor disproved here. The average environmental conditions were also assumed to be roughly equivalent, with the exception of the target plant species. Under these assumptions, differences in the visit sequence result from differences in target plant species.

The description of the visit sequence includes all possible acts and transitional probabilities between acts. A transitional probability is the probability that, given that the butterfly has performed a specified behavior, the next behavior performed will be a given act. This probability is potentially affected by a number of factors. To meet the requirements for a Markov chain, transitional probabilities must be constant over time and be affected only by the type of acts immediately preceding the transition (i.e., not be affected by the butterflies' previous histories). The number of immediately preceeding acts known to affect a transitional probability is the order of the Markov chain.

The requirement for transitional probabilities to remain constant over time and not be influenced by history is termed stationarity. It is frequently recommended that data be initially tested for stationarity (Chatfield and Lemon 1970, Slater 1973). While it is never possible to prove stationarity in the absolute sense, the more obvious

factors can be checked for influences on the transitional probabilities.

The sequence performed by butterflies visiting the broccoli target plant (comparison I) was tested for stationarity. It was not possible to test whether events occurring prior to the entry of the butterflies into the target area influenced transitional probabilities, but it was assumed that any such influence would tend to average out between plant types. In any sequence of behaviors, the transitional probabilities between acts may change during the course of a sequence due to changing levels of motivation and/or due to information gained during the sequence (for examples see Lemon and Chatfield 1971, Oden 1977, Fraser and Nelson 1984). Broccoli data were analyzed to answer the following questions: 1) Do the transitional probabilities between two given acts change as the sequence progresses, and 2) Does the occurrence of certain crucial events in the sequence (i.e., landing and curling) affect transitional probabilities between acts?

Effect of Step Number

A sequence step was defined as corresponding to the performance of one behavior pattern. Therefore, the number of steps in the sequence equals the number of behaviors performed, and the nth step in the sequence corresponds to the nth behavior performed (Oden 1977).

An easy way to check for non-stationarity during the sequence is to compare frequencies of various acts at

different steps of the sequence (Oden 1977). Table 17 gives these frequencies for visits to broccoli. Because the relative proportions of various acts appear to change as the visit progresses, initial examination of this table leads to the conclusion that data are not stationary. However, this apparent non-stationarity could be due to the definition of the various acts rather than to a true trend; of the nine transitions, one, flutter to flutter, was forbidden as defined. By definition, a flutter was considered to continue until the butterfly performed a different type of act (land, contact, or end). The reduction in the relative proportion of butterflies fluttering at step two could simply be due to the high number fluttering at step one which were, by definition, prevented from fluttering on the second step.

To check data for stationarity, and to correct for the influence of the forbidden flutter-to-flutter transition, three transition matrices were constructed: one each for transitions from a flutter, a contact, and a land, as a function of step number (data includes behaviors only up to the first curl). These matrices are shown in Table 18. Each matrix was tested for independence of transitional frequency from step number. The G-statistics obtained were not significant (flutter transitions, $G=5.73$, $df=6$, $P=.454$; contact transitions, $G=4.01$, $df=8$, $P=.856$; land transition, $G=7.68$, $df=8$, $P=.465$). Thus, until the first curl (or through step 4) the transitional probabilities remain

Table 17. Number of butterflies performing a flutter, a contact, a land, a land-curl, or an end on steps 1 through 4 of visits to the broccoli target (comparison I).

Step Number	Flutter	Contact	Land	Land-Curl	End
1	158	24	22	49	____
2	7	41	26	84	46
3	16	17	7	26	7
4	2	10	6	16	7

Behavior is included only up to the first curl.

Table 18. Number of butterflies performing specified transitions to all possible behaviors following a flutter, a contact, and a land as a function of step number.

Step Number	SECOND BEHAVIOR: Flutter	Contact	Land	Land-Curl	End
FROM A FLUTTER AS THE FIRST BEHAVIOR:					
1 to 2	*	33	22	65	38
2 to 3	*	3	1	3	0
3 to 4	*	3	1	7	5
			G =5.73, df =6, P =.454		
FROM A CONTACT AS THE FIRST BEHAVIOR:					
1 to 2	4	5	2	9	4
2 to 3	7	11	2	16	5
3 to 4	1	6	2	7	1
			G =4.01, df =8, P =.856		
FROM A LAND AS THE FIRST BEHAVIOR:					
1 to 2	3	3	2	10	4
2 to 3	9	3	4	7	2
3 to 4	1	1	3	2	1
			G =7.68, df =8, P =.465		

* The flutter-to-flutter transition is forbidden by definition.

constant. This indicates that the data up to the first curl are stationary with respect to step number.

Effect of Key Events

It was hypothesized that the occurrence of two "key" events--landing and curling--could change the transitional probabilities between acts. Landing had the potential to affect transitional probabilities in that butterflies potentially received additional information about the plant after landing. Curling could affect transitional probabilities by changing the internal state (motivation) of a butterfly.

The transitional frequencies between acts were visually inspected to detect differences between behavior prior to and following the first land. There were only minimal differences in transitional probabilities. Thus, the event of landing does not change transitional probabilities.

To test whether the transitional probabilities change after the performance of a curl, four matrices were constructed. Each matrix included the transitional frequencies from one of four behaviors--a flutter, contact, land and land-curl--as a function of "experience." "Experience" categories included: 1) behaviors prior to the first curl, 2) behaviors from the first curl up to the second curl, and 3) behaviors from the second to the third curl. These matrices are shown in Table 19. A G-test was performed to test whether the transitional frequencies were independent of experience. The transitional frequencies

Table 19. Number of butterflies performing specified transitions to all possible behaviors following a flutter, a contact, a land, and a land-curl as a function of "experience".

Experience Cateogory	SECOND BEHAVIOR: Flutter	Contact	Land	Land-Curl
FROM A FLUTTER AS THE FIRST BEHAVIOR:				
Before first curl	*	39	24	75
After first curl	*	6	4	28
After second curl	*	4	8	17
		G =8.15, df =4, P =.087		
FROM A CONTACT AS THE FIRST BEHAVIOR:				
Before first curl	12	22	6	32
After first curl	2	3	0	5
After second curl	2	5	1	5
		G =2.02, df =6, P =.918		
FROM A LAND AS THE FIRST BEHAVIOR:				
Before first curl	13	7	9	19
After first curl	2	0	1	10
After second curl	4	1	3	4
		G =8.79, df =6, P =.186		
FROM A LAND-CURL AS THE FIRST BEHAVIOR:				
After first curl	45	2	8	24
After second curl	31	6	1	4
		**G =15.24, df =3, P =.002		

* The flutter-to-flutter transition is forbidden by definition.

from a flutter, a contact, and a land without a curl were independent of experience (flutter transitions: G=8.14, df=4, p=.087; contact transitions: G=2.02, df=6, p=.918; land-no curl transitions: G=8.79, df=6, P=.186). However, the transitional frequencies from a land with a curl were not independent of experience (G=15.25, df=3, P=.002). A butterfly was more likely to flutter or contact, and less likely to land or land-curl following the second curl as compared to after the first curl.

Figure 17 shows the relative proportions of four possible acts (flutter, contact, land-no curl, and land-curl) at four key points in the visit sequence: 1) as the first behavior in a visit, 2) following the first land or contact in a visit, 3) following the first curl, and 4) following the second curl. The frequencies of these acts are not independent of the "key points" in the sequence listed above (G=87.91, df=9, P=4.3x10-15). Thus, although the sequence of behaviors up to the first curl is stationary, the performance of a curl changes the transitional probabilities of at least the first act following a curl.

As Figure 17 reveals, the probability of fluttering decreases following the first land or contact (as compared to the probability of fluttering as the first behavior in a visit), but increases again after a curl has been performed. The probability of contacting or landing without curling increases after the first land or contact has been

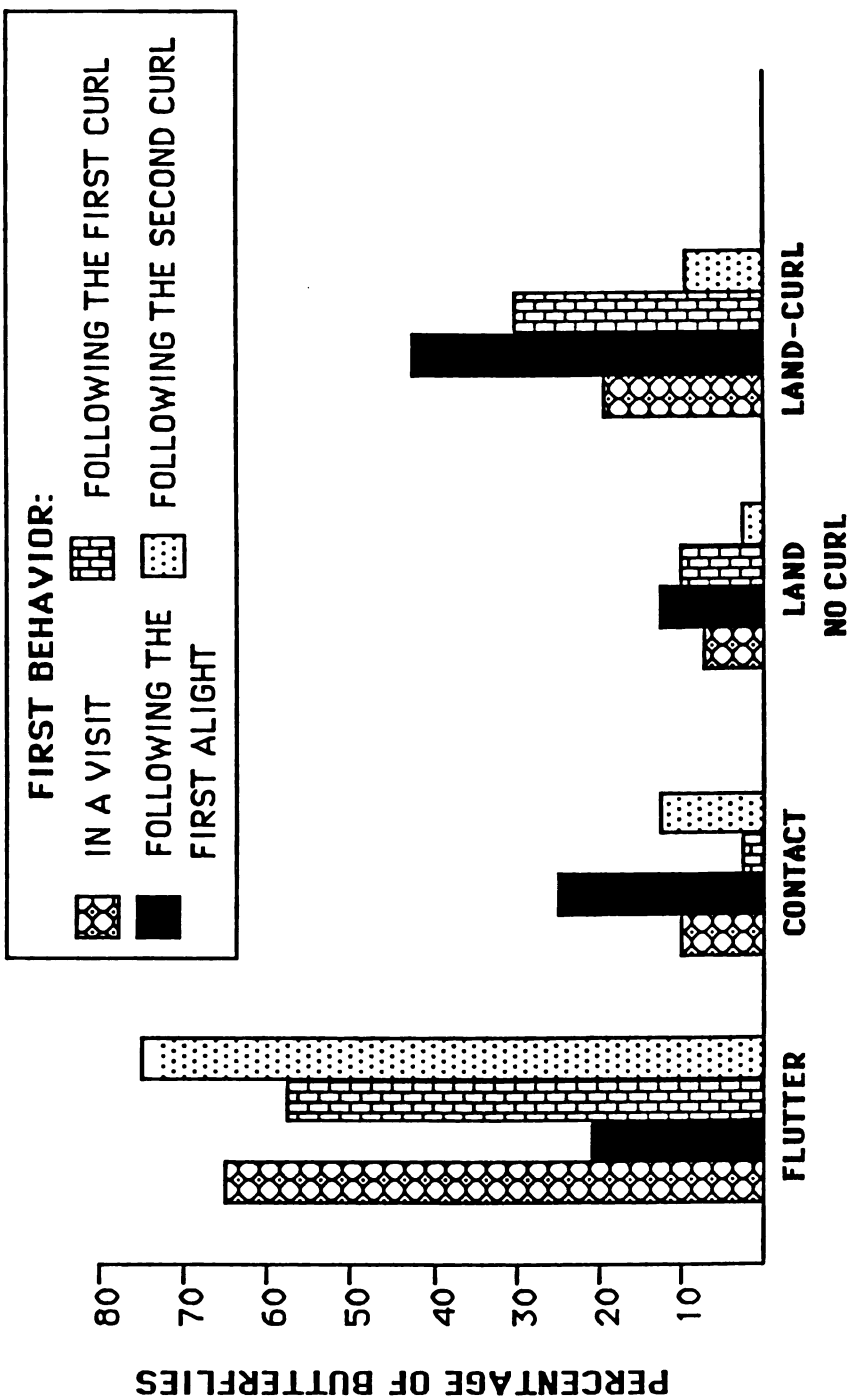


Figure 17. Percentage of butterflies fluttering, contacting, landing, and landing with a curl as the first behavior: 1) in a visit, 2) following the first alight, 3) following the first curl, and 4) following the second curl.

made (compared to the probability of landing or curling as the first behavior in a visit), and, likewise, decreases after a curl has been performed. Collectively, this indicates the existence of a discrete behavioral unit--the "curl sequence"--which can be defined as the series of acts leading up to a curl. The transitional probabilities of the various acts are similar at the beginning of the visit and after a curl has been performed. The curl sequence is most likely to begin with a flutter. The probability of curling increases if at least one prior behavior has been performed in the particular curl sequence. This implies that the butterflies do not curl in bouts, but rather, after curling, start the curl sequence over again.

Determination of the Order of the Chain

As the previous analysis indicates, the visit sequence is not stationary. The transitional probabilities between acts are affected by the event of curling. Therefore, in this section data only up to the first curl are included in calculations.

The next step in the analysis is to determine the number of preceding behaviors that influence the probability of performing an act, and thus establish the order of the Markov chain. Initially the data are tested for independence of acts immediately following one another. If succeeding acts are independent of preceding acts, then the conditional probability of act j occurring given that act i has just occurred is equal to the unconditional probability

of act j occurring (Chatfield and Lemon 1970). A sequence of independent events is called a "zeroth-order" Markov chain (Slater 1973).

If data do not fit the independence model, then they are tested for fit to a first order Markov chain, where the probability of performing a given act depends only on the immediately preceding act and not on earlier ones. If this model is also rejected, the next step is to test for fit to a second order Markov chain, where the probability of performing a given act depends only on the two preceding acts. This proceedure is repeated until the order of the Markov chain is determined (Fagen and Young 1978).

The usual test for independence is to construct a matrix listing the transitional frequencies from preceding behaviors (rows) to following behaviors (columns), and to conduct a Chi-Square or G-test of independence. With these data, however, the forbidden flutter-to-flutter transition could result in erroneous conclusions with this method (Slater 1973). The method used with these data was a test for quasi-independence given by Goodman (1968). The entire table is collapsed four ways to yield four subtables (see Table 20). The subtable containing the impossible transition is eliminated from consideration. Chi-square tests are performed on the remaining subtables, and their sum is used as the test statistic. The degrees of freedom for this statistic is the sum of the degrees of freedom of the three individual subtables, or the degrees of freedom of

Table 20. Chi-Square test for quasi-independence of preceding behavior from following behavior on a table including an impossible transition (flutter-to-flutter).

ORIGINAL TABLE:* Preceeding Behavior	Following Behavior: Flutter	Contact	Land	Land-Curl	End
Flutter	____	39	24	75	43
Contact	12	22	6	32	10
Land	13	7	9	19	7

SUBTABLE A: Preceeding Behavior	Following Behavior: Contact	Land	Land-Curl	End
Contact	22	6	32	10
Land	7	9	19	7

Chi-Square = 52, df=3

SUBTABLE B: Preceeding Behavior	Following Behavior: Flutter	Not Flutter
Contact	12	70
Land	13	42

Chi-Square = 79, df=1

SUBTABLE C: Preceeding Behavior	Following Behavior: Contact	Land	Land-Curl	End
Flutter	39	24	75	43
Not Flutter	29	15	51	17

Chi-Square = 31, df=3

SUBTABLE D:** Preceeding Behavior	Following Behavior: Flutter	Not Flutter
Flutter	____	181
Not Flutter	13	112

* The original table is broken into four subtables and a Chi-Square test is performed on each subtable.
** The subtable containing the impossible transition is eliminated.

the original table minus one for the missing cell.

The results are shown in Table 20. The overall Chi-Square is 8.84, which is not significant at the .05 level (P=.264, df=7). This implies that the acts performed in an individual "curl sequence" (i.e., before curling) are independent. The sequence approximates a "zeroth-order" Markov chain. Therefore, the sequence is not structured internally, but rather represents the random performance of acts (random in the sense of independent, not in the sense of being equally probable). The probability of a butterfly performing a given act is, therefore, affected only by the internal and external conditions. Assuming the internal motivation of butterflies visiting different target plants is equal, the probability distribution for the various acts is altered only by environmental conditions; specifically, the target plant species. This allows for direct comparisons among sequences performed in response to different target plant species.

Visits to Different Target Plant Species

Figures 18, 19, and 20 show descriptions of the visit sequence to three different target plants: broccoli, tansy, and mustard. The acts in these sequences are quasi-independent in that they depend on the preceding act only because of the forbidden flutter-to-flutter transition. Because of this artificial dependence, the transitional probabilities from a flutter and from a land or contact are depicted separately. The probability of performing a given

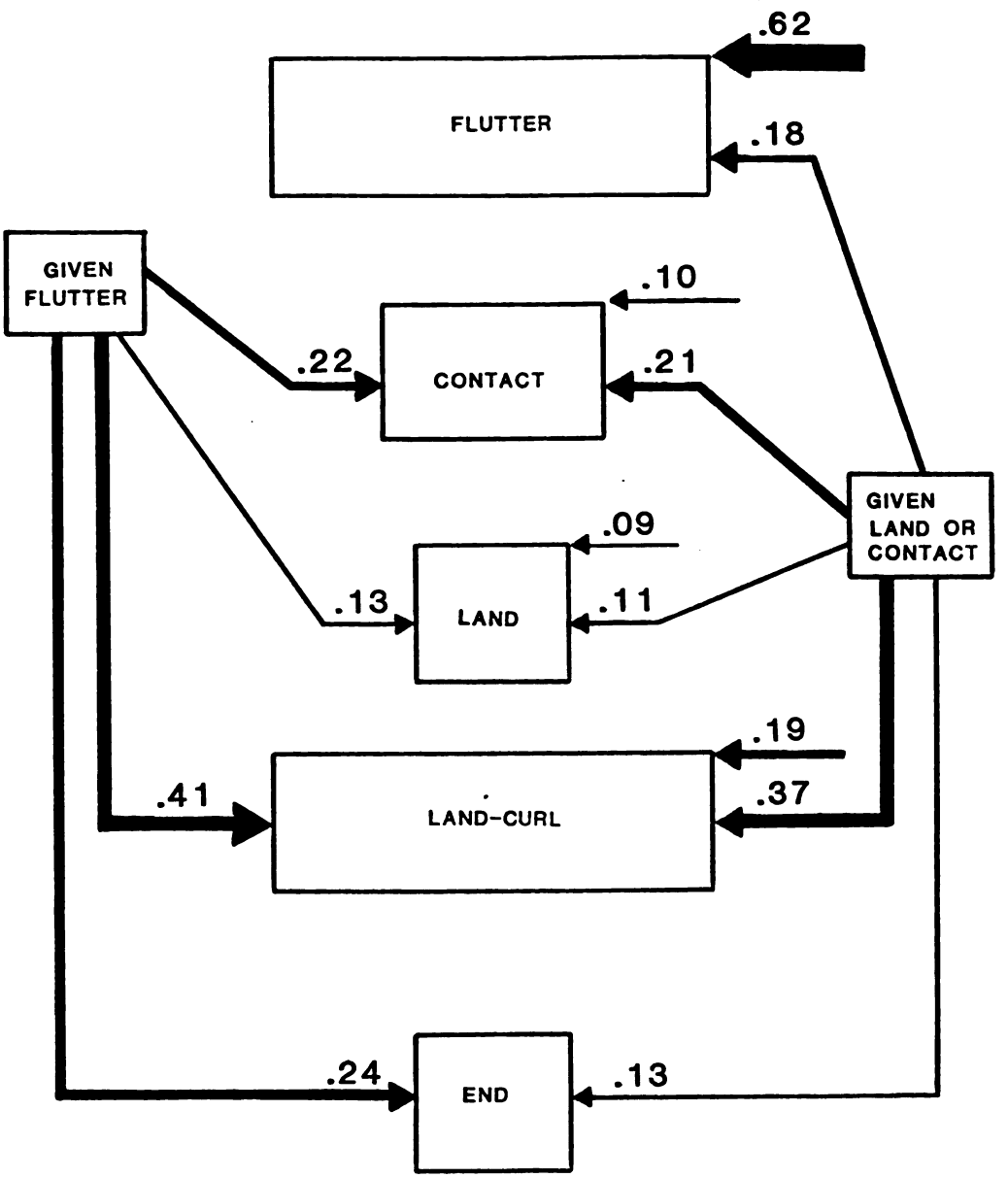


Figure 18. The visit sequence to the broccoli target (comparison I). The size of the boxes is proportional to the relative frequency of the behavior. The width of the arrows is proportional to the transitional probability between behaviors (given next to the arrow). The relative proportion of the behavior as the first act in a visit is shown by the arrow in the upper right corner of each box.

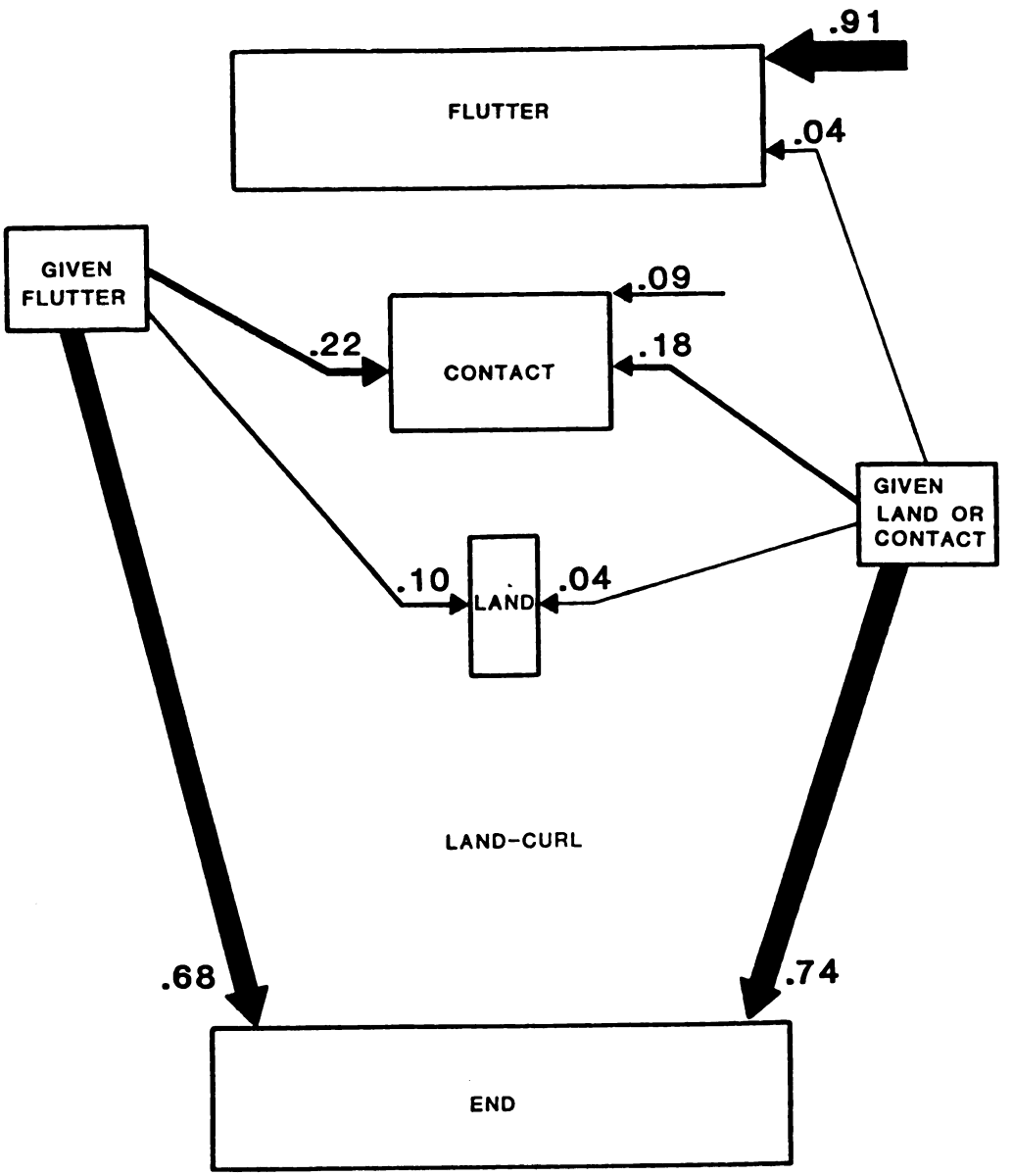


Figure 19. The visit sequence to the tansy target (comparison I). The size of the boxes is proportional to the relative frequency of the behavior. The width of the arrows is proportional to the transitional probability between behaviors (given next to the arrow). The relative proportion of the behavior as the first act in a visit is shown by the arrow in the upper right corner of each box.

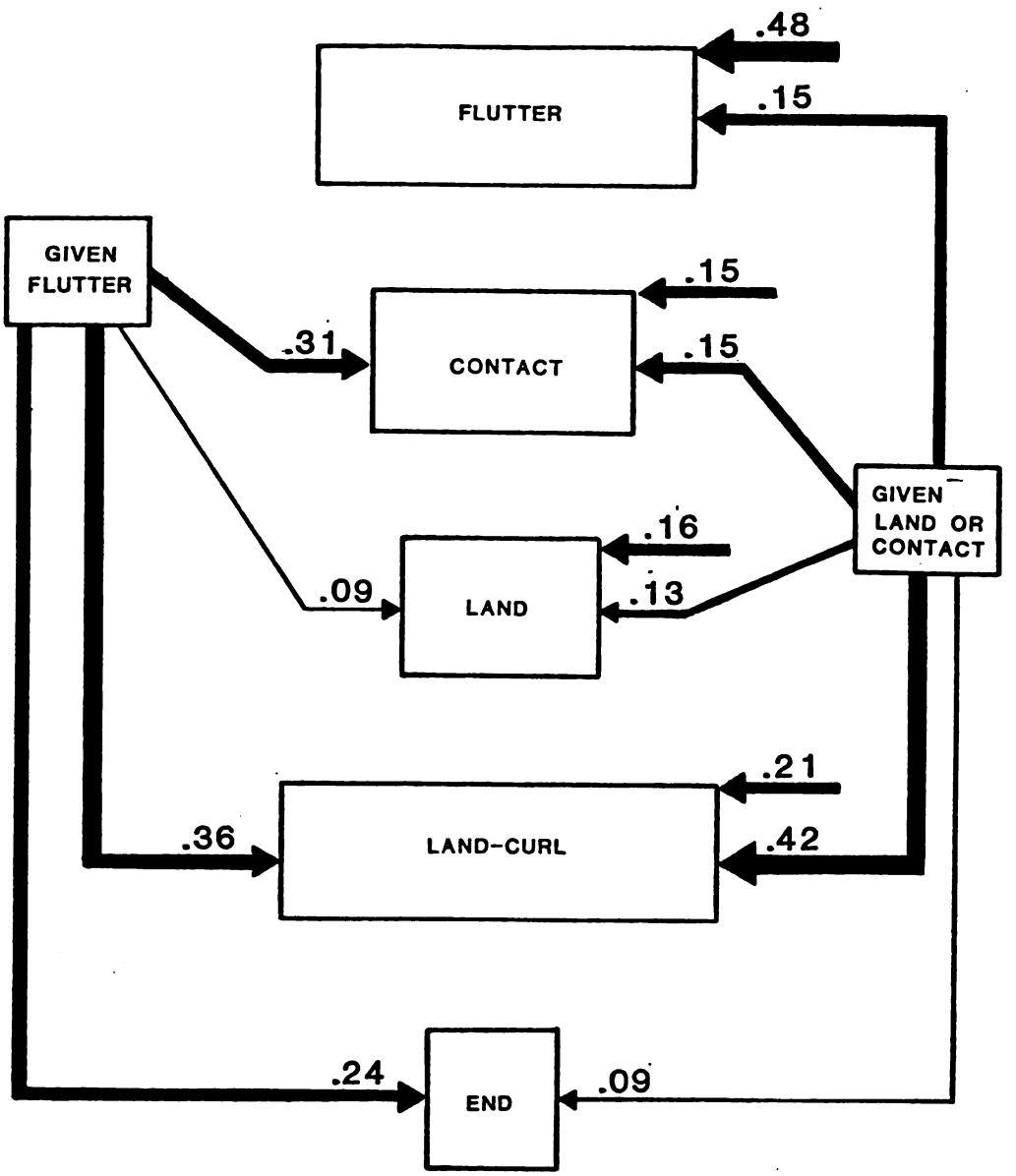


Figure 20. The visit sequence to the mustard target (comparison III). The size of the boxes is proportional to the relative frequency of the behavior. The width of the arrows is proportional to the transitional probability between behaviors (given next to the arrow). The relative proportion of the behavior as the first act in a visit is shown by the arrow in the upper right corner of each box.

act as the first behavior in a visit is also shown separately.

There are a number of similarities between visits to the three different plant species. The act of fluttering is more common than either a contact, or a land without a curl. The large number of flutters is most likely a result of the high probability of fluttering as the first act in a visit (.62 broccoli, .42 mustard, .91 tansy). The probability of fluttering after landing or contacting is considerably lower than the probability of fluttering as the first act in a visit, and is lower for tansy (.04) than for broccoli (.18) or for mustard (.21). The difference in the probability of fluttering after alighting between hosts and tansy is probably a result of an increased probability of ending after alighting on tansy (.74) as compared to the probability of ending after alighting on broccoli (.13) or on mustard (.09).

A butterfly is more likely to contact a plant than to land on it without curling. This difference is especially pronounced in the visit sequence to tansy.

The probability of contacting in the midst of a sequence (i.e., after having performed previous visit behaviors) is higher than the probability of contacting as the first act in a visit, but only slightly.

The various transitional probabilities are very similar for broccoli and mustard. This indicates that, despite differences between the two host species, common

host-specific stimuli elicit a host-visit sequence. There is no way of knowing, from these data, just what these host-specific stimuli are, but they certainly include more than just contact stimuli.

A major difference between sequences toward hosts and toward the non-host, tansy, is in the probability of ending after a land or contact, vs ending after a flutter. The probability of ending is greater after a flutter than after a land or a contact for hosts and greater after a land or contact than after a flutter for the non-host tansy. It should be emphasized that the category flutter includes butterflies having made contact with the plant, and that the data were stationary, i.e., the probability of ending after a flutter was no less after having landed as before having landed. Immediately after landing or contacting the probability of ending decreases in sequences toward hosts, but it increases again after fluttering. Therefore, the absence of host-specific contact stimuli appears to induce butterflies to terminate sequences to non-hosts after alighting. In sequences to hosts, however, stimuli perceived during the flutter stage seem to be of primary importance in determining whether butterflies will continue the visit.

IVB: Post-Curl

During a visit sequence butterflies frequently made multiple curls. Differences between host plants in the tendency to promote multiple curls could cause differences in acceptability. Since broccoli is more acceptable than mustard, it was hypothesized that butterflies visiting broccoli would make more curls than butterflies visiting mustard. To test for this, the proportion of butterflies ending after curling was calculated for the first four curls on broccoli and mustard. It was predicted that a higher proportion of butterflies visiting mustard would end after curling than butterflies curling on broccoli.

The results are shown in Figure 21. In calculating these results, only sequences observed until the butterfly left the target area were included. This amounted to 116 sequences for broccoli and 38 sequences for mustard.

The proportion of butterflies ending after each respective curl was very similar for broccoli and mustard; the sole exception was on the third curl. Twenty-two percent of the butterflies curling 3 times left the mustard target plant without curling a fourth time as compared to 57% for broccoli. These percentages are significantly different at the .05 level by a test for the equality of two percentages (Sokal and Rholf 1969) (t_s=1.966, $P<.05$). However, the percentage of butterflies ending after other curls is not significantly different between broccoli and

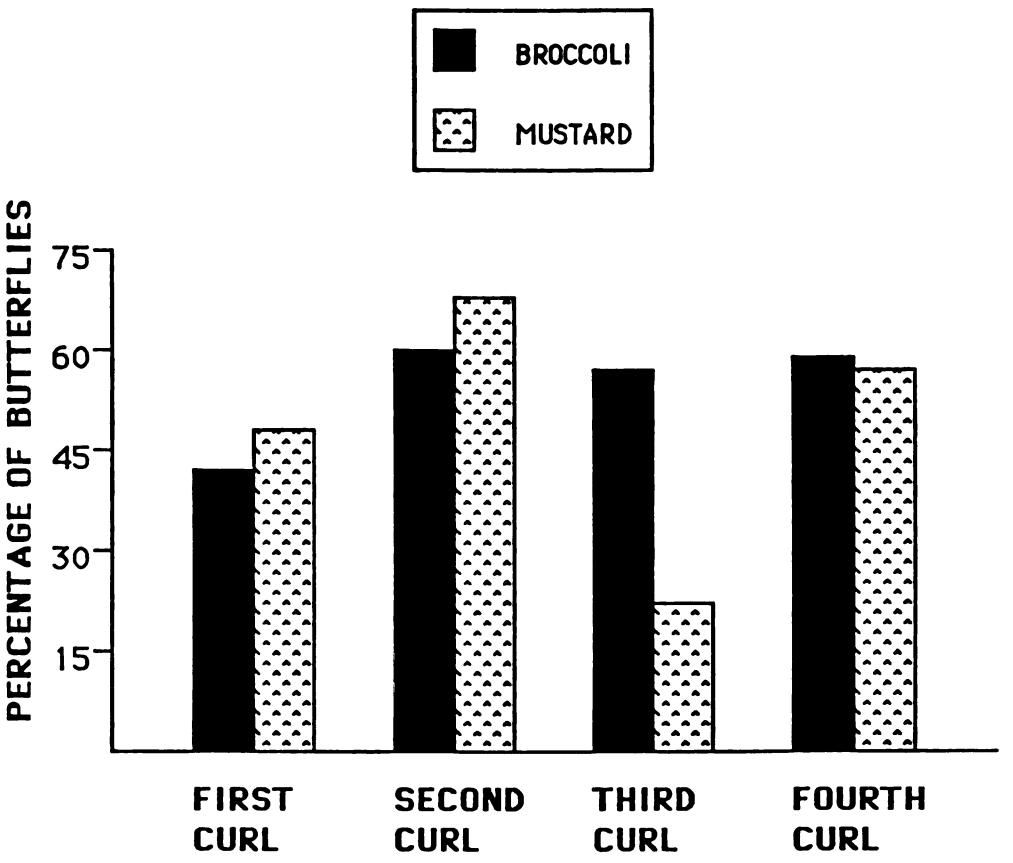


Figure 21. Percentage of butterflies ending (not making additional curls), after curling on broccoli and mustard, as a function of curl number.

mustard and, probably, these two host plants do not differ in their tendency to promote multiple curls.

Relative Discrimination

Comparisons Within a Sequence

As has been shown previously, discrimination by P. rapae does not involve simply a differential response after alighting. Rather, discrimination between hosts and non-hosts occurs at all stages and at most steps of the ovipositional sequence. The purpose of this section is to assess the relative degree of discrimination occurring at different stages and steps of the sequence to clarify how differential responses at the various stages and steps result in differences in relative acceptability.

To compare discrimination at different stages and steps, the normalized transmission, a measure taken from information theory, is used. The normalized transmision is well suited to this purpose because, being a relative measure, normalized transmissions from different experiments, or even from different species can be compared directly (Steinberg 1977).

The following is a brief discussion of information theory, including an explanation of measures on which the normalized transmission is based. This material is abstracted from papers by Steinberg (1977), Losey (1978), Estabrook (1967), and Steinberg and Conant (1974). The

interested reader is referred to these works for additional information and further clarification.

Information theory deals with the amount of uncertainty or entropy in a character. A character is a class of events and the events within a class are called the states of the character. For example, the character of sex has two states: male and female. The states within a character may also be more arbitrarily defined. For example, the character age may contain states corresponding to chronological age or may simply contain the states young and old. In this study, two characters are considered: target plant species and observed behavior pattern.

The basic unit of information is the "bit" (Shannon and Weaver 1949), which is defined as the average number of yes-no questions needed to determine the state of a character (Steinberg 1977). For example, if a group of animals were 50% male and 50% female, it would require on the average one bit of information (one yes-no question) to determine the sex of any individual animal. The maximum information required to determine the state of a character with n states is $\text{Log}_2 n$. Maximum information is required when all states are equally probable. When states are not equally probable, the determination of the amount of information required must be weighted by the probability of each state. The general formula for determining the amount of information required to detemine the state of character X is:

$$H(X) = -\Sigma P(i) \text{Log}_2 P(i)$$

where there are n states of character X and P(i) is the probability that character X assumes state i. In general, P(i) is not known. Rather, it is estimated from the maximum likelihood estimator:

$$P(i) = \frac{\text{Total number of occurrences of event i}}{\text{Total number of occurrences of all events}}$$

(Steinberg 1977)

For example, if a given population is 30% male and 70% female then the average amount of information required to determine the sex of any organism is:

$$H(X) = -[(.3 * \log_2 .3) + (.7 * \log_2 .7)] = .881.$$

Although up to this point H(X) has been discussed in terms of amount of information required to determine the state of a character, it should be realized that H(X) is also a measure of randomness or, conversely, predictability of a character. Characters that are unpredictable have an H(X) close to the maximum value. Conversely, predictable characters have an H(X) closer to zero. In the examples discussed above, when the sex ratio was 1:1, H(X) was 1 (the maximum value). When the sex ratio was 7:3, H(x) was .881. There was less uncertainty or unpredictability about the sex of an organism in this latter case. If all organisms were male, the unpredictability, H(X), would be 0.

Events may be classified according to more than one character. In this study, each sequence was classified according to the target plant species and the type of behavior exhibited by butterflies. A matrix may be constructed with the rows being the state of one character

(target plant species) and the columns being the state of the second character (behavior pattern). The amount of information needed to determine the row character, X (target plant species), can be calculated using the formula:

$$H(x) = N \log_2 N - \Sigma Fi \log_2 Fi$$

where Fi = the frequency of observations in the ith row (row totals) and N = the total frequency of observations in the matrix (grand total).

Similarly, the amount of information required to determine the column character Y (behavior pattern) can be determined by the formula:

$$H(Y) = N \log_2 N - \Sigma Fj \log_2 Fj$$

where Fj is the frequency of observations in the jth column (column totals).

The amount of information needed to determine the state of both characters in the matrix is given by the formula:

$$H(X,Y) = N \log_2 N - \Sigma \; Fij \log_2 Fij$$

where Fij = the frequencies of observations in the ith row and the jth column (cell totals).

The usual reason for constructing such a matrix is to determine the relatedness between two characters. To do so the conditional uncertainty must be calculated. Conditional uncertainty is the amount of information remaining unknown about character Y assuming the state of character X is known. Conditional uncertainty is given by the formula:

$$H(Y/X) = H(X,Y) - H(X)$$

With reference to the above example, the conditional uncertainty is the amount of information still needed to determine a butterfly's behavior assuming the target plant species is known. It should be evident that the more character Y (behavior) is influenced by character X (target plant species), the lower the conditional uncertainty, H(Y/X), will be.

The transmission, T(X;Y) is the differences between H(Y) and H(Y/X). It is, roughly, the amount the uncertainty of Y is reduced by knowing X. In the above example, T(X;Y) is the amount of information the target plant species conveys about the butterflies' behavior.

Transmission is a measure of relatedness or communication. The X character (target plant species) can be thought of as a signal and the Y character (behavior) as a response. Steinberg (1977) points out that communication is said to occur when a signal changes the probability of a behavioral response. T(X;Y) is a measure of this change. When T(X;Y) is zero, no communication occurs. As T(X;Y) approaches H(Y), the amount of communication increases.

The normalized transmission, t(x;Y) is given by the formula:

$$t(x;Y) = \frac{T(X;Y)}{H\ (Y)}$$

When expressed as a percentage, it gives the percentage of the total information needed to determine the state of character Y, that is obtained by knowing the state of character X. For example, if t(x;Y) in the example given

above were .12, this would mean that 12% of the uncertainty about a butterfly's behavior is eliminated by knowing the target plant species.

Because t(x;Y) is a relative measure, normalized transmissions from different circumstances can be directly compared to get an idea of the relative degree of communication occurring in different circumstances (Steinberg 1977). This makes the measure ideal for comparing relative degree of discrimination occurring at different stages and steps of the ovipositional sequence.

Level II: Relative Discrimination at Different Stages of the Ovipositional Sequence

To compare the relative degree of discrimination occurring at the three stages of the ovipositional sequence--movement, response, and alight--the normalized transmission for the three transitions--movement to response (Seq-->V), response to alight (V-->l-c), and alight to curl (l-c-->cu)--were calculated for comparisons I and III. The normalized transmissions were multiplied by 100% and presented as the percent communication from plant to butterfly (Figure 22).

The percent communication in comparisons I and III was very similar at equivalent stages. About 9% of the unpredictability in the butterflies' behavior was eliminated by knowing the target plant species at the movement to response transition. This compares with an approximately 10% reduction in unpredictability at the response to alight

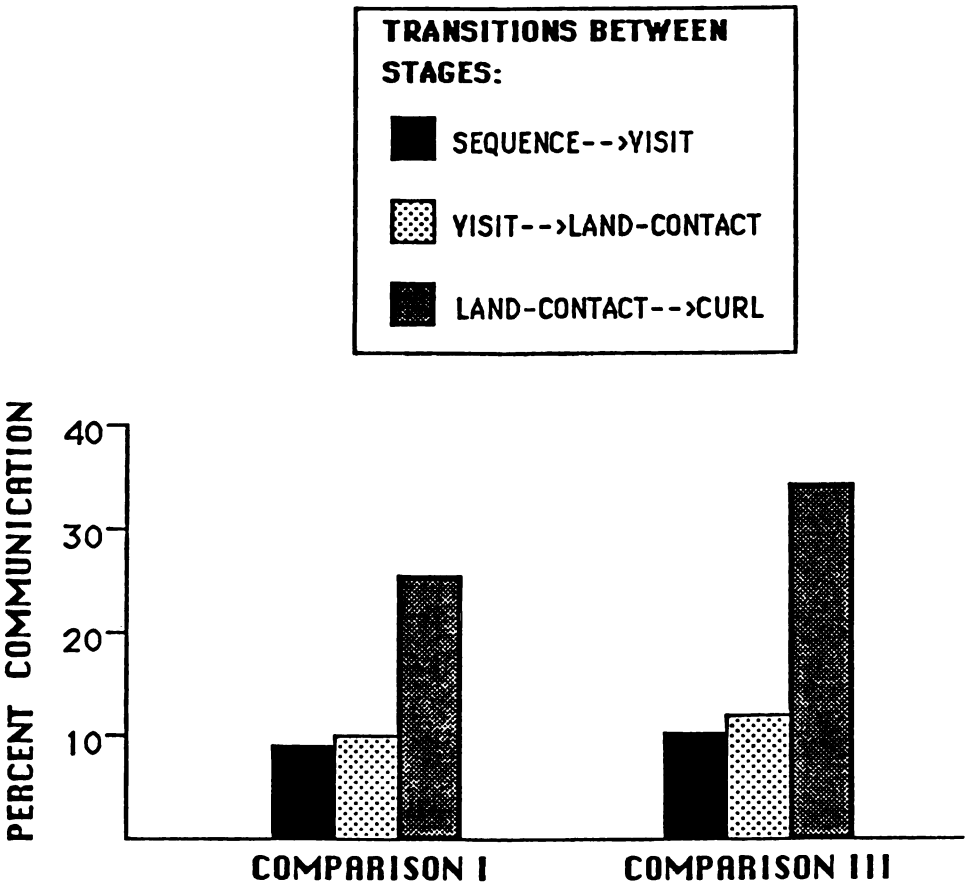


Figure 22. Percent communication from plant to butterfly during different stages of the ovipositional sequence.

transition and a 25% to 35% reduction at the alight to curl transition.

Two points are worthy of note. First, as the sequence progresses, the degree of communication increases. This is the trend one would logically expect if butterflies are assessing the plant at all stages of the sequence. The amount of information gathered about the plant should increase as the sequence progresses, and therefore, so should the degree to which the butterfly's behavior is influenced by the plant.

Secondly, the highest degree of discrimination occurs after alighting. This is in keeping with the idea of the primacy of perception of host-specific contact chemicals in host plant identification. However, it is clear that contact chemicals are not solely responsible for the total amount of discrimination shown between plants, as a good deal of discrimination takes place prior to alighting.

Level III: Relative Discrimination at Different Steps of the Ovipositional Sequence

To compare the degree of discrimination occurring at different steps of the ovipositional sequence, the total sequence was divided into a series of six steps representing the following five transitions: 1) movement from the soil space to the plant space (s-->p), 2) movement from the plant space to visit (p-->V), 3) first act exhibited in a visit (flutter, contact or land), 4) behavior after a first

flutter (f--> land, contact or end), and 5) behavior after a first alight (1-c --> cu, end or continue).

The normalized transmissions for each of these transitions for plant comparisons I and III were calculated and are presented as the percent communication from plant to butterfly (normalized transmission x 100%) (Figure 23).

As with the percent communication at different stages (see above), the percent communication at different steps is very similar for comparisons I and III. Percent communication is relatively low at the soil space step (only .9% of the uncertainty in the butterflies' behavior at this stage is eliminated by knowing the target plant species for comparison I and only.7% for comparison III). This low degree of communication probably results from the large number of butterflies entering the target area for reasons other than response to the target plant.

During the plant space step about 10% of the uncertainty in the butterflies' behavior is explained by the target plant species. The percent communication occurring at this step is probably a much better estimate of communication occurring in the movement stage, as many irrelevant sequences have been eliminated by butterflies leaving the soil space without entering the plant space (s-->end).

Knowing the target plant species reduced the uncertainty about the butterflies' first act in a visit about 3%. Thus, the target plant species determines whether

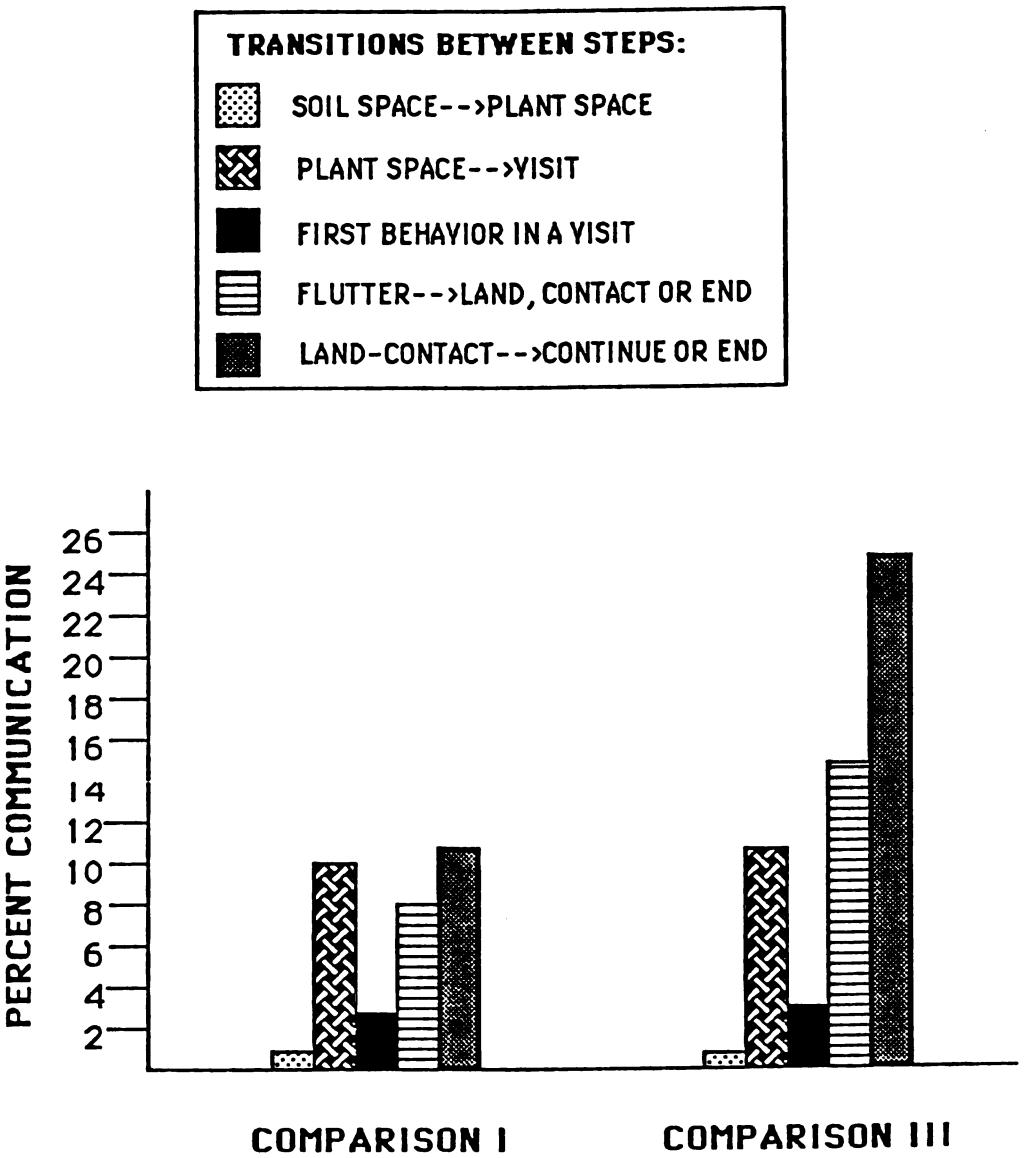


Figure 23. Percent communication from plant to butterfly during different steps in the ovipositional sequence.

butterflies will respond to the plant (visit) more than it determines the first behavior in a response.

In contrast with the 3% reduction in uncertainty about the butterfly's first behavior, knowing the target plant species reduces the uncertainty of behavior after a flutter approximately 8 to 15% and about 11 to 25% after a first land or contact. This indicates that a butterfly gains information concerning the nature of the plant during the course of a visit. Slightly more information is gained by alighting than by fluttering, but significant information is gained during the act of fluttering. A butterfly gains more information while fluttering than while approaching the plant.

As with the previous section, the amount of information gained by the butterfly increases as the sequence progresses.

Degree of Discrimination Occurring between Different Plant Types

Discrimination between plant species has been shown to exist at all stages and several steps of the ovipositional sequence. In addition, discrimination between different types of plants occurs at single stages and steps of the sequence. At almost all transitions between steps in the sequence the transitional probabilities of hosts differed significantly from those of non-hosts, thus establishing the existance of discrimination between these two plant types. At some steps discrimination between hosts of different

acceptabilities occurred. Occasionally, discrimination between different species of non-hosts also occurred.

The purpose of the present section is to compare the degree of discrimination occurring at the same stage or step of the ovipositional sequence between the following plant types: hosts vrs non-hosts, hosts of differing acceptabilities and different species of non-host. Because plant comparison III included two species of host (broccoli and mustard) and two species of non-host (lettuce and tansy), data from this comparison were used.

The index used to determine relative discrimination between different plant types was percent relative discrimination. This is the percentage of the maximum difference in the butterflies' response that is accounted for by the difference in response toward the plant types in question. It is calculated by the formula:

$$\% \text{ Relative Discrimination} = \frac{R1 - R2}{M.D.} \times 100\%$$

where R1 = the response to one plant type, R2 = the response to the second plant type, and M.D. = the maximum difference (defined below).

The response in the above formula is determined by dividing the number of butterflies advancing to the next stage or step of the ovipositional sequence for the plant type in question by the number of butterflies entering the previous stage or step in the ovipositional sequence for that plant type.

The maximum difference is calculated by subtracting the lowest response from the highest response in the comparison for the particular transition in question.

The percent relative discrimination between hosts and non-hosts is:

$$\frac{R(\text{hosts}) - R(\text{non-hosts})}{M.D.} \times 100\%$$

The percent relative discrimination between hosts is:

$$\frac{R(\text{broccoli}) - R(\text{mustard})}{M.D.} \times 100\%$$

And, the percent relative discrimination between non-hosts is:

$$\frac{R(\text{lettuce}) - R(\text{tansy})}{M.D.} \times 100\%$$

Level II: Stages of Oviposition

The percent relative discrimination for hosts vs non-hosts, hosts of differing acceptabilities and different species of non-hosts, for each stage of the ovipositional sequence is shown in Figure 24. During the movement and the alighting stage, relative discrimination is highest between hosts and non-hosts, less between different species of host, and minimal between non-hosts. This indicates that host-specific stimuli are the most important determinants of response during these stages. That host specific stimuli vary in quantity and/or quality (as perceived by the butterflies) is shown by the moderate degree of discrimination occurring between hosts of differing acceptabilities. Little discrimination occurred between

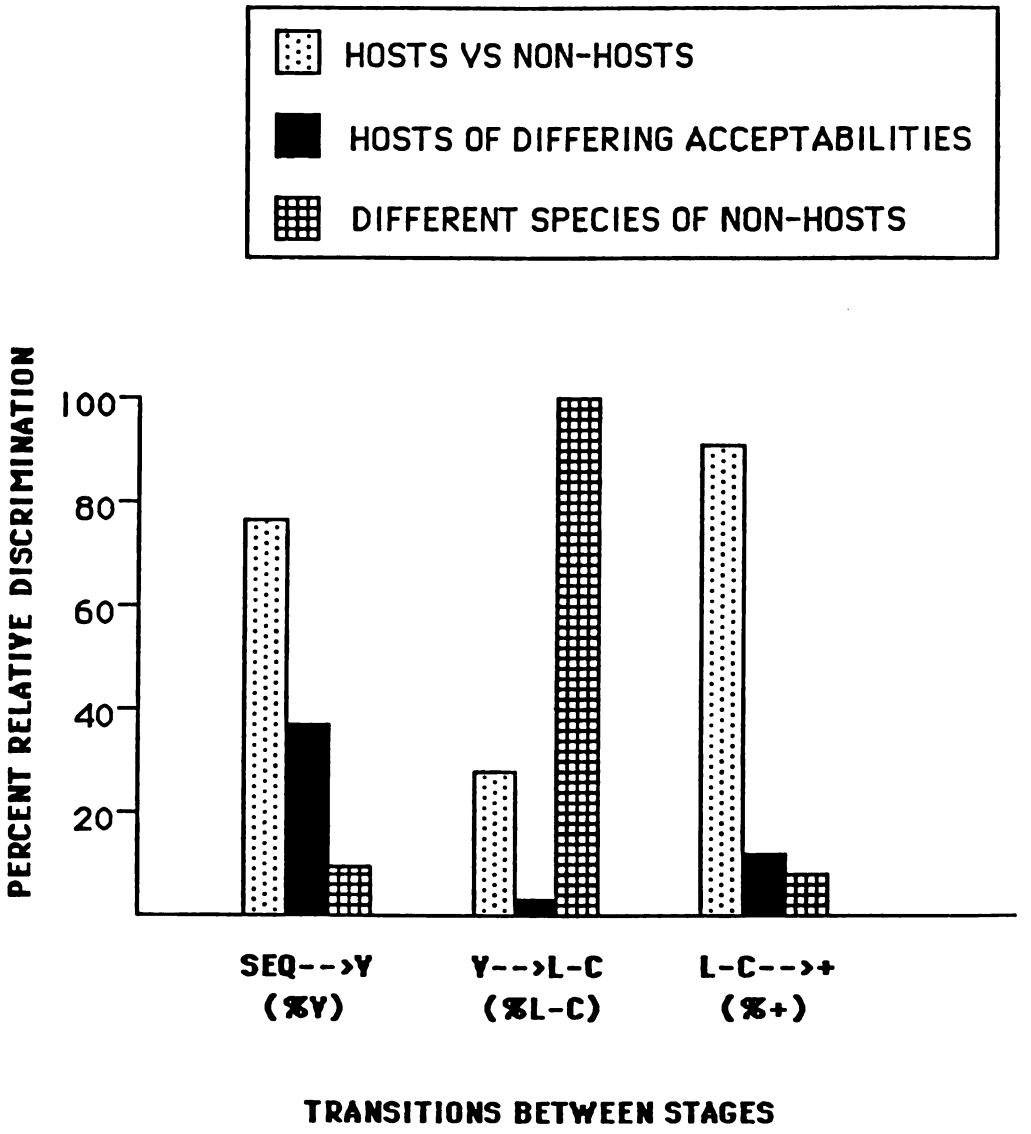


Figure 24. Percent relative discrimination between hosts and non-hosts, hosts of differing acceptabilities, and different species of non-hosts during different stages of the ovipositional sequence.

lettuce and tansy in these stages despite their different morphologies, and the reputed repellent effect of tansy.

During the response stage, discrimination between the two non-host species is very high during the response stage, higher than that between hosts and non-hosts. Discrimination between hosts is minimal at this stage. This indicates that host specific stimuli is relatively less important in eliciting alighting than are general plant characterisitics, such as visually perceived stimuli (e.g., the lettuce target) and/or the presence or absence of a repellent compound (e.g., the tansy target).

Level III: Steps of Oviposition

The percent relative discrimination for hosts vs non-hosts, hosts of differing acceptabilities, and different species of non-host at each step of the ovipositional sequence is shown in Figure 25. Both steps in the movement stage (s-->p and p-->v) show the same pattern. The relative degree of discrimination is highest for hosts vs non-hosts, lower between hosts, and lower still between the two non-hosts. As discussed previously, this indicates that host-specific stimuli are the most important factors eliciting an approach to the plant. Differences in the quality and/or quantity of host plant stimuli are relatively less important, and differences in general plant stimuli are of relatively minor importance.

The step corresponding to the first behavior in a visit is presented twice, once representing the difference in the

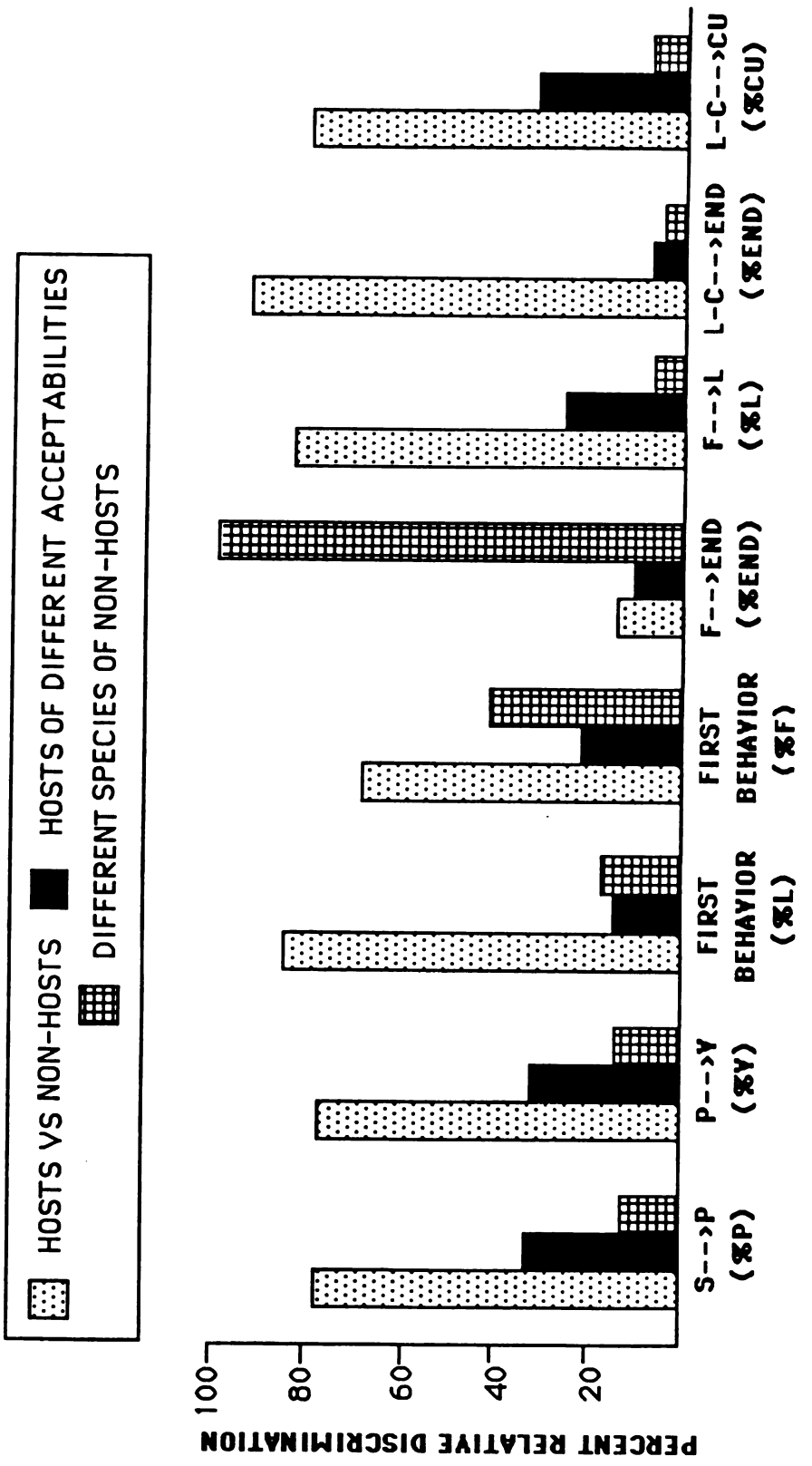


Figure 25. Percent relative discrimination between hosts and non-hosts, hosts of differing acceptabilities, and different species of non-hosts, during different steps of the ovipositional sequence.

proportions of first flutters, the second time representing the difference in the proportions of first landings. In both cases, maximal discrimination occurs between hosts and non-hosts. This indicates that host-specific stimuli are more important in determining the first behavior of visiting butterflies than are general plant stimuli or differences in host-specific stimuli.

The degree of discrimination among non-hosts is higher than that between hosts for the first behavior in a visit. This difference is large for the proportion of first flutters, and minimal for the proportion of first lands. This indicates that differences in general plant stimuli influence the probability of fluttering more than do quantitative and/or qualitative differences between hosts, but that these two types of stimuli affect the probability of landing about equally.

The behavior following an initial flutter is also presented twice, once representing the proportions of flutters that were followed by a butterfly leaving the target area (f-->end); the second time representing the proportions of flutters resulting in a land (f-->l). Host-specific stimuli are very important in determining landing after a flutter, as indicated by the high degree of discrimination occurring between hosts and non-hosts at this point. Host-specific stimuli are much less important in determining the proportion of fluttering butterflies that left the target area. For the flutter to end transition

(f-->end), the degree of discrimination is highest among non-hosts. This indicates that differences in general plant characteristics, such as morphological differences and/or the presence or absence or repellent characteristics, are important in determining the proportion of fluttering butterflies that leave the target area.

Behavior after the first land or contact is depicted twice, once representing the proportion of alighting butterflies that left the target area (1-c-->end), the second time representing the proportion of alighting butterflies that curled (1-c-->cu). The degree of discrimination, for both proportions, is greatest between hosts and non-hosts, indicating that host-specific stimuli are the most important determinanats of behavior after alighting. Quantitative and/or qualitative differences in host-specific stimuli are moderately important in determining the proportion of alighting butterflies that curled, as indicated by the moderate degree of discrimination occurring between hosts at this point. Such differences apparently most influence the proportion curling. Differences between non-host species apparently have minimal influence on post-alighting behavior.

Miscellaneous Results and Discussion

Correlation of Number of Visits to Number of Eggs

Because behavioral sequences of only a fraction of the butterflies entering the target area during a sampling

interval were recorded, a check on the accuracy of the sampling method is needed. Two independent measures of butterfly responsiveness during a sampling interval were recorded: the number of visits to the target plant (using the sequence sampling method) and the total number of eggs laid on the target plant. Correlations between these two independent measures were performed for the broccoli target (comparison I), the mustard target (comparison III), and the broccoli-tansy target (comparison IV).

Significant correlation coefficients were obtained for all three target plants (Figures 26, 27, 28). The correlation coefficient was .758 (P (r=0)=.006) for broccoli, 0.856 (P(r=0)=.001) for mustard, and .866 (P(r=0)=.037) for broccoli-tansy. This indicates that the sampling method accurately measured differences in the day-to-day responsiveness of the butterflies. Therefore, it can be assumed that this method also accurately measured differences in P. rapae responsiveness toward different species of target plant.

Increase in Butterfly Responsiveness over the Season

Because the broccoli and tansy targets were included in most plant comparisons, data were taken on these plants during the entire study period. An examination of the results in Tables 7 through 15 reveal that some transitional frequencies for the broccoli and tansy targets progressively increase from one comparison to the next. For example, the

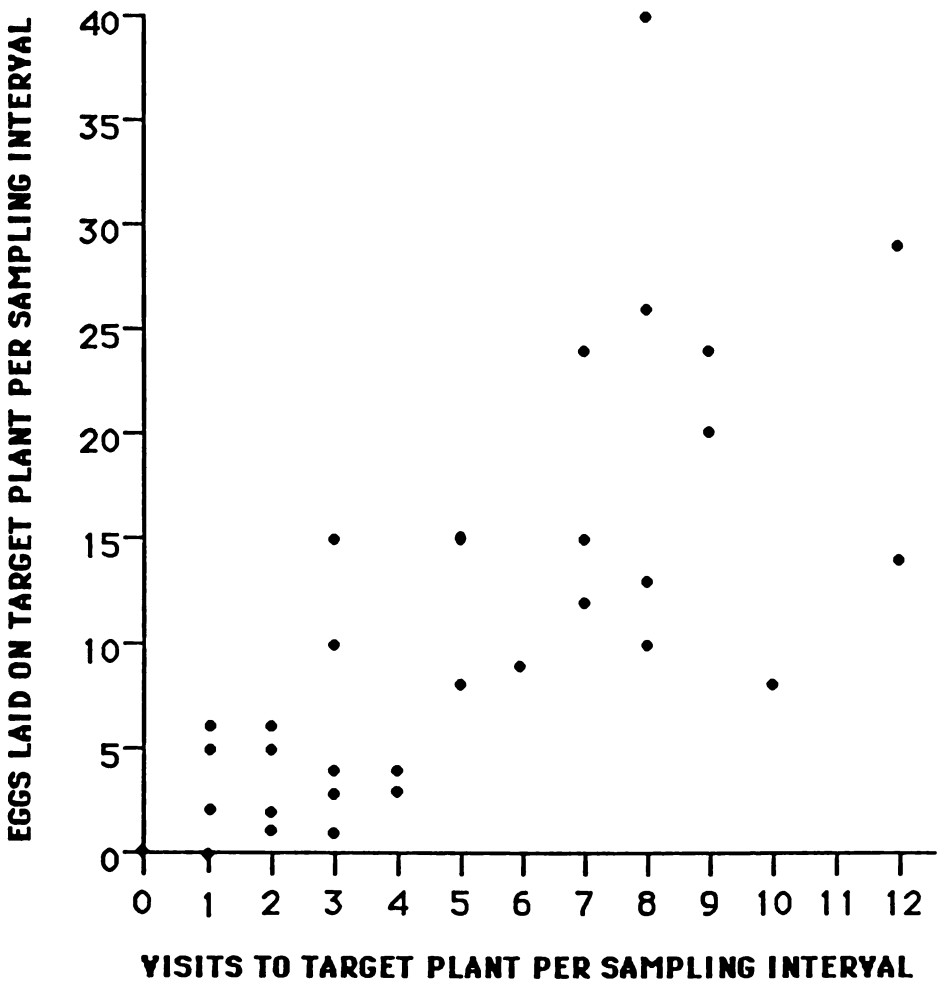


Figure 26. Eggs laid per sampling interval vs visits per sampling interval for broccoli (comparison 1). r=.758.

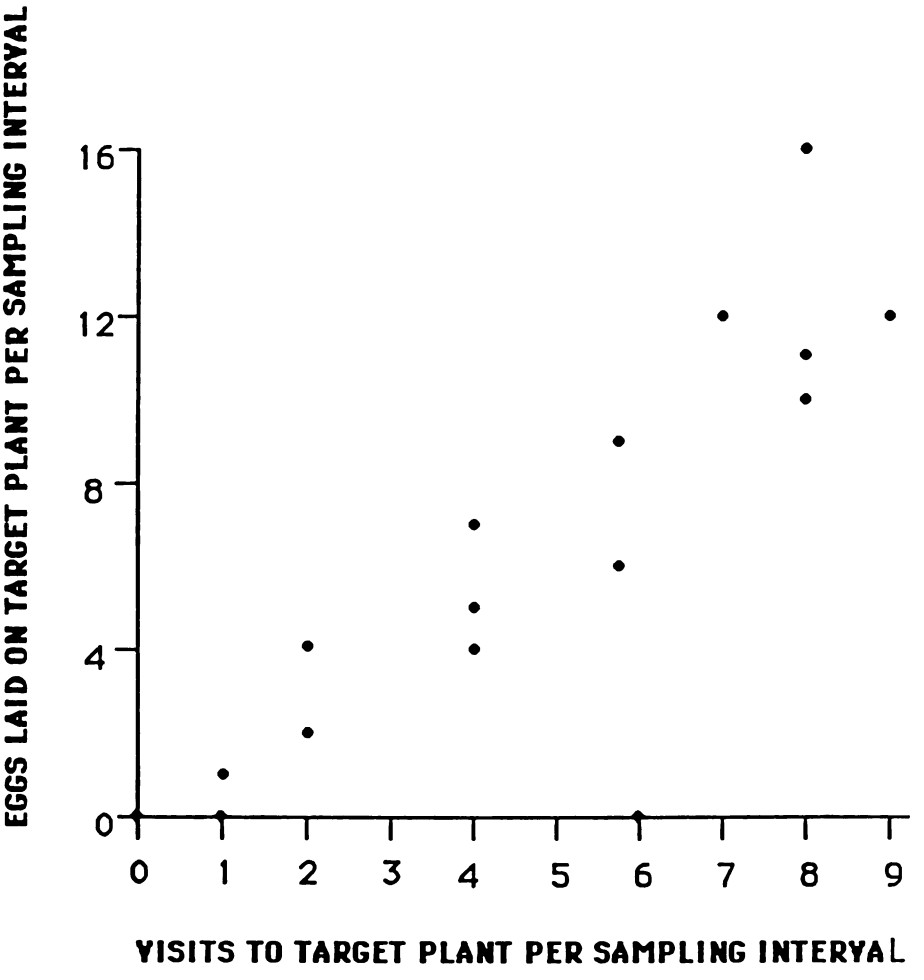


Figure 27. Eggs laid per sampling interval vs visits per sampling interval for mustard (comparison III)> r=.856

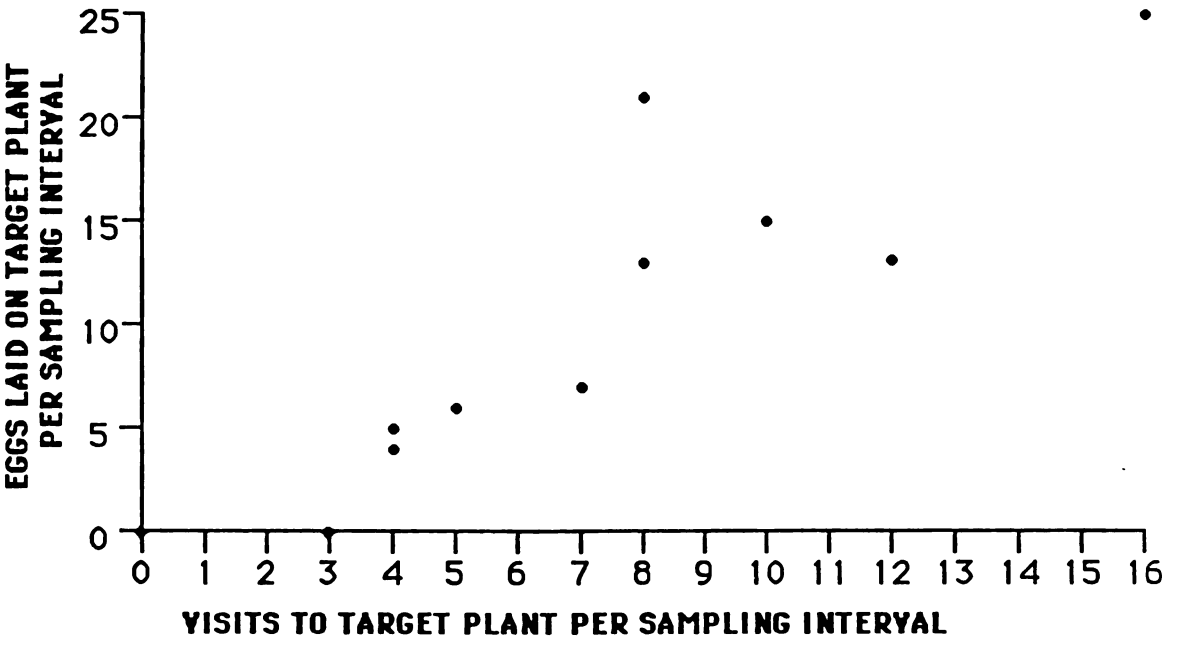


Figure 28. Eggs laid per sampling interval vs visits per sampling interval for broccoli-tansy (comparison V). r=.866.

proportion of butterflies flying into the soil space that flew into the plant space (s-->p) was 0.458 for broccoli in comparison II, 0.514 in comparison III, and 0.591 in comparison V. The same proportions for the tansy target were 0.350 in comparison II, 0.401 in comparison III, 0.436 in comparison IV and 0.496 in comparison V.

Because data were taken on successively numbered comparisons progressively later in the season the trend noted above may indicate an increase in the measured responsiveness of butterflies as the study season progressed. To check this, the percentage of butterflies advancing from one step to the next (for the transitions s-->p, p-->v, f-->l and l-->cu) for broccoli in comparison II were compared to the percentages for the same steps for broccoli in comparison V. Comparisons II and V were used because no overlap occurred in sampling dates, comparison II being done between July 21 and August 21 and comparison V being done between September 6 and October 17. This proceedure was repeated for tansy. Percentages for the same step, and the same target plant, but in different comparisons, were tested for significant differences using a test for equality of two percentages (Sokal and Rholf 1969).

With the exception of the percentage p-->V for tansy, the proportion of butterflies advancing from any one step to the succeeding one was greater in comparison V than in comparison II at every step for both the broccoli and the tansy target (Table 21). The percentage of butterflies

Table 21. Percentage of butterflies making the same transition between behaviors for the same plant (broccoli or tansy) in different comparisons (different sampling dates).

TRANSITIONS	COMPARISON II	COMPARISON V	t*	P**
BROCCOLI:				
Soil Space to Plant Space (s-->p)	45.8	59.1	-4.27	<.005
Plant Space to Visit (p-->V)	32.2	42.1	-2.44	<.02
Flutter to Land or Contact (f-->l-c)	66.1	82.2	-2.08	<.05
Land or Contact to Curl (l-c-->+)	82.2	88.6	-1.20	>.05
TANSY:				
Soil Space to Plant Space (s-->p)	35.0	49.6	-4.78	<.005
Plant Space to Visit (p-->V)	13.7	05.6	2.97	<.01
Flutter to Land or Contact (f-->l-c)	25.9	36.4	-6.36	>.05

* t = t-statistic,
** P = probability.

flying from the outer (soil) space to the inner (plant) space (s-->p) was significantly higher in comparison V than in comparison II for both tansy and broccoli. The percentage of butterflies entering the plant space that visited the plant (p-->V) was significantly higher in comparison V for broccoli and significantly lower in comparison V for tansy. The proportion of fluttering butterflies that alighted was significantly higher in comparison V for the broccoli target, but not for the tansy target. There was no significant difference in the percentage of alighting butterflies that curled on broccoli. Therefore, the idea that the measured responsiveness of butterflies increased as the study season progressed is partially supported by these data.

There are two alternate reasons for the measured responsiveness to increase during the course of the study: either a change in the judgments made by the observer or an actual change in the behavior of butterflies. There is evidence supporting the latter explanation. The mean number of eggs laid per sampling interval on broccoli is higher for those comparisons done later in the season (see Table 6, p 78). The mean number of eggs laid per sampling interval on broccoli is 7.13 in comparison II, 11.94 in comparison III, and 12.07 in comparison V. The number of eggs laid on a target plant during a sampling interval was measured independently of the number of visits to the plant,

indicating that the observed increase in responsivness was a real phenomenon and not a result of observer bias.

There are many possible explanations for the increase in butterfly responsiveness as the season progressed. First, there was a change in the wild vegetation in the cage. During the season the wild plants continued to grow and the vegetation as a whole became more dense. This change may have increased the probability of ovipositing butterflies entering the target area.

A second possibile explanation for the increase in responsiveness is unintentional artificial selection. Since the eggs used to continue the P. rapae culture were laid by butterflies in the cage, the females most responsive to hosts in the cage left the most progeny. The culture may have become increasingly more adapted to cage life. The butterflies used at the end of the study had been ovipositing in the cage for two to four generations.

Whatever the explanation, the difference in the proportion of butterflies advancing from any given step to the next among different target plant species remains relatively constant from one comparison to the next. For example, the difference between broccoli and tansy in the percentage of butterflies flying from the soil space to the plant space was 10.8% for comparison I and 9.5% for comparison V. The difference between broccoli and tansy in the percentage of fluttering butterflies that alighted (f-->l-c) was 40.2% for comparison I and 45.8% for

comparison V. Therefore, this increase in responsiveness probably had little effect on results.

Ending Behavior

Butterflies entered the target area for a variety of reasons, including response to the target plant. While it is virtually impossible to evaluate the motivation of butterflies entering the target area, by observing what they did after leaving the target area it was possible to infer, to some extent, their motivation upon exiting. The general hypothesis tested in this section was that the motivation of butterflies would be affected by their experience with the target plant, and therefore, the ending behavior (i.e., what a butterfly did after leaving the target area) of butterflies that had progressed to different steps of the sequence before exiting would differ.

Ending behavior was recorded whenever possible for observed sequences. Descriptions of the ending behaviors can be found at the bottom of Table 3 (p 50). Ending behaviors were grouped into three categories: oviposition, feeding, and "other." Feeding behaviors included behaviors directed toward real or artificial flowers: fluttering around a flower (ff), contacting a flower (cf), and landing on a flower (lf). Ovipositional behaviors included fluttering around a reserve host (fh), contacting a reserve host (ch), contacting wild vegetation (cv), and landing on a host or non-host and exhibiting behaviors associated with

oviposition, such as drumming or curling (lh-ov, lv-ov). The ovipositional category is further subdivided into behaviors directed toward hosts (fh, ch, lh-ov) and those directed toward non-hosts (cv, lv-ov).

Ending behaviors classified in the "other" category include: flying toward another butterfly (S), flying upward into the air (A), fluttering around non-hosts (fv), and landing on hosts (lh) or on non-hosts (lv), but not exhibiting behaviors associated with oviposition.

The total number of ending behaviors in each category was calculated for the broccoli target (comparison I). The specific hypotheses that were tested include:

1. It was hypothesized that the closer a butterfly that was motivated to oviposit was to the target host, the more likely it was to recognize the host and direct ovipositional behavior toward it. Therefore, it was predicted that a lower proportion of those butterflies leaving the target area after entering the plant space (p-->end) would exhibit ending behaviors in the ovipositional category than butterflies leaving the target area after entering the soil space (s-->end).

2. It was hypothesized both that most of the butterflies visiting hosts were motivated to oviposit and that the act curl was a consummatory act, i.e., an act, which, when completed, reduces the internal motivation to perform that act. Therefore, it was predicted that a higher proportion of the butterflies visiting the plant but not

curling (V-->end; includes the transitions f-->end and l-c-->end) would exhibit ending behavior in the ovipositional category than either butterflies that left the target area without visiting (s-->end and p-->end) or butterflies that curled.

3. It was hypothesized that the experience of tarsal contact with hosts would increase the ability of butterflies to distinguish between hosts and non-hosts. Therefore it was predicted that, of the butterflies exhibiting ending behavior in the ovipositional category, a larger proportion of those alighting on the target host (l-c-->end and curl) would direct their ending behavior toward hosts, than butterflies that had not alighted.

Figure 29 shows the proportion of butterflies exhibiting ending behavior in each of the three ending categories as a function of how far they progressed through the ovipositional sequence. As expected, the proportion of butterflies exhibiting ending behavior in the ovipositional category generally increased as the sequence progressed. The proportion exhibiting ending behavior in the feeding category decreased and the proportion in the "other" category remained relatively constant.

A total of 7.4% of the butterflies ending after entering the soil space (s-->end) exhibited ending behavior in the ovipositional category, compared to 3.6% for butterflies ending after entering the inner plant space (p-->end). These two percentages are significantly

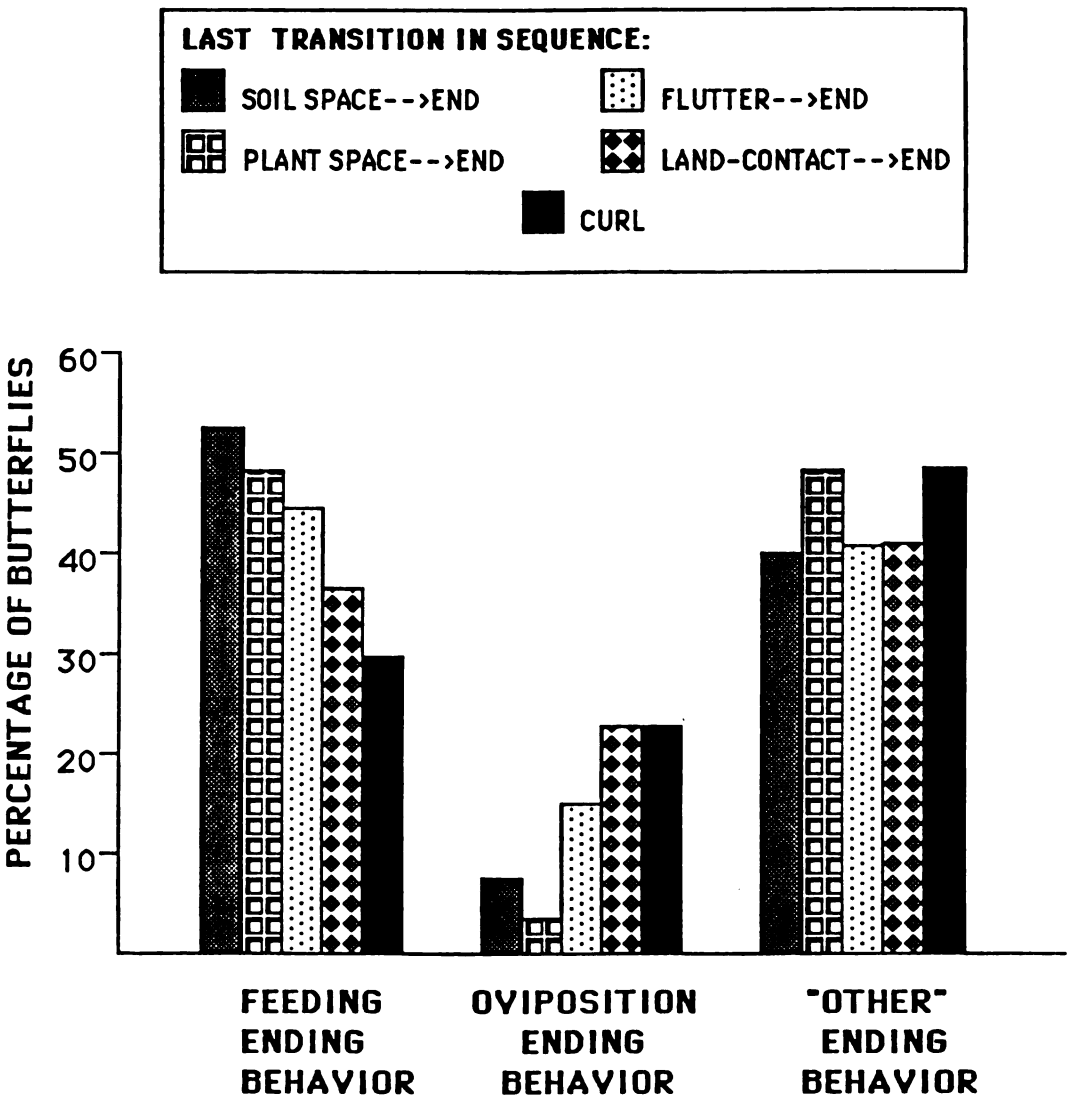


Figure 29. Percentage of butterflies performing ending behaviors in the feeding, oviposition, and ending categories as a function of how far they progressed through the sequence

different (using a test for the equality of two percentages, Sokal and Rholf 1969, $t= 2.13$, $p<.025$). This indicates that butterflies closer to hosts are more likely to recognize and respond to them.

The proportion of butterflies exhibiting ovipositional ending behavior is higher for butterflies that visit the plant, but do not curl than for butterflies not visiting the plant. However, contrary to expectation, the proportion of butterflies exhibiting ovipositional ending behavior does not decrease significantly after curling has occurred. Therefore, the idea that the curl is a consummatory act, decreasing internal motivation, is not supported by these data.

Figure 30 shows the proportion of butterflies exhibiting ovipositional ending behavior directed toward hosts (rather than toward non-hosts) as a function of how far they progressed in the sequence. Although the proportions appear to differ, the samples are small and no two percentages differ significantly. Therefore, the idea that contact with host foliage increases the butterflies' ability to discriminate between hosts and non-hosts is not supported by these data.

Total Time

As mentioned previously, the sampling method used in this study was to record an approximately equal number of sequences for each target species used on any given sampling

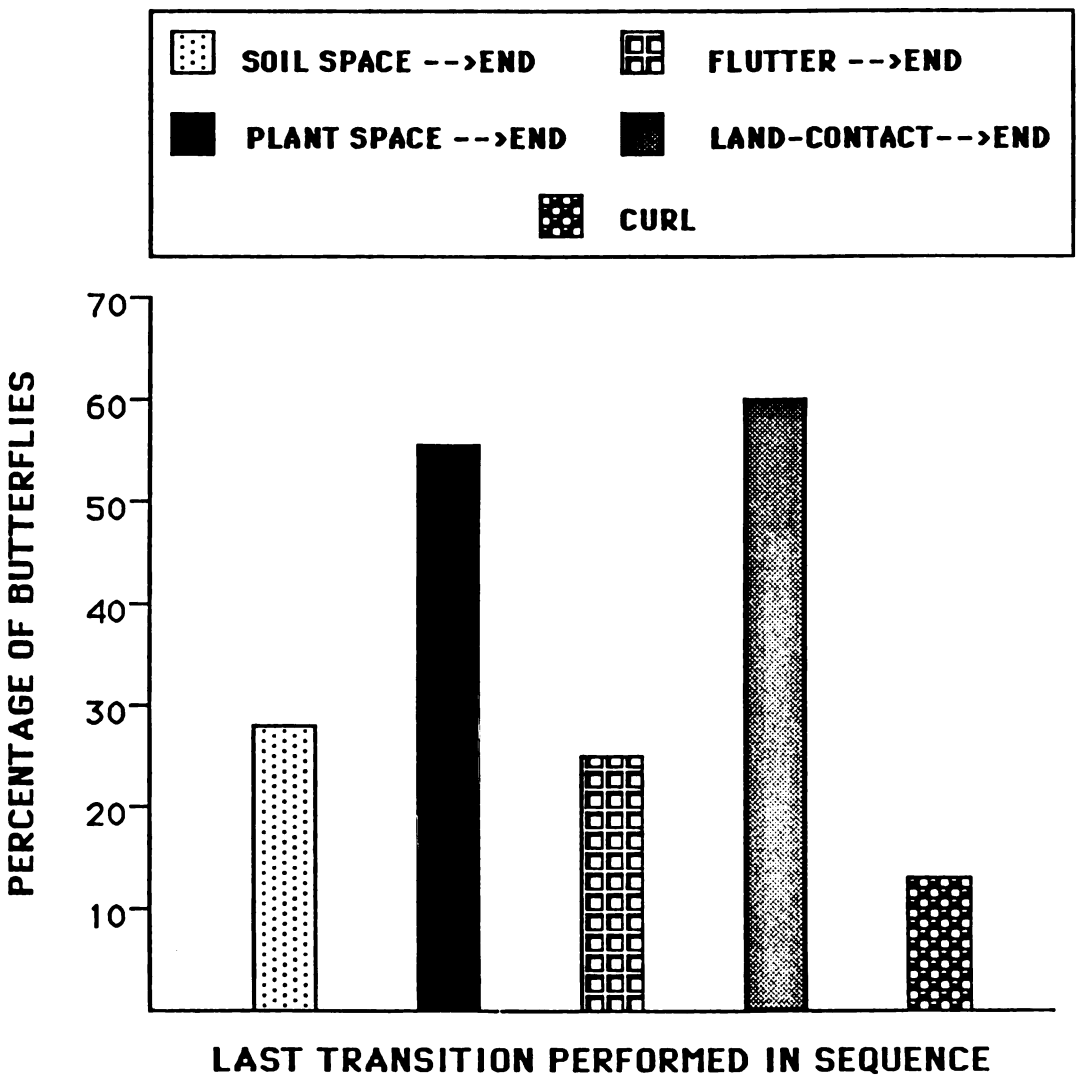


Figure 30. Percentage of butterflies exhibiting ending behavior classed as "ovipositional" that directed their ending behavior toward hosts rather than toward non-hosts as a function of how far they progressed in the ovipositional sequence.

date. As a result, the length of the sampling intervals varied. If the length of sampling intervals was, on the average, different for different species of target plant, then a bias might occur that could affect results. To check for this possibility, the sampling interval lengths for the different target plant species in a single comparison were analyzed for significant differences using a two-way ANOVA (randomized block design with days as blocks).

While the length of sampling intervals varied significantly among different sampling dates (as would be expected from differences in weather conditions) it did not differ significantly among different target plant species (Table 22). Upon initial consideration, it may seem that sampling intervals should be shorter for hosts than for non-hosts because butterflies would be stimulated to approach hosts and, therefore, more would fly into the target area. However, since a higher proportion of butterflies visiting hosts progressed farther in the sequence, the sequence length was longer and took longer to record. Presumably, these two effects cancelled each other out, resulting in no difference in sampling interval length between hosts and non-hosts.

Table 22. Mean length of time of sampling intervals (time taken to record sequences) for different target plant species.

Comparison	Plant Species	Mean Length of Time for Sampling Interval (Minutes)
I	Broccoli	18.8
	Tansy	18.0
		F=.901, df=1, P=.350
II	Broccoli	19.5
	Tansy	18.0
	Pot	19.3
	Sage	19.5
		F=.319, df=3, P=.811
III	Broccoli	16.6
	Tansy	16.5
	Mustard	15.7
	Lettuce	15.2
		F=.479, df=3, P=.699
IV	Tansy	14.3
	Lettuce	14.7
	Soybean	16.3
		F=.585, df=2, P=.572
V	Broccoli	14.3
	Tansy	13.8
	Broccoli-Tansy	15.5
		F=.608, df=2, P=.556

GENERAL DISCUSSION

Methods

The methods used in this study are well-suited to discrimination studies for several reasons. First, an ideal way to study a behaviorally-based phenomenon such as discrimination, is to study the behavior directly. Results based on indirect data, such as the number of eggs laid, or damage done, while useful for many purposes, may lead to erroneous conclusions about behavior. Jones (1977) gives the following example. Kobayashi (1965), observing the egg distribution of Pieris rapae in Japan, found that egg distribution changed with egg density, tending toward a uniform distribution at high densities and a clumped distribution at lower densities. He suggested the butterflies changed their behavior at high densities. Jones (1977) studied the movement behavior of P. rapae and found that no such change in behavior either occurs or is necessary to account for the change in egg distribution. Rather, the observed change in distribution with density was a statistical result of two parameters--the probability of laying an egg during a visit and the probability of a repeat visit to a host--which jointly determined the number of eggs a butterfly laid on a host.

Secondly, there are distinct advantages to studying behavior as a sequence. Most complex behaviors such as oviposition consist of a temporally-ordered series of

separate responses, each elicited by its own set of sensory stimuli. Studying discrimination behavior as a sequence allows for determination of the amount of discrimination occuring during different responses. Since the influence of a specific stimulus on response may vary throughout the sequence, this determination may be important to purposes of the study. For example, Kennedy (1965) points out that attempting to control the spread of a virus spread by an aphid vector by masking an odor stimuli would be futile because the odor works only as an arrestant when the aphid is close to the plant, not as a long range attractant. Only by examining the aphids' behavior as a sequence of separate stages could this determination be made.

Thirdly, dividing a sequence of behaviors several different ways may be advantageous. Making multiple divisions of a sequence of behavior is justified in that behavior is, in reality, a continuum. "The stream of behavior may be sliced up many ways" (Drummond 1981). Because <u>any</u> division of the sequence is artificial, the validity of the divisions used can only be judged by the understanding they promote. Making multiple divisions is advantageous in that, while finer divisions result in a greater understanding of the behavioral components of the sequence (e.g. the actual acts), coarser division allows discrimination to be judged within the context of the entire sequence (for example, it allows for the assessment of the

respective roles of pre-alighting vs post-alighting discrimination).

The choice of behavioral units to record is dictated by the desired divisions of the sequence. In this study, the smallest reliably observable behavioral units were chosen. This allowed for a more detailed study of behavior than is possible in most field studies of free-flying butterflies. In addition, the smallest units of behavior were recorded because it is always possible to consolidate behavioral units into higher categories and thus study a more coarsly-divided sequence, but it is not possible to subdivide behaviors already recorded (Lehner 1979).

Fourth, the use of butterflies confined to a field cage is ideal for discrimination studies because it maxmizes the advantages and minimizes the disadvantages of using either butterflies confined to small laboratory cages or wild, free-flying butterflies. While the behavior of butterflies confined to small indoor cages is relatively easy to observe and between treatment variation can be kept to a minimum, problems arise when generalizing results obtained with these severely confined butterflies to the behavior of natural populations. This is, perhaps, especially true when the subject of investigation is discrimination.

The degree to which discrimination patterns observed in severely confined colonies of butterflies can be considered natural is questionable. First, the conditions of confinement may prevent the expression of certain behavior

patterns. For example, butterflies kept in small cages cannot be expected to exhibit normal host-finding behavior (Papaj and Rausher 1983). Secondly, the habitat of such confined animals is often a gross oversimplification of normal conditions. Thus, such animals are usually deprived of stimulus situations which release normal behaviors. In addition, such caged animals are often intentionally deprived of essential stimuli in order to increase their responsiveness during experiments. A common result of such deprivation, both intentional and unintentional, is a lowering of the threshold of stimuli required to release a given response (Singer 1982, Lorenz 1981). Consequently, deprived animals often exhibit responses toward objects that would not normally release such responses. The net result may be abberent patterns of discrimination.

> "If insects in small cages cannot exhibit normal host location, neither are they likely to display normal host postalighting behavior. Thus confined, the insects' inability to search normally will lead to irregular rates of encounter with the host plants. This, in turn, will lead to irregular levels of discrimination and this will cause irregular patterns of postalight selectivity". Papaj and Rausher 1983.

The field cage used in this study was much larger than small laboratory cages often used for studies of ovipositional behavior and contained a "natural habitat". Thus, the complications discussed above were minimized.

Other problems arise when using free-flying butterflies in behavioral studies. The first concerns the observability of behavior. That which cannot be observed cannot be

described and recorded. It is often difficult to observe the behavior of insects because of their small size. Detailed observations would require a close proximity to free-flying butterflies which is sometimes difficult to maintain with free-flying butterflies. A second problem lies with the heterogeneity of habitats that a free-flying butterfly is likely to encounter. It has been shown that differences in habitat can affect the behavior of phytophagous insects in general and P. rapae in particular (Stanton 1983, Root and Kareiva 1984, Cromartie 1975, Smith 1976). Since discrimination in this study was assessed on the basis of differences in behavior toward various plant species, it was crucial that such differences be due to differences among the plants themselves and not due to differences in local habitat. The use of a field cage in this studied allowed the observer to be close to the butterflies and also ensured a heterogenous habitat.

In sum, four different aspects of the methods used in the present study are particularly well-suited to discrimination studies in general. These include; direct observation of behavior, observation of ovipositional behavior as a sequence, analysis of the sequence divided several different ways, and the use of butterflies in a field cage.

Hypotheses and Results

The following discussion summarizes the major hypotheses, predictions and results in the first section of the results as they concern discrimination between: 1) hosts vs non-hosts, 2) hosts of differing acceptabilities, 3) different species of non-hosts, and 4) repellent vs non-repellent plants.

Hosts vs Non-Hosts

Cabbage butterflies exhibit significant discrimination between hosts and non-hosts during all stages and most steps of the ovipositional sequence (Table 23). In virtually every plant comparison (the sole exception to be discussed later), a higher proportion of butterflies exhibited a response toward hosts than toward non-hosts during each sequence step. This higher degree of responsiveness toward hosts occurred even in comparison III, which included two host species differing greatly in external morphology. These results imply that host-specific stimuli exists toward which cabbage butterflies preferentially respond. These host specific stimuli are perceived at all stages and steps of oviposition, including those steps prior to tarsal contact with a plant.

The results support the idea that cabbage butterflies are able to perceive host-specific plant stimuli and, as a result, discriminate between hosts and non-hosts: 1) while at least short distances from hosts plants, 2) during the

Table 23: Summary of the hypotheses, predictions, and results from the first section of the results for hosts vs non-hosts.

Key for Results:

* Significant difference between response toward hosts and toward non-hosts for the indicated comparison.

+ The difference between response toward hosts and toward non-hosts is as predicted from the hypothesis, but the difference is not significant at the .05 level.

0 The difference between response toward hosts and toward non-hosts is not as predicted from the hypothesis.

Table 23.

General Assumption: Host plants generate host-specific stimuli which butterflies perceive. Perception of these stimuli results in butterflies responding preferentially toward hosts.

Results Hypotheses	Analysis Sections	Predictions	Comparisons I	II	III	V
1. Host-specific stimuli are perceived while the butterfly is at least short distances from the plant. A butterfly responds by approaching and visiting the plant.	2A	A higher proportion of butterflies entering the target area will visit host than non-hosts.	*	*	*	*
	3A-1	A higher proportion of butterflies entering the soil space will fly into the plant space if the target plant is a host rather than a non-host.	*	*	*	*
	3A-3	A higher proportion of butterflies flying into the plant space will visit target hosts than target non-hosts.	*	*	*	*
2. Host-specific stimuli are perceived by approaching or visiting butterflies.	2B	A higher proportion of visiting butterflies will land on or contact hosts than non-hosts.	*	*	0	*
	3B-1	A higher proportion of visiting butterflies will immediately land (as their first behavior) on hosts than on non-hosts.	*	+	+	+

Table 23 cont.

Results Hypotheses	Analysis Sections	Predictions	Comparisons I	II	III	V
	3B-2	A higher proportion of fluttering butterflies will contact or land on hosts than on non-hosts.	*	*	*	*
3. Host-specific stimuli (contact chemicals), perceived after alighting, are releasers of the curl response. The absence of host-specific contact chemicals induces an alighting butterfly to end the visit.	2C	A much higher proportion of alighting butterflies will curl on hosts than on non-hosts.	*	*	*	*
	3C-2	The proportion of butterflies curling on any one land or contact will be much greater for hosts than for non-hosts.	*			
	3C-2	The proportion of butterflies ending on any one land or contact will be much greater for non-hosts than for hosts.	*			

approach and the visit, and 3) after alighting on a plant. In addition, the results on relative discrimination also indicate that the host specific stimuli responsible for eliciting a given response differ, however subtly, for different responses, as the degree of discrimination changes as the sequence progress (Figures 22, p 157 & Figure 23, p 1606). One possible reason for the change in the degree of discrimination is that host-specific contact chemicals, which have been shown to be important to egg deposition (Hovanitz and Chang 1964, Renwick and Radke 1983, Traynier 1984), are perceived only after landing. As supporting evidence, relative discrimination between hosts and non-hosts was greatest during the alighting stage. But contact chemicals cannot be the total explanation for the change in the degree of discrimination during the sequence as the relative discrimination differs even among pre-alight sequence steps.

Discrimination between hosts and non-hosts is incomplete only during the visit stage, specifically during the flutter to land-contact transition. However, butterflies exhibit significant discrimination between hosts and non-hosts during all other transitions in the visit stage. Thus, although host-specific stimuli may not be of prime importance in determining the response of a fluttering butterfly, the evidence indicates that host-specific stimuli are primarily responsible for eliciting all other responses, including other responses in a visit.

Hosts of Differing Acceptabilities

Despite the fact that broccoli received a significantly higher number of eggs than did mustard (Table 6, p 78), only during the movement stage of the ovipositional sequence was discrimination between mustard and broccoli significant (Table 24). Nevertheless, even during responses where the difference in the proportion of butterflies responding to broccoli and mustard was not significant, the results were generally as predicted from the hypotheses: a lower proportion of butterflies at any one particular step responded to mustard than to broccoli. This was true for all three transitions between successive stages of oviposition and for five out of the seven transitions between steps that were tested for differences in response.

In light of this, it is probable that discrimination between the highly acceptable broccoli and the less acceptable mustard occurred throughout the ovipositional sequence, but that the difference in response for any one step was minimal. Minimal differences in the proportion of butterflies responding to broccoli and mustard at several steps in the overall sequence can lead to significant differences in the number of eggs laid on the two plants. The probability that a butterfly, entering the target area, will lay an egg on the plant is the product of the probabilities that the butterfly will continue the sequence at <u>each</u> transition between responses in the sequence.

Table 24: Summary of the hypotheses, predictions, and results from the first section of the results for hosts of differing acceptabilities.

Key for Results:

* Significant difference between response toward broccoli and toward mustard, for the indicated comparison.

+ The differences between the response toward broccoli and toward mustard is as predicted from the hypothesis, but the difference is not significant at the .05 level.

0 The difference between the response toward broccoli and toward mustard is not as predicted from the hypothesis.

Table 24.

General Assumption: Host plants differ quantitatively and/or qualitatively in host-specific stimuli as perceived by butterflies. These differences in stimuli result in differences in the degree of response exhibited by butterflies, which in turn result in differences in acceptability.

Hypotheses	Analysis Sections	Predictions	Results Comparison III
1. Differences in host-specific stimuli result in hosts of higher acceptability being recognized sooner, or be a higher proportion of butterflies than hosts of lower acceptability.	2A	A higher proportion of butterflies entering the target area will visit broccoli (a more highly acceptable host) than mustard.	*
	3A-1	A higher proportion of butterflies entering the soil space will fly into the target space with broccoli as the target plant than with mustard.	+
	3A-3	A higher proportion of butterflies entering the plant space will visit the broccoli target than the mustard target.	+
2. Differences in host-specific stimuli perceived by a responding butterfly will influence the nature of the visit.	2B	A higher proportion of visiting butterflies will land on or contact broccoli than mustard.	+
	3B-1	A higher proportion of visiting butterflies will land on broccoli as the first act in a visit than on mustard.	0

Table 24 cont.

Hypotheses	Analysis Sections	Predictions	Results Comparison III
	3B-2	A higher proportion of fluttering butterflies will land on or contact broccoli than mustard.	+
3. Differences in host-specific contact stimuli will affect post-alighting behavior.	2C	A higher proportion of alighting butterflies will curl on broccoli than on mustard.	+
	3C-2	A higher proportion of butterflies end or continue after any given alight on mustard than on broccoli.	0

Consequently, small differences in the probability of responding at these various transitions can result in significant differences in the probability of completing the sequence. For example, small differences in the proportion of butterflies responding to broccoli and to mustard at all sequence steps resulted in a differences in the proportion of butterflies entering the movement stage that progressed through the sequence and ultimately curled (Seq-->cu) of 14.9% vs 8.5% for broccoli and mustard respectively. This percentage is significantly different (using a test for equality of two percentages, Sokal and Rholf 1969, $ts = 3.54$, $P<.05$).

Therefore, in general, these results support the idea that hosts differ in the quantity or quality of host specific stimuli as perceived by butterflies and that these differences result in differences in the degree of response, which, in turn, result in differences in acceptability. The results suggest that differences in host-specific stimuli definitely affect the responses of the movement stage and probably also affect responses in the visit and alight stages, but the evidence for the latter is less clear cut.

One last result requires discussion. Mustard proved to be much more acceptable for resting than broccoli. As yet, little attention has been paid to factors eliciting resting behavior in butterflies, although it has been recognized as a behavior (Vaidya 1969, Root and Kareiva 1984, Stanton 1984). It is interesting that, contrary to the findings of

Vaidya (1969) for the lemon citrus butterfly, Papilio demoleus, the optimal stimulus situation for resting and oviposition are not the same in P. rapae.

Different Species of Non-Host

During most stages and steps of the ovipositional sequence, cabbage butterflies exhibit little, if any, discrimination among various non-host species (Table 25). With one exception, the proportion of butterflies responding at any one step or stage was virtually identical for different non-host species. The exception was behavior toward target non-hosts in comparisons III and IV during the response stage. Significantly more visiting butterflies alighted on lettuce than on any other non-host species (Table 8, p 84). The higher proportion of butterflies alighting on lettuce resulted from differences in the behavior of fluttering butterflies. Significantly more of those butterflies fluttering around lettuce landed or contacted than those fluttering around other non-hosts species (Table 14 pg 109). However, all other responses in the response stage were similar.

Although to humans lettuce appears visually similar to the host mustard, the butterflies' response toward the lettuce target was, with the above exception, more similar to that toward other non-host species (tansy and soybean) and quite different from that toward the host mustard. Thus, the idea that lettuce is perceived by butterflies as

Table 25: Summary of the hypotheses, predictions, and results from the first section of the results for different non-host species.

Key for Results:

* Significant difference between response toward lettuce and toward other non-host species, as predicted from the hypothesis, for the indicated comparison.

+ The difference between the response toward lettuce and toward other non-host species is as predicted from the hypothesis, but the difference is not significant at the .05 level.

0 The difference between the response toward lettuce and toward other non-host species is not as predicted from the hypothesis.

Table 25.

General Assumptions: General plant stimuli (non-host-specific) affect the butterflies' response. Lettuce is perceived as visually similar to the host mustard by butterflies. Visually perceived stimuli influence a butterfly's response.

Hypotheses	Analysis Sections	Predictions	Results Comparisons III	IV
1. Visually perceived aspects of plants influence the approach and visit response.	2A	A higher proportion of butterflies entering the target area will visit lettuce than other non-host species.	+	+
	3A-1	A higher proportion of butterflies entering the soil space will fly into the plant space with the lettuce target than with other non-host targets.	0	0
	3A-3	A higher proportion of butterflies entering the plant space will visit lettuce than other non-host species.	+	+
2. Visual stimuli perceived by an approaching or visiting butterfly influence the nature of the visit.	2B	A higher proportion of visiting butterflies will land on or contact lettuce than other non-host species.	*	*
	3B-1	A higher proportion of visiting butterflies will land on lettuce, as the first act in a visit, than on other non-host species.	+	

Table 25 cont.

Hypotheses	Analysis Sections	Predictions	Results Comparisons III	IV
	3B-2	A higher proportion of fluttering butterflies will land on or contact lettuce than other non-host species.	*	
3. Host-specific contact chemicals are the releasers of curling. non-host species.	2C	The proportion of alighting butterflies curling will not differ between non-host species.	no significant difference	
	3C-2	The proportion of butterflies curling, continuing, and ending after any given alight will not differ for different non-host species.	no	

similar to the host mustard and that visual stimuli are important in eliciting an approach or a visit is not supported by the results. This is not to say that these results suggest that visual stimuli are unimportant during the movement stage of oviposition, only that visual characteristics that we perceive lettuce as sharing with mustard do not affect butterfly behavior. This suggests that visual characteristics possessed in common by lettuce and hosts are important only in inducing a fluttering butterfly to alight. Lettuce is similar to both mustard and broccoli in having broad, rather flat leaves. Whatever this common characteristic is, other responses in the response stage are not affected.

As was expected, no discrimination between non-hosts was shown by butterflies during the alight stage. This is consistent with the idea that host-specific contact chemicals are releasers of post-alighting ovipositional behavior, in particular the curl response (Renwick and Radke 1983, Traynier 1984). Of all alights on non-hosts, only one resulted in a curl and it is interesting to note that this was an alight on the lettuce target. The visit sequence of the individual that curled on lettuce was: lcu c c c c, which indicates the butterfly immediately landed and curled on the lettuce target and followed this behavior by four contacts. The initial act performed in this visit (lcu) was something to be observed only in visits to hosts. In addition, the four contacts subsequently performed were

unusual in that the probability of continuing after alighting on non-hosts is low. However, because this was an isolated incident few, if any, conclusions can be drawn.

Repellent vs Non-Repellent Plants

The results obtained from the two "repellent" target plants, tansy and sage, suggest that these plants, traditionally considered to repel P. rapae, have no such effect (Table 26). With the exception of the previously discussed difference in behavior of butterflies fluttering in response to lettuce and tansy, no significant discrimination occurs between tansy and other non-host species at any stage or step of the ovipositional sequence. Neither does significant discrimination occur at any step of the sequence between the two "repellent" plants, tansy and sage; such a difference would be expected if these two plants differed in repellent properties.

Although these results do not support the idea that tansy and sage are repellent to P. rapae, neither do they support the idea, suggested by Latheef and Ortiz (1983b), that they are attractive. Rather, the behavior of butterflies toward these alleged repellent plants is similar to their behavior toward other non-host species.

Even though the results suggest that tansy, by itself, is not repellent to cabbage butterflies, it is still possible that the presence of tansy near a host plant would reduce the butterflies' degree of responsiveness toward the

Table 26.

General Assumption: Tansy generates repellent plant stimuli which butterflies are able to perceive and which deter the butterflies' response toward the plant.

Hypotheses	Analysis Sections	Predictions	Results Comparisons III	IV	V
1. Repellent plant stimuli are perceived from at least short distances. Perception of these stimuli inhibits the approach and visit to the plant.	2A	A lower proportion of butterflies entering the target area will visit tansy than other non-host species.	+	+	
	2A	A lower proportion of butterflies entering the target area will visit broccoli-tansy than broccoli alone.			+
	3A-1	A lower proportion of butterflies entering the soil space will fly into the target space with the tansy target than with other non-host targets.	0	0	
	3A-1	A lower proportion of butterflies entering the soil space will fly into the plant space with the broccoli-tansy target than with the broccoli-target alone.			0
	3A-3	A lower proportion of butterflies entering the plant space will visit tansy than other non-host species.	+	+	
	3A-3	A lower proportion of butterflies entering the plant space will visit broccoli-tansy than broccoli alone.			

Table 26: Summary of the hypotheses, predictions, and results from the first section of the results for repellent vs non-repellent plants.

Key for Results:

* Significant difference between response toward: 1) tansy and other non-host species, or 2) broccoli-tansy and broccoli alone, as predicted from the hypothesis for the indicated comparison.

+ The difference between the response toward: 1) tansy and other non-host species, or 2) broccoli-tansy and broccoli alone, is as predicted from the hypothesis, but the difference is not significant at the .05 level.

0 The difference between the response toward: 1) tansy and other non-host species, or 2) broccoli-tansy and broccoli alone, is not as predicted from the hypothesis.

Table 26 cont.

Hypotheses	Analysis Sections	Predictions	Results Comparisons III	IV	V
2. Repellent plant stimuli, perceived by an approaching or visiting butterfly influence the nature of the visit, resulting in inhibition of the alight response.	2B	A lower proportion of visiting butterflies will land on or contact tansy than other non-host species.	*	0	
	2B	A lower proportion of visiting butterflies will land on or contact broccoli-tansy than broccoli alone.			+
	3B-1	A lower proportion of butterflies will land, as the first act in a visit, on tansy than on other non-host species.	+		
	3B-1	A lower proportion of butterflies will land, as the first act in a visit, on broccoli-tansy than on broccoli alone.			+
	3B-3	A lower proportion of fluttering butterflies will land or contact on tansy than on other non-host species.	*		
	3B-3	A lower proportion of fluttering butterflies will land or contact on broccoli-tansy than on broccoli alone.			*

host simply by interfering with the host signal (stimuli) perceived by the butterflies. The results from the broccoli-tansy combination target are contradictory. In the first place, the acceptability of the broccoli-tansy combination did not differ significantly from that of broccoli. This would suggest that tansy has no inhibitory effect on the ovipositional behavior of butterflies toward broccoli. This is in part confirmed by the fact that in all stages and most of the steps of the ovipositional sequence (the sole exception is discussed below), the proportion of butterflies responding to broccoli-tansy does not differ significantly from the proportion responding to broccoli. However, with the exception of the soil space to plant space transition (s-->p), the results are as predicted from the hypotheses; a lower proportion of butterflies at any given step or stage responded to broccoli-tansy than to broccoli alone. For example, a lower proportion of butterflies visited, alighted on, and curled on broccoli-tansy than on broccoli alone. The first behavior in visits to broccoli-tansy was more like that toward non-hosts (more flutters, less lands) and butterflies were more likely to contact (rather than land) on broccoli-tansy than on broccoli.

Even so, the minor differences in the proportion of butterflies responding have little cumulative effect on the overall proportion of butterflies completing the sequence. The percentage of all butterflies entering the target area that curled on the target plant (Seq-->V) was 20.1% for

broccoli and 15.4% for broccoli-tansy. These two percentages are not significantly different (by a test for equality of two percentages, Sokal and Rholf 1969, ts= 1.87, P>.05).

The only exception to the above discussion was the flutter to land-contact transition (f-->l-c). A significantly lower proportion of fluttering butterflies alighted on broccoli-tansy than on broccoli (Table 14, p 109). This result suggests that tansy perhaps does have a minor deterrent effect on fluttering butterflies, possibly due to an odor. However, the overall effect on the total sequence is negligible.

The Sequence

Although it has been generally accepted that ovipositional behavior consists of a sequence of responses (Dethier 1953, Beck 1963, 1965, Kennedy 1965), it is not always studied as such. Investigations of ovipositional behavior may focus only on a single response or on the number of eggs laid on the plant. In such cases too much emphasis may be placed on a single stimulus as a determinant of ovipositional behavior.

In this study discrimination was assessed within the context of the entire sequence and differences in the degree of response between hosts and non-hosts were found to occur at every sequence step. Discrimination resulting from differences in the degree of response toward two objects at

multiple sequence steps is probably quite common. For example, conspecific eggs, which deter oviposition by the large white butterfly (Pieris brassicae), are perceived at several steps of the ovipositional sequence and exert a deterrent effect via a number of different stimuli (Rothschild and Schoonhoven 1977, Behan and Schoonhoven 1978, Klijnstra 1982). During approach and fluttering further response is deterred by visual perception of the yellow eggs on the plant and by olfactory perception of a volatile component of the oviposition deterrent chemical deposited with eggs. After alighting, deterrent chemicals perceived via the tarsi appear to inhibit further response. Finally, the oviposition deterrent pheromone is also perceived through abdomenal chemoreceptors, resulting in a reduction of the number of eggs laid by an ovipositing female.

In addition, although not explicitly tested, the results imply that different sensory stimuli are involved in different sequence responses. This is consistent with several experimental results (Saxena and Goyal 1978, Saxena and Saxena 1975, Copp and Davenport 1978).

Discrimination patterns involving differential responses at multiple points of the ovipositional sequence and involving information gained from multiple stimulus sources are probably advantageous evolutionarily. Because a sequence involves several responses, an object must possess the right stimulus configuration for each response in order

for the sequence to be completed and this makes mistakes in oviposition much less likely. In addition, because discrimination is shown in several of the sequece responses, a butterfly's investment (in terms of time, energy, and vulnerability to predators) will be proportional to the degree to which the object responded to possesses the characteristics of a host. Plants that are obviously or grossly different from hosts will be eliminated early in the sequence. On the average, only those plants that most closely resemble hosts (and are, therefore, most likely to be hosts) will receive a major investment in time and energy.

The relative discrimination occurring at each stage or step in the sequence increases as the sequence progresses, indicating that the longer butterflies interact with the plant, the more precise the information they gain about the plant's identity. If the stimuli influencing each response differs somewhat (Kennedy 1965), then the butterflies' behavior is being influenced by an ever increasing number of different stimuli. As Miller and Strickler (1984) have pointed out, the more kinds of stimuli affecting an insects host-finding behavior, the higher the chance that the plant the insect finds will be a suitable host.

Pre-Alighting Discrimination

The results of this study have shown that ovipositing cabbage butterflies do not land indiscriminately on plants.

This is in contrast to the observations of Traynier (1979) whose caged butterflies flew with equal frequency to pieces of cabbage leaves, lettuce leaves and green and yellow index cards. The explanation for this difference in results may be a difference in methodology. Traynier used naive females confined to small cages devoid of anything green (before experiments). Lettuce leaves, cabbage leaves and index cards were presented to these females separately, so their simultaneously expressed, differential responsiveness toward the objects cannot be assessed. Insects in a no-choice situation may appear to exhibit equivalent responsiveness toward different objects when, in reality, their responses would be quite different if the objects were offered simultaneously. For example, Yamamoto et al. (1969) observed that, in the absence of hosts, tobacco hornworm moths (Manduca sexta) approached and oviposited on artificial leaves sprayed with host extract but in the presence of a normal host their response toward the artificial leaves was lessened. In contrast to Traynier's (1979) study, the present study was, in reality, a choice situation in that a wide variety of hosts and non-hosts was always available in the field cage.

A second major difference in methodology between Traynier's (1979) study and the present study is that his butterflies were deprived of all plant or plant-like stimuli until the experiment. As discussed previously, deprived animals often experience the phenomenon of threshold

lowering resulting in less specificity in the stimuli required to elicit a given response. "It is a general observation, however, that as animals become increasingly deprived, they become decreasingly finicky" (Dethier 1982). Because the butterflies used in this study had vegetation (hosts and non-hosts) available at all times, they were not deprived and therefore were probably more specific in their responses than were Traynier's butterflies.

Other experiments using deprived butterflies have led to different conclusions. For example, the observations of David and Gardiner (1962) that caged P. brassicae females "fluttered eagerly" and apparently with equal intensity toward hosts and non-hosts outside of the cage led to the conclusion that olfaction played no role in host-plant finding in this insect. Since then, evidence has been uncovered indicating that host-specific volatiles do indeed influence ovipositional behavior of P. brassicae (Rothschild and Schoonhoven 1977, Behan and Schoonhoven 1978, Mitchell 1978).

Discrimination exhibited during the pre-alighting stages of the sequence contributes significantly to the overall discrimination among plants. Although the results on relative discrimination show that the degree of discrimination occuring at the alighting stage was higher than at any other stage of the sequence (Figure 22, p 157; Figure 23, p 160), alighting occurs in the latter part of the sequence and a significant number of butterflies have

been eliminated from sequences toward non-hosts (as compared to sequences toward hosts) prior to this. For example, only 22 butterflies alighted on tansy compared to 222 alighting on broccoli (Table 8, p 84). Approximately equal numbers of butterflies initiated sequences toward these two plants (1397 and 1394 for broccoli and tansy, respectively). Pre-alighting discrimination, although seemingly minimal, resulted in a ten-fold reduction in the number of butterflies alighting on tansy.

The results of this study have shown that pre-alighting discrimination was greater than post-alightinging discrimination between 2 hosts of different acceptabilities (broccoli and mustard). This agrees with results obtained by Wolfson (1980) who found that the number of P. rapae eggs laid on black mustard plants (Brassica nigra) was not correlated with the total sinigrin content of the plant. If chemicals are perceived only after alighting, then chemical differences between plants are irrelvent to pre-alighting behavior during which the most significant discrimination between hosts of different acceptabilities occurs. Traynier (1984) has shown that P. rapae females do discriminate during pre-alighting behavior between varieties of cabbage differing in outward appearance.

Renwick and Radke (1983) found that host extract concentration affected the number of P. rapae eggs received by artificial ovipositional substrates. Initially, these results may appear to be in conflict with those of Wolfson

(1980). However, because the artificial ovipositional substrates were presumably equal in appearance, pre-alighting discrimination would not occur in this situation. This leaves only post-alighting discrimination to affect differences in the number of eggs laid. In addition, the fact that Renwick and Radke's experiments were conducted in small laboratory cages, suggests that differences in concentration of host-specific contact chemicals may be more relevent to the distribution of eggs on a single host (which is the result of behavioral responses occuring after initial pre-alight discrimination) rather than to differences in the number of eggs laid on the two plants.

Although the purpose of this study was not to investigate the sensory basis of discrimination, the results provide at least a basis for speculation and further study. The results support the ideas that host-specific stimuli are primarily responsible for eliciting both the visit and the approach response (Table 7, p 80 & Table 8, p 84). It is difficult to speculate on what this set of host-specific characterisitics are. Because it is likely to be host-specific, odor is the logical candidate . Although a number of studies have led to the conclusion that odor plays no role in Pieris rapae ovipositional behavior (Hovanitz and Chang 1964, Renwick and Radke 1983), there are problems in methodology that jeopardize that conclusion, namely the use of deprived butterflies, the use of butterflies confined to small laboratory cages, and the failure to record actual

ovipositional behaviors. Although this means that an influence of host-specific volatiles on the approach and visit response can not be ruled out, it is still unlikely that host odor is entirely responsible for the higher degree of response shown toward hosts, as odor gives little information as to exact location.

It is possible that visual stimuli are solely responsible for eliciting the approach and visit. Vision almost certainly plays some role in this behavior, especially the visually perceived aspect of color (Traynier 1984, Miyakawa 1976, Hovanitz and Chang 1964), but to totally account for the higher proportion of approaches and visits to hosts, visual stimuli would have to be fairly host specific, and color is not (Prokopy and Owens 1983). The fact that lettuce and mustard are seen by humans as more similar than either are to broccoli, but that the responses of butterflies to mustard and broccoli are more similar than either are to lettuce may seem, at first, to exclude visual stimuli from being a major factor in eliciting response. However, it is possible that distinguishing characteristics go unnoticed by humans and that mustard and lettuce are not seen as similar by butterflies.

Wide variation in appearance among hosts also leads to the inference that visually perceived stimuli are not the major factors eliciting the approach and visit. Broccoli and mustard are distinct in overall shape, leaf shape and color. However, broccoli and mustard may share visual

characteristics easily overlooked by humans, but easily perceived by butterflies. Alternatively, individual P. rapae females may vary in their response, some individuals responding preferentially toward broccoli, others responding preferentially toward mustard. Individual variation in the degree of response exhibited toward hosts differing in visually perceived characterisitics has been shown to exist in some butterflies (Rausher 1978, Tabashnik et. al. 1981, Rausher and Papaj 1983). Individual differences in ovipositional behavior were impossible to detect in this study, as the individuals were not marked.

If individual variation in the degree of response toward different hosts occurs in P. rapae, it could be due either to innate differences or to an effect of experience. The host-finding behavior of some other butterfly species is affected by the type of plants it has previously landed on (Stanton 1984, Rausher 1978), thus suggesting a role of experience. Traynier (1979) found that tarsal contact with host foliage increased the tendency of P. rapae to land and oviposit. Host chemicals have an excitatory influence on P. rapae and, in such circumstances, learning may occur. In a later study, Traynier (1984) discovered that P. rapae does learn to associate the appearance of an ovipositional substrate with the contact chemical stimulation it provides.

Partial discrimination between hosts and non-hosts occurs during the response stage of the ovipositional sequence. The results suggest that host-specific stimuli

are important in determining the first act in a visit, but not in determining behavior after an initial flutter (Table 13, p 105; Table 14, p 109). Of the specific stimuli potentially affecting the behavior of fluttering butterflies, odor is one candidate, especially repellent odors. Behan and Schoonhoven (1978) report that the aversion pheromone associated with conspecific eggs in Pieris brassicae is detected while the butterflies flutter over the leaves. In the present study, the significantly lower proportion of fluttering butterflies alighting on the broccoli-tansy target as compared with the broccoli target (Table 14, p 109), may have been due to a repellent odor of tansy.

A second possible influence on the behavior of fluttering butterflies is leaf shape. Broccoli, mustard and lettuce all have rather large, wide and simple (undivided) leaves while the leaves of the other non-hosts (soybean, tansy and sage) are not of this type. Experimental findings have suggested that leaf shape influences pre-alight discrimination in several butterfly species (Rausher 1978, Stanton 1982). Observations of Feeny et al. (1983) suggest that Papilio polyxenes selectively responds to plants possessing finely dissected leaves like those of their umbelliferous hosts. If P. rapae, during pre-alighting ovipositional behavior, responded preferentially toward plants with undivided leaves, a large number of non-host species would be eliminated from consideration. Personal

observation of free-flying P. rapae suggests that this may be the case. Very few plants possessing compound leaves receive attention. In contrast, butterflies often flutter around non-hosts with broad, simple leaves, such as dandelion or dock. Whatever these general plant characteristics affecting the behavior of fluttering butterflies are, they appear to be important in the final acceptance of a host plant by a butterfly. This is shown in that, once initiated, a visit to a host is more likely to be terminated following a flutter than following a contact or a land (Figure 18, p 144; Figure 20, p 145).

Post-Alighting Discrimination

Most of the emphasis has been placed on host-specific contact chemicals as determinants of P. rapae ovipositional behavior. The results of this study suggest that host-specific chemicals have a major influence on post-alighting ovipositional behavior, but that other stimuli are also involved. As results from Traynier (1984) indicate, host-specific contact chemicals are probably the major releasers of curling. In this study, from 77% to 89% of all butterflies alighting on hosts curled, while only one butterfly alighting on a non-host curled. However, the data from butterflies alighting on broccoli-tansy suggest that stimuli other than host-specific contact chemicals also influence post-alighting ovipositional behavior.

Traynier (1979) found that contact with host foliage resulted in an increase in the probability of landing and laying. Extrapolating from this, the probability of curling and continuing might be expected to increase as the number of alights increased. However, results from this study do not support this (Figure 30, p 182). Therefore, although initial contact with host foliage has an excitatory effect on P. rapae, the results of this study suggest that after the first alight the internal motivation of the butterflies' remains constant. This indicates that the factors determining the alight on which a butterfly will first curl are extrinsic, belonging to the plant. The probability that a butterfly will alight on a site possessing adequate stimuli to elicit a curl response remains constant throughout a visit. Since internal motivation does not change, the probability that a butterfly will curl on any given alight remains constant. This view is consistent with the finding of Renwick and Radke (1983) that butterflies are able to discriminate between two sides of an index card, one containing cabbage extract, the other lacking that extract. Since butterflies normally do not walk on leaves to any great extent, they apparently find suitable ovipositional sites by repeated alightings.

Further Questions

Several questions needing research are suggested by the results of this study. One concerns the distances from

which cabbage butterflies recognize hosts. These results have shown that cabbage butterflies are stimulated to approach hosts preferentially from at least short distances. The actual distances involved may be considerably greater, but this cannot be ascertained from the data. A number of factors potentially affect the distances from which hosts are recognized. Plant size has already been shown to influence the probability of P. rapae landing on a plant (Jones 1977). Size probably exerts this effect by increasing the distance over which hosts are seen by P. rapae, as has been shown for the pierid butterfly, Anthocharis cardamines (Courtney 1982). A second factor potentially influencing the distance from which hosts are recognized is neighboring vegetation. A host surrounded by non-hosts may not be as easily detected by Pieris rapae as isolated hosts would be. This has already been shown to occur in the butterfly Battus philenor and its Aristolochia hosts (Rausher 1981).

Another question awaiting further research is whether the results of this study are generally applicable to free-flying P. rapae. Although the butterflies used in this study were provided with a relatively large and complex habitat, they were, nonetheless, confined. Under natural conditions, P. rapae females cover approximately 700 meters on daily flights, ending up approximatly 2 km from their starting point during the course of their lifetime (Jones et al. 1980). While butterflies confined to small cages might

be expected to exhibit lower degrees of discrimination due to the phenomenon of threshold lowering, those confined to large field cages may exhibit higher degrees of discrimination than free-flying butterflies. This would be likely to occur if butterflies are capable of learning to associate the visual appearance of a plant with contact chemicals perceived after alighting, as has been shown already for P. rapae (Traynier 1984). Because butterflies confined to a field cage are exposed to limited vegetational diversity, they may learn faster and better than free-flying butterflies.

Perhaps the most striking issue remaining to be answered is--precisely which stimuli elicit the responses in the ovipositional sequence, especially responses in the pre-alighting portion of the sequence? The fact that discrimination occurs at every step of the sequence indicates that the optimal stimulus configuration eliciting each response is host-specific. A number of different stimuli, potentially influencing ovipositional behavior, but whose role has not yet been investigated have already been mentioned: odor, plant shape, leaf shape, etc. It is some as yet unknown set of perceived stimuli to which butterflies respond.

The experimental approach used in this study is ideal for investigating the perceptual basis of discrimination. the advantages have already been stressed: Animals are not deprived and, therefore, are less likely to exhibit abnormal

discrimination patterns due to threshold lowering and the effect of a stimulus pattern on acceptability can be traced to its influence on one or more responses in the sequence.

In addition, the experimental approach used in this study would be ideal for testing directly the idea that the response-influencing stimuli change over the course of the sequence (Kennedy 1965). In the present method, each response is recorded separately. Thus, it is possible to determine if the influence of a given stimulus changes at different responses, and whether the major stimuli influencing response differ for different responses.

The fact that the amount of communication from plant to butterfly increases as the sequence progresses suggests that the number of different stimuli affecting a response also increases as the sequence progresses. Because each response is recorded separately, this could also be tested using the present method.

The methods of analysis used in this study, especially Markov chain analysis and Information analysis are useful tools for investigating such questions. The chief advantage of the Markov chain analysis is that it allows comparisons of sequences that involve multiple transition possibilities at each step. For the P. rapae ovipositional sequence described in this study, the number of possible transitions involved are limited up until the visit. This portion of the sequence is somewhat deterministic in that the behaviors possible at any given step depend, in part, on the

preceeding behavior. For example, butterflies may visit the plant only if they have entered the plant area (s-->p) and not if they have left the target area (s-->end). The semi-deterministic nature of the sequence up to this point makes it possible to compare sequence steps among different plant types by use of a Chi-Square or G test.

At the visit step of the sequence, however, the number of possible behaviors both preceeding and proceeding transitions at any given step increase greatly. In order to compare sequences during this phase of oviposition, one can either focus on a key outcome (such as was done on Levels II and III), or use Markov chain analysis to produce exact descriptions of sequences. Comparisons of Markov chain descriptions of ovipositional sequences in P. rapae would be valuable to determine: 1) the influence of specific stimuli, or sets of stimuli, on ovipositional behavior, 2) whether inter-individual variation in ovipositional behavior occurs, and 3) whether intra-individual differences in ovipositional behavior occur (e.g., whether learning takes place). In addition, the Markov model of oviposition, once perfected, should predict the number of eggs a plant will receive. Predictive models of P. rapae ovipositional behavior which focus mostly on movement behavior have already been created (Jones 1977, Root and Kareiva 1984). These models explain mostly the effects of plant density, distribution, and variety on the abundance and distribution of eggs in a field. The value of the Markov model of the visit sequence

proposed above is that it could predict the number of eggs individual plants would receive on the basis of stimulus characteristics possessed by those plants.

The use of information analysis, in particular the normalized transmission index, is another potentially valuable tool for investigations of P. rapae ovipositional behavior specifically, and plant-insect interactions in general. Two aspects of the normalized transmission index make it especially useful in such investigations. First, normalized transmission is a measure of communication. It has been used as a measure of communication between two interacting animals (Dingle 1969, Conanat 1974). As far as I know, it has not been used to measure the influence of a non-animal, such as a plant, on an animal's behavior. However, this measure seems ideally suited to this purpose.

The second aspect of the normalized transmission index which makes it a valuble tool for studying insect-plant interactions is that it is a relative measure. This makes it possible to compare directly the influence of different

stimuli on the same sequence step, or the influence of the same stimulus on different sequence steps.

In summary, this study raises far more questions about the cause of P. rapae ovipositional behavior than it answers. The chief value of this study, therefore, is that it gives a basis for further research by: 1) providing a description of ovipositional behavior, 2) analyzing how

ovipositional behavior varies when directed toward different plant species, and 3) suggesting specific questions and methods of research to answer these questions.

Control Implications

The results of this study have implications for the control of P. rapae larvae on economically important crops. First, the determination of where discrimination occurs in the ovipositional sequence is important to control. The responses showing maximal discrimination are the "weak links" of the chain for control purposes. Factors contributing to plant resistance via non-preference work by making a plant less acceptable to an insect. This implies that these factors reduce the probability of response for one or more behaviors in the sequence. Discrimination is measured by differences in the degree of response. Where discrimination is minimal, there is little potential to alter the probability of response by manipulating stimuli. Conversely, the presence of maximal discrimination indicates that the probability of response can be lowered by changing the stimuli eliciting that response. The degree to which the probability of response can potentially be lowered is proportional to the degree of discrimination observed.

Secondly, the finding that P. rapae discriminates between hosts and non-hosts prior to alighting has important control implications. Plant resistance to P. rapae infestation results from non-preference by ovipositing

females (Radcliffe and Chapman 1966a, 1966b, Dickson and Eckenrode 1975). Any plant characteristic affecting the probability that a female will lay an egg also affects resistance. While host-specific thioglucosides undoubtedly have a major influence on the behavior of P. rapae females after alightment, increasing resistance by reducing thioglucoside content is not desireable since these chemicals are very important constituents of humanly-desired crucifer flavor (MacLeod 1976). Non-chemical characteristics affecting pre-alighting ovipositional behavior hold more promise for manipulation by breeders. For example, the resistance shown by some strains of red cabbage may be due to a reduced probability of alighting, although this has not been investigated. Discovering and manipulating factors affecting the probability of alighting may hold promise for producing resistant varieties of cruciferous crops.

CONCLUSIONS

The results of this study indicate that:

1. Virtually all P. rapae ovipositional behaviors are elicited by host-specific stimuli.
2. Quantitative and/or qualitative variation in host-specific stimuli between 2 different host species

(broccoli and mustard) primarily affect the movement stage of oviposition.

3. Variation in general plant stimuli (non-host-specific) influences only the behavior of fluttering butterflies.
4. Tansy, a reputed "repellent" plant deters butterfly response only during the flutter step, and then only minimally.
5. Butterflies become increasingly discriminating as the ovipositional sequence progresses.
6. For most stages and steps of the ovipositional sequence, the most important stimuli affecting response are host-specific. General plant stimuli are relatively more important than host-specific stimuli only in determining the behavior of fluttering butterflies.

LIST OF REFERENCES

LIST OF REFERENCES

Beck, S.D. 1963. Behavioral aspects of host plant specificity. Proc. N. Cent. Br. ESA 18:26-27.

_____1965. Resistance of plants to insects. Annu. Rev. Entomol. 10:207-232.

Behan, M. and L.M. Schoonhoven. 1978. Chemoreception of an oviposition deterrent associated with eggs in Pieris brassicae. Ent exp & appl. 24:163-179.

Bjorkman, R. 1976. Properties and function of plant myrosinases. In: J.G. Vaughan, A.J. MacLeod and B.M.G. Jones, Eds. The Biology and Chemistry of the Cruciferae. Academic Press. London. pp 191-205.

Bliss, C.I. 1958. The analysis of insect counts as negative binomial distributions. Proc 10th Intnl. Cong. Entomol. 2:1015-1031.

Blurton-Jones, N.G. 1968. Observations and experiments on the causation of threat displays of the great tit (Parus major). Anim. Behav. Monogr. 1:75-158.

Brewer, G.J. and H.J. Ball 1981. A feeding deterrent effect of a water extract of tansy (Tanacetum vulgare L., Composite) on three lepidopterous larvae. J. Kansas Entomol. Soc. 54:733-736.

Brower, J.E. and J.H. Zar 1977. Field and Laboratory Methods for General Ecology. Wm. Brown Co, Dubuque, Iowa. 194pp.

Brues, C.T. 1920. The selection of food plants by insects, with special reference to lepidopterous larvae. Am. Nat. 54:313-332.

Cane, V.R. 1978. On fitting low-order Markov chains to behaviour sequences. Anim. Behav. 26:332-338.

Chatfield, C. and R.E. Lemon 1970. Analysing sequences of behavioural events. J. theor. Biol. 29:427-445.

Chew, F.S. 1975. Coevolution of pierid butterflies and their cruciferous foodplants. I. The relative quality of available resources. Oecologia (Berl.) 20:117-127.

_____1977. Coevolution of pierid butterflies and their cruciferous foodplants. II. The distribution of eggs on potential foodplants. Evolution 31:568-579.

Chun, M.W. and L.M. Schoonhoven. 1973. Tarsal contact chemosensory hairs of the large white butterfly Pieris brassicae and their possible role in oviposition behavior. Ent exp & appl. 16:343-357.

Copp, N.H. and D. Davenport 1978. Agraulis and Passiflora II. Behavior and sensory modalities. Biol. Bull. 155:113-124.

Courtney, S.P. 1982. Coevolution of pierid butterflies and their cruciferous foodplants. IV. Crucifer apparency and Anthocharis cardamines (L.) oviposition. Oecologia (Berl.) 52:258-265.

Crane, J. and H. Fleming 1953. Construction and operation of butterfly insectaries in the tropics. Zoologica 38:161-172.

Cranshaw, W.S. 1984. Effect of a hay mulch and of a companionate planting on cabbage pest populations. Great Lakes Entomol. 17:9-12.

Cromartie, W.J. 1975. Effect of stand size and vegetational background on the colonization of cruciferous plants by herbivorous insects. J. Appl. Ecol. 12:517-533.

David, W.A.L. and B.O.C. Gardiner 1962. Oviposition and the hatching of the eggs of Pieris brassicae (L.) in a laboratory culture. Bull. Entomol. Res. 53:91-109.

_____1966. Mustard oil glucosides as feeding stimulants for Pieris brassicae larvae in a semi-synthetic diet. Ent. exp & appl. 9:247-255.

Dethier, V.G. 1953. Host plant perception in phytophagous insects. Trans 9th Int. Congr. Entomol. 2:81-89.

_____1969. Whose real world? Am. Zool. 9:241-249.

_____1976. The importance of stimulus patterns for host-plant recognition and acceptance. In: T. Jermy Ed. The Host Plant in Relation to Insect Behavior and Reproduction. Akademiai, Budapest. pp 67-70.

_____1982. Mechanism of host-plant recognition. Ent. exp & appl. 31:49-56.

Dickson, M.H. and C.J. Eckenrode. 1975. Variation in Brassica oleracea resistance to cabbage looper and imported cabbage worm in the greenhouse and field. J. Econ. Entomol. 68: 757-760.

Dingle, H. 1969. A statistical and information analysis of aggressive communication in the mantis shrimp Gonodactylus bredini Manning. Anim. Behav. 17:561-575.

Drummond, H. 1981. The nature and description of behavior patterns. In: P.P.G. Klopfer and P.H. Bateson, Eds. Perspectives in Ethology. Vol 4. pp 1-31.

Ehrlich, P.R. and P.H. Raven. 1964. Butterflies and plants: A study in coevolution. Evolution 18:586-608.

Erickson, J.M. and P. Feeny 1974. Sinigrin: A chemical barrier to the black swallowtail butterfly, Papilio polyxenes. Ecology 55:103-111.

Esau, K. 1977. Anatomy of Seed Plants, 2nd Ed. John Wiley & Sons. New York. 550pp.

Estabrook, G.F. 1967. An information theory model for character analysis. Taxon 16:86-97.

Fagen, R.M. and D.Y. Young. 1978. Temporal patterns of behavior: durations, intervals, latencies and sequences. In: P.W. Colgan, Ed. Quantitative Ethology. John Wiley and Sons, New York. 364pp

Feeny, P. 1977. Defensive Ecology of the Cruciferae. Ann. Mo. Bot. Gard. 64:221-234.

Feeny, P., K.L. Paauwe, and N.J. Demong 1970. Flea beetles and mustard oils: Host plant specificity of Phyllotreta cruciferae and P. striolata adults (Coleoptera: Chrysomelidae). Ann. Entomol. Soc. Am. 63:832-841.

Feeny, P., L. Rosenberry, and M. Carter 1983. Chemical aspects of oviposition behavior in butterflies. In: S. Ahmad Ed. Herbivorous Insects: Host-seeking Behavior and Mechanisms. Academic Press. New York. pp 27-76.

Finch, S. 1978. Volatile plant chemicals and their effect on host plant finding by the cabbage root fly (Delia brassicae). Ent. exp & appl. 24:150-159.

Fox, R.M. 1966. Forelegs of butterflies I. Introduction: Chemoreception. J. Res. Lepid. 5:1-12.

Fraser, J. and M.C. Nelson. 1984. Communication in the courtship of the madagascan hissing cockroach I. Normal courship. Anim. Behav. 32:194-203.

Gangwere, S.K. 1965. Food selection in the Oedipodinae grasshopper Arphia sulphurea (Fabricius). Amer. Mid. Naturl. 74:67-75.

Goodman, L.A. 1968. The analysis of cross-classified data: Independence, quasi-independence, and interactions in contingency tables with or without missing entries. J. Amer. Stat. Ass. 63:1091-1131.

Gossard, T.W. and R.E. Jones 1977. The effects of age and weather on egg-laying in Pieris rapae L. J. Appl. Ecol. 14:65-71.

Gupta, P.D. and A.J. Thorsteinson. 1960. Food plant relationships of the diamond-back moth (Plutella maculipennis (Curt.)). II. Sensory regulation of oviposition of the adult female. Ent. exp & appl. 3:305-314.

Harcourt, D.G. 1961. Spatial pattern of the imported cabbageworm, Pieris rapae (L.) (Lepidoptera: Pieridae), on cultivated Cruciferae. Can. Entomol. 98:945-952.

_____1963. Biology of cabbage caterpillars in eastern Ontario. Proc. Entomol. Soc. Ont. 93:61-75.

_____1966. Sequential sampling for the imported cabbageworm, Pieris rapae (L.). Can. Entomol. 98:741-746.

Harrison, P.K. and R.W. Brubaker 1943. The relative abundance of cabbage caterpillars on cole crops grown under similar conditions. J. Econ. Entomol. 36:589-592.

Hemingway, J.S., H.J. Schofield and J.G. Vaughan 1969. Volatile mustard oils of brassica juncea seeds. Nature 192:993.

Hovanitz, W. and V.C.S. Chang 1963. Comparison of the selective effect of two mustard oils and their glucosides to Pieris larvae. J. Res. Lepid. 2:281-288.

_____1964. Adult oviposition responses in Pieris rapae. J. Res. Lepid. 3:159-172.

Hsiao, T.H. and G. Fraenkel 1968. Selection and specificity of the colorado potato beetle for solanaceous and nonsolanaceous plants. Ann. Entomol. Soc. Amer. 61:493-503.

Hunter, B.T. and B. Hines 1971. Gardening without Poisons. Houghton Mifflin, Boston. 318pp.

Ilse, D. 1956. Behaviour of butterflies before oviposition. J. Bombay Nat. Hist. Soc. 53:486-488.

Ives, P.M. 1978. How discriminating are cabbage butterflies? Aust. J. Ecol. 3:261-276.

Jermy, T. 1966. Feeding inhibitors and food preferences in chewing phytophagous insects. Ent. exp. & appl. 9:1-12.

Jones, R.E. 1977. Movement patterns and egg distribution in cabbage butterflies. J. Anim. Ecol. 46:195-212.

Jones, R.E., N. Gilbert, M. Guppy and V. Nealis 1980. Long distance movement of Pieris rapae. J. Anim. Ecol. 49:629-642.

Josefsson, E. 1967. Distribution of thioglucosides in different parts of Brassica plants. Phytochemistry (Oxf.) 6:1617-1627.

Kennedy, J.S. 1965. Mechanisms of host plant selection. Ann. appl. biol. 56: 317-322.

Kjaer, A. 1963. The distribution of sulphur compounds. In: T. Swain Ed. Chemical Plant Taxonomy. Academic Press. London. pp 453-473.

_____1976. Glucosinolates in the Cruciferae. In: J.G. Vaughan, A.J. MacLeod and B.M.G. Jones, Eds. The Biology and Chemistry of the Cruciferae. Academic Press. London. pp 207-219.

Klijnstra, J.W. 1982. Perception of the oviposition deterrent pheromone in Pieris brassicae. Proc. 5th Int. Symp. Insect-plant relationships, Wageningen 1982. Pudoc, Wageningen. pp 145-151.

Kobayashi, S. 1965. Influence of parental density on the distribution pattern of eggs in the common cabbage butterfly, Pieris rapae crucivora. Res. Popul. Ecol. 7:109-117.

_____1966. Process generating the distribution pattern of eggs of the common cabbage butterfly, Pieris rapae crucivora. Res. Popul. Ecol. 8:51-61.

Latheef, M.A. and R.D. Irwin 1979a. Factors affecting oviposition of Pieris rapae on cabbage. Environ. Entomol. 8:606-609.

_____1979b. The effects of companionate planting on lepidopteran pests of cabbage. Can. Entomol. 111:863-864.

Latheef, M.A. and J.H. Ortiz 1983a. Influence of companion plants on oviposition of imported cabbageworm, Pieris rapae (Lepidoptera: Pieridae), and cabbage looper, Trichoplusia ni (Lepidoptera: Noctuidae), on collard plants. Can. Entomol. 115:1529-1531.

_____1983b. The influence of companion herbs on egg distribution of the imported cabbageworm, Pieris rapae (Lepidoptera: Pieridae), on collard plants. Can. Entomol. 115:1031-1038.

Lawrence, G.H.M. 1951. Taxonomy of Vascular Plants. Macmillan Co. New York. 823pp.

Lehner, P.N. 1979. Handbook of Ethological Methods. Garland STPM Press. New York. 403pp.

Lemon, R.E. and C. Chatfield. 1971. Organization of song in cardinals. Anim. Behav. 19:1-17.

Lorenz, K.Z. 1981. The Foundations of Ethology. Simon and Schuster. New York. 380pp.

Losey, G.S. Jr. 1978. Information theory and communication. In: P.W. Colgan Ed. Quantitative Ethology. John Wiley and Sons. New York. pp 44-78.

Lundgren, L. 1975. Natural plant chemicals acting as oviposition deterrents on cabbage butterflies (Pieris brassicae (L.), P. rapae (L.), and P. napi (L.)). Zool. Scr. 4:253-258.

MacLeod, J.A. 1976. Volatile flavour compounds of the Cruciferae. In: J.G. Vaughan, A.J. MacLeod and B.M.G. Jones Eds. The Biology and Chemistry of the Cruciferae. Academic Press. London. pp 307-330.

Maguire, L.A. 1983. Influence of collard patch size on population densities of lepidopteran pests (Lepidoptera: Pieridae, Plutellidae). Environ. Entomol. 12:1415-1419.

_____1984a. Choosing host plant patch sizes for experiments on Pieris rapae (L.) populations (Lepidoptera: Pieridae). Environ. Entomol. 13: 459-463.

_____1984b. Influence of surrounding plants on densities of Pieris rapae (L.) eggs and larvae (Lepidoptera: Pieridae) on collards. Environ. Entomol. 13:464-468.

Mathews, D.L., P.S. Michalak and R.J. MacRae 1983. Effect of traditional insect-repellent plants on insect numbers in a mixed planting system. Proc 4th Intern. Federation of Organic Agriculture Movements (IFOAM). Boston Mass. 1981. pp 117-177.

McKillip, B.B. (Ed.) 1973. Getting the Bugs out of Organic Gardening. Rodale Press. Emmaus Pennsylvania. 115pp.

Miller, J.R. and K.L. Strickler 1984. Finding and accepting host plants. In: W.J. Bell and R.J. Carde, Eds. Chemical Ecology of Insects. Chapman Hall Ltd. pp 127-157.

Mitchell, N.D. 1978. Differential host selection by Pieris brassicae L. (the large white butterfly) of Brassica oleraceae L. subs. oleraceae (the wild cabbage). Ent exp.& appl. 22:208-219.

Miyakawa, M. 1976. Flower-visiting behavior of small white butterfly, Pieris rapae crucivora. Ann. Zool. Jap. 4:261-273.

Moss, J.E. 1933. The natural control of the cabbage caterpillars, Pieris spp.. J. Anim. Ecol. 2:210-231.

Munakata, K. 1977. Insect feeding deterrents in plants. In: H.H. Shores and J.J. McKelvey Jr. Eds. Chemical Control of Insect Behavior: Theory and Application. John Wiley & Sons. New York. pp 93-102

Nair, K.S.S., F.L. McEwen and V. Snieckus 1976. The relationship between glucosinolate content of cruciferous plants and oviposition preferences of Hylema brassicae (Diptera: Anthomyiidae). Can. Entomol. 108:1031-1036.

Nieuwhof, M. 1969. Cole Crops. Leonard Hill Books. London. 353pp.

Obara, Y. 1970. Studies on the mating behavior of the white cabbage butterfly, Pieris rapae crucivora Boisduval. III. Near-ultra-violet reflection as the signal of intraspecific communication. Z. vgl. Physiol. 69:99-116.

Obara, Y. and T. Hidaka 1968. Recognition of the female by the male, on the basis of ultra-violet reflection, in the white cabbage butterfly, Pieris rapae crucivora Boisduval. Proc. Jpn. Acad. 44:829-832.

Oden, N. 1977. Partitioning dependence in non-stationary behavior sequences. In: B.A. Hazlett Ed. Quantitative Methods in the Study of Animal Behavior. Academic Press. New York. pp203-220.

Opler, P.A. and G.O. Krizek 1984. Butterflies East of the Great Plains. An Illustrated Natural History. John Hopkins Univ. Press. Baltimore. 294 pp.

Papaj, D.R. and M.D. Rausher 1983. Individual variation in host location by phytophagous insects. In: S. Ahmad Ed. Herbivorous Insects: Host-seeking Behavior and Mechanisms. Academic Press. New York. pp 77-124.

Prokopy, R.J. and E. D. Owens 1983. Visual detection of plants by herbivorous insects. Annu. Rev. Entomol. 28:337-364.

Radcliffe, E.B. and R.K. Chapman 1965. The relative resistance to insect attack of three cabbage varieties at different stages of plant maturity. Annl. Entomol. Soc. Amer. 58:897-902.

_____1966a. Varietal resistance to insect attack in various cruciferous crops. J. Econ. Entomol. 59:120-125.

_____1966b. Plant resistance to insect attack in commercial cabbage varieties. J. Econ. Entomol. 59:116-120.

Rahman, M. 1968. Oviposition by Pieris rapae L. in the insectory. Pak. J. Sci. 20:278-280.

Rausher, M.D. 1978. Search image for leaf shape in a butterfly. Science 200:1071-1073.

_____1981. The effect of native vegetation on the susceptibility of Aristolochia reticulata (Aristolochiaceae) to herbivore attack. Ecology 62:1187-1195.

Rausher, M.D. and D.R. Papaj 1983. Host plant selection by Battus philenor butterflies: Evidence for individual differences in foraging behaviour. Anim. Behav. 31:341-347.

Renwick, J.A.A. and C.D. Radke 1983. Chemical recognition of host plants for oviposition by the cabbage butterfly, Pieris rapae (Lepidoptera: Pieridae). Environ. Ent. 12: 446-450.

Richards, O.W. 1940. The biology of the small white butterfly (Pieris rapae), with special reference to the factors controlling its abundance. J. Anim. Ecol. 9:243-288.

Rodman, J.E. and F.S. Chew 1980. Phytochemical correlates of herbivory in a community of native and naturalized Cruciferae. Biochem. System. Ecol. 8:43-50.

Root, R.B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (Brassica oleracea). Ecol. Monographs 43:95-120.

Root, R.B. and P.M. Kareiva 1984. The search for resources by cabbage butterflies (Pieris rapae): Ecological consequences and adaptive significance of Markovian movements in a patchy environment. Ecology 65:147-165.

Rothschild, M. and L.M. Schoonhoven 1977. Assessment of egg load by Pieris brassicae (Lepidoptera: Pieridae). Nature 266:352-355.

Rothschild, M. and J.W. Fairbairn 1980. Ovipositing butterfly (Pieris brassicae) distinguishes between aqueous extracts of two strains of Cannabis sativa L. and THC and CBI. Nature 286: 56-59.

Rumsey, W.E. and F.E. Brooks 1909. Cabbageworms and suggestions for destroying them. W. Virginia Agri. Exp St Bulletin 120.

Saxena, K.N. and S. Goyal 1978. Host-plant relations of the citrus butterfly Papilio demoleus L: Orientational and ovipositional responses. Ent. exp. & appl. 24:1-10.

Saxena, K.N. and R.C. Saxena 1975. Patterns of relationships between certain leafhoppers and plants. Part IV. Sequence of stimuli determining arrival on a plant. Ent exp & appl. 18:207-212.

Scheffler, W.C. 1980. Statistics for the Biological Sciences. Addison-Wesley Co. Mass. 276 pp.

Schoonhoven, L.M. 1977. Insect chemosensory responses to plant and animal hosts. In: H.H. Shorey and J.J. McKelvey Jr. Eds. Chemical Control of Insect Behavior: Theory and Application. John Wiley and Sons, New York. pp7-14.

Scudder, S.H. 1887. The introduction and spread of Pieris rapae in North America, 1860-1886. Mem. Boston Soc. Nat. Hist. 4:53-69.

Shannon, C.E. and W. Weaver. 1969. The Mathematical Theory of Communication. Univ. of Illinois Press, Urbana.

Shapiro, A.M. 1974. Host-plant utilization by Pieris napi populations in California (Lepidoptera: Pieridae). Psyche 81:361-366.

_____1975. Ecological and behavioral aspects of coexistence in six crucifer-feeding pierid butterflies in the Central Sierra Nevadas. Amer. Midl. Natur. 93:424-433.

Singer, M.C. 1982. Quantification of host preference by manipulation of oviposition behavior in the butterfly Euphydryas editha. Oecologia (Berl.) 52:224-229.

Slater, P.J.B. 1973. Describing sequences of behavior. In: P.P.G. Bateson and P.H. Klopfer Eds. Perspectives in Ethology. Plenum Press. New York. pp131-152.

Smith, J.G. 1976. Influence of crop background on aphids and other phytophagous insects on brussels sprouts. Ann. appl. Biol. 83:1-13.

Sokal, R.R. and F.J. Rholf 1969. Biometry W.H. Freeman and Co., San Francisco. 776pp.

Solereder, H. 1908. Systematic Anatomy of the Dicotyledons, vol 1. Clarendon Press, Oxford. 644pp.

Stanton, M.L. 1982. Searching in a patchy environment: Foodplant selection by Colias p. eriphyle butterflies. Ecology 63:839-853.

_____1983. Spatial patterns in the plant community and their effects on insect search. In: S. Ahmad Ed. Herbivorous Insects: Host-seeking Behavior and Mechanisms. Academic Press. New York. pp 125-157.

_____1984. Short-term learning and the searching accuracy of egg-laying butterflies. Anim. Behav. 32:33-40.

Steinberg, J.B. 1977. Information theory as an ethological tool. In: B.A. Hazlett Ed. Quantitative Methods in the Study of Animal Behavior. Academic Press. New York. pp47-74.

Steinberg, J.B. and R.C. Conant 1974. An informational analysis of the inter-male behaviour of the grasshopper Chortophaga viridifasciata. Anim. Behav. 22:617-627.

Stevens, W.C. 1924. Plant Anatomy. P. Blakestons and Sons. Philadelphia. 398pp.

Stone, J.L.S. and H.J. Midwinter 1975. Butterfly Culture: A Guide to Breeding Butterflies, Moths and Other Insects. Blanford Press. Dorset. 104pp.

Tabashnik, B.E., H. Wheelock, J.D. Rainbolt, and W.B. Watt 1981. Individual variation in oviposition preference in the butterfly, Colias eurytheme. Oecologia (Berl.) 50: 225-230.

Thorsteinson, A.J. 1952. The chemotactic responses that determine host specificity in an oligophagous insect (Plutella maculipennis (Curt.) Lepidoptera). Can. J. Zool. 31:52-72.

_____1958. Acceptability of plants for phytophagous insects. Proc. 10th Intnl. Congr. Entomol. 2 1956. pp 599-601.

_____1960. Host selection in phytopagous insects. Annu. Rev. Entomol. 5:193-218.

Traynier, R.M.M. 1979. Long-term changes in the oviposition behaviour of the cabbage butterfly, Pieris rapae, induced by contact with plants. Physiol. Entomol. 4:87-96.

_____1984. Associative learning in the ovipositional behaviour of the cabbage butterfly, Pieris rapae. Physiol. Entomol. 9:465-472.

Twinn, C.R. 1924. Studies in the life history, bionomics and control of the cabbage worm in Ontario. 54th Ann. Rep. Entomol. Soc. Ont. 1923:82-86.

van Emden, H.F. 1972. Aphids as phytochemists. In: J.B. Harborne, Ed. Phytochemical Ecology. Academic Press, London. pp 25-43.

van Emden, H.F. and M.A. Bashford. 1969. A comparison of the reproduction of Brevicoryne brassicae and Myzus persicae in relation to soluble nitrogen concentration and leaf age (leaf position) in the brussels sprout plant. Ent. exp. & appl. 12:351-364.

von Uexkull, J. 1957. A stroll though the world of animals and men: A picture book of invisible worlds. In: C.H. Schiller, Ed. Instinctive Behavior. International Universities Press, Inc. 328pp.

Vaidya, V.G. 1969. Investigations on the role of visual stimuli in the egg-laying and resting behaviour of Papilio demoleus L. (Papilionidae, Lepidoptera). Anim. Behav. 17:350-355.

Verschaffelt, E. 1911. The cause determining the selection of food in some herbivorous insects. Proc. Acad. Sci. Amsterdam 13:536-542.

Wensler, R.J.D. 1962. Mode of host selection by an aphid. Nature 195:830-831.

Wolfson, J.L. 1980. Oviposition response of Pieris rapae to environmentally induced variation in Brassica nigra. Ent. exp. & appl. 27:223-232.

Yamamoto, R.T., R.Y. Jenkins, and R,K. McClusky 1969. Factors determing the selection of plants for oviposition by the tobacco hornworm Maduca sexta. Ent. exp. & appl. 12:504-508.

APPENDICES

APPENDIX A

Sampling dates during which different plant comparisons were tested.

Appendix A

Sampling dates during which different plant comparisons were tested.

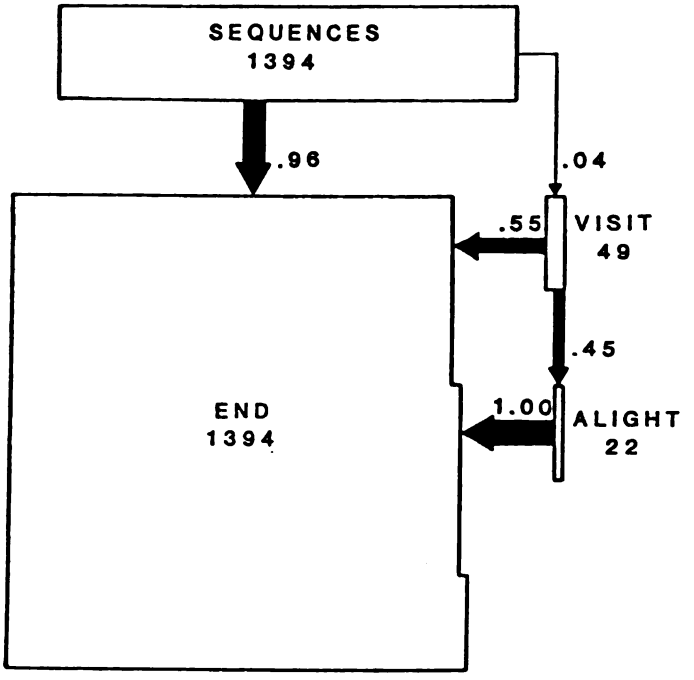
Date	Plant Comparison Number I	II	III	IV	V
July 12	X				
July 13	X				
July 19	X				
July 21	X	X			
July 22	X				
July 23	X	X			
July 24	X	X			
July 25	X	X			
July 28	X	X			
July 30	X	X			
July 31	X	X			
August 1	X	X			
August 2	X	X			
August 5	X	X			
August 9	X	X			
August 10	X				
August 13	X	X			
August 14	X	X	X		
August 15	X	X	X		
August 16	X	X	X		
August 17	X	X	X		
August 20	X	X	X		
August 21	X	X	X		
August 25	X		X		
August 26	X		X		
August 28	X		X		
August 30	X		X	X	
September 2	X		X	X	
September 6	X		X	X	X
September 8	X		X	X	X
September 10	X		X	X	X
September 11	X		X	X	X
September 17	X				X
September 18	X		X	X	X
September 19	X				X
September 20	X		X	X	X
September 21	X		X	X	X
September 22	X		X	X	X
October 2	X				X
October 3	X				X
October 12	X				X
October 17	X				X

APPENDIX B

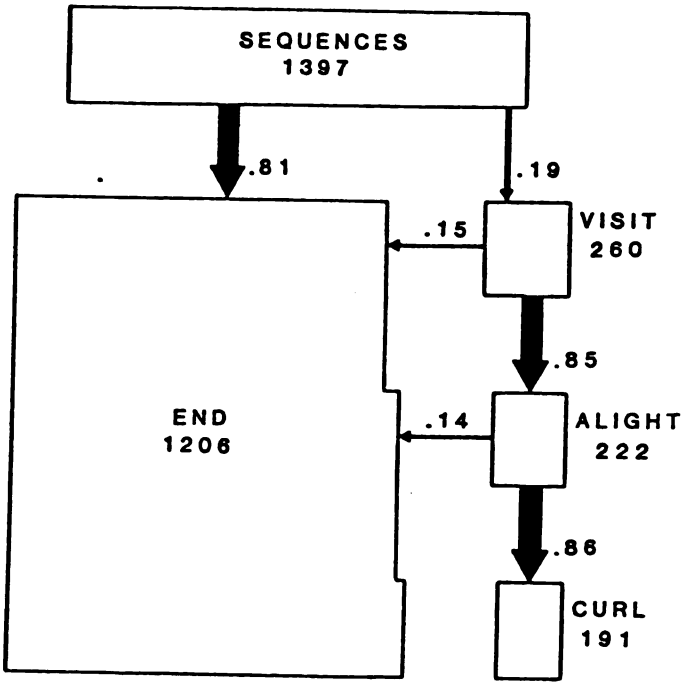
Number of butterflies entering each stage of the ovipositional sequence for the plant species in each comparison.

The width of each box is proportional to the number of butterflies entering the stage (given in or near the approprate box). The width of each arrow is proportional to the transitional probability (given next to each arrow). The total area of each box is not significant.

Appendix B

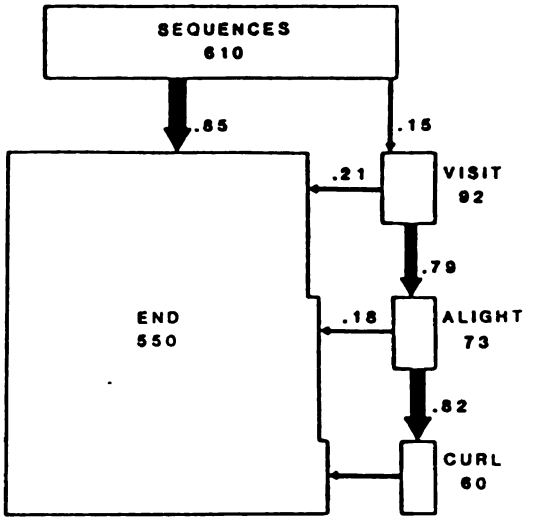


COMPARISON 1 : BROCCOLI

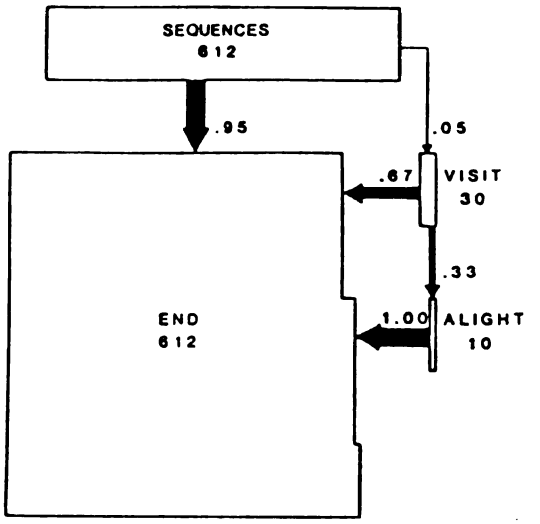


COMPARISON I : TANSY

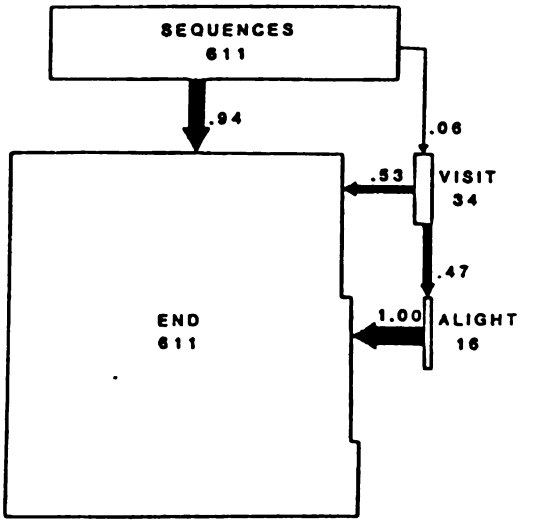
Appendix B (cont.)



COMPARISON II : BROCCOLI

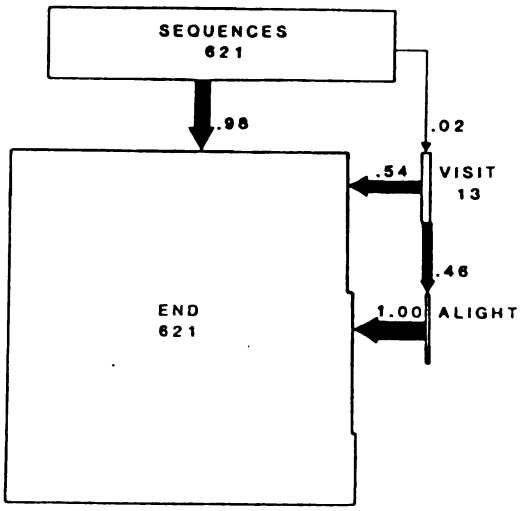


COMPARISON II : TANSY

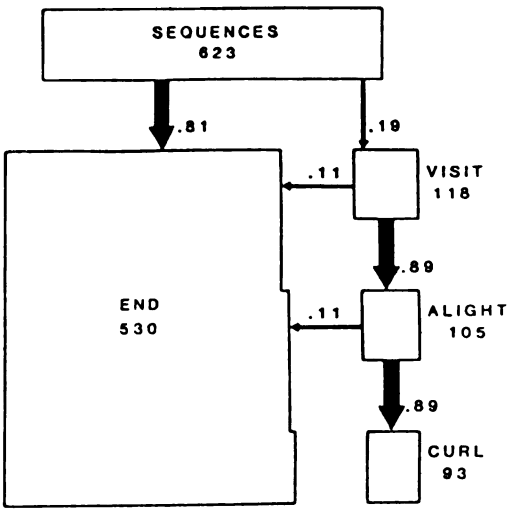


COMPARISON II : SAGE

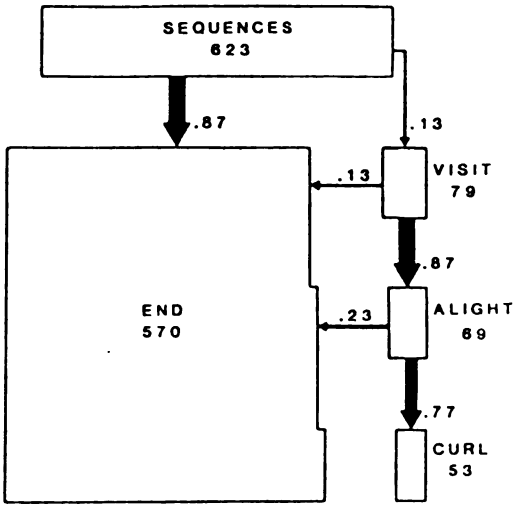
Appendix B (cont.)



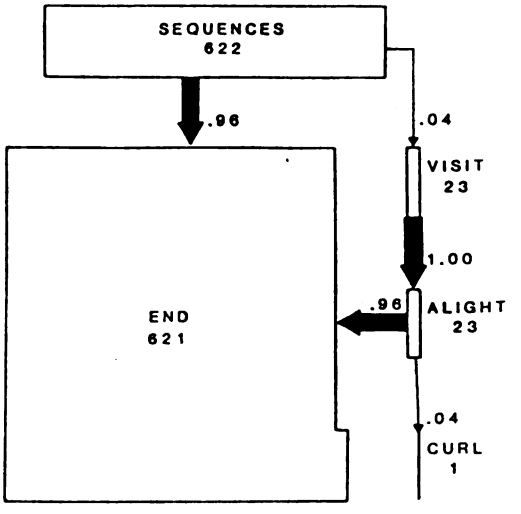
COMPARISON III : TANSY



COMPARISON III : BROCCOLI

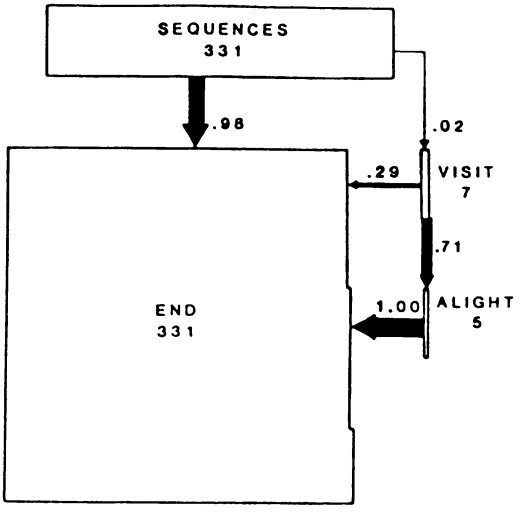


COMPARISON III : MUSTARD

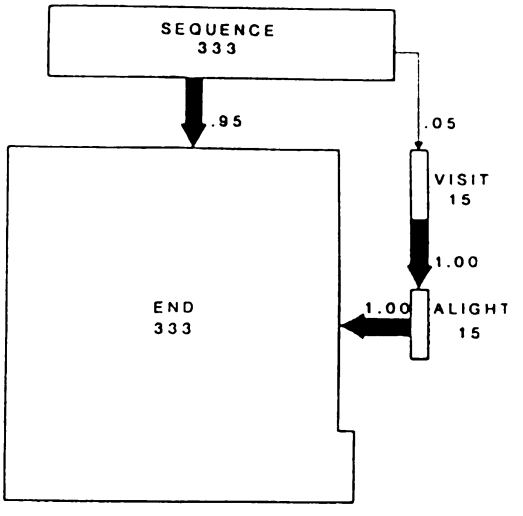


COMPARISON III : LETTUCE

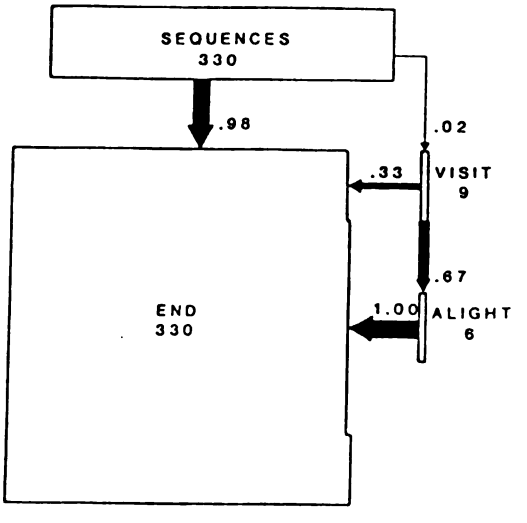
Appendix B (cont.)



COMPARISON IV : TANSY

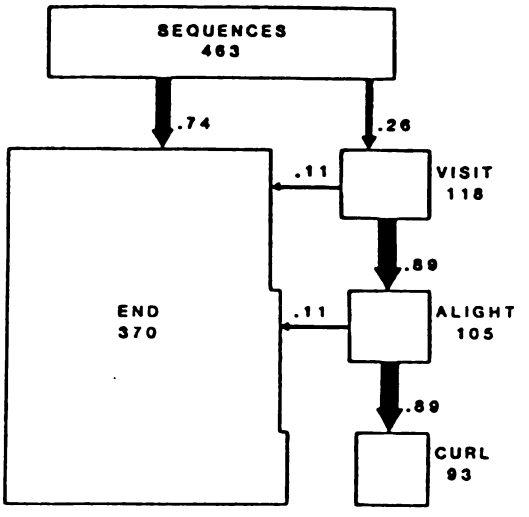


COMPARISON IV : LETTUCE

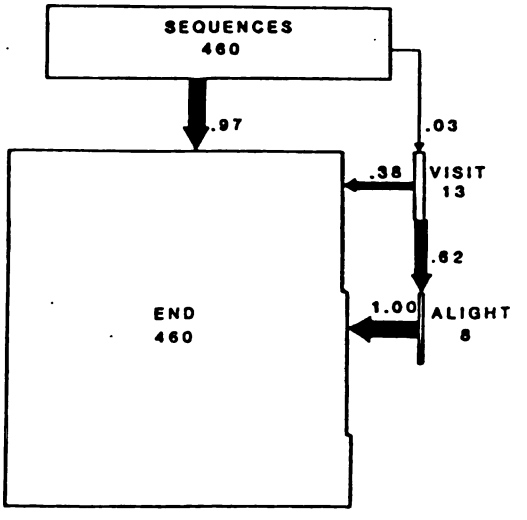


COMPARISON IV : SOYBEAN

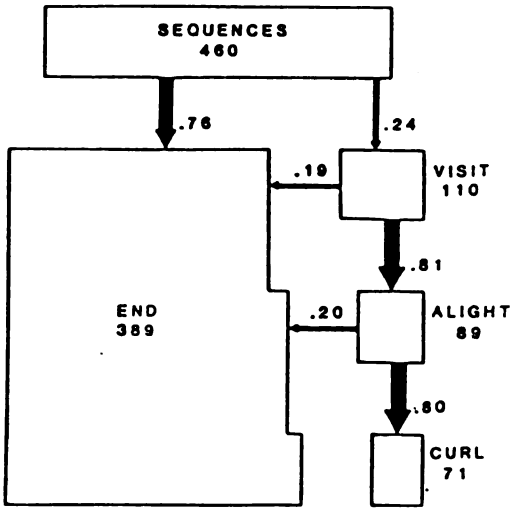
Appendix B (cont.)



COMPARISON V : BROCCOLI



COMPARISON V : TANSY



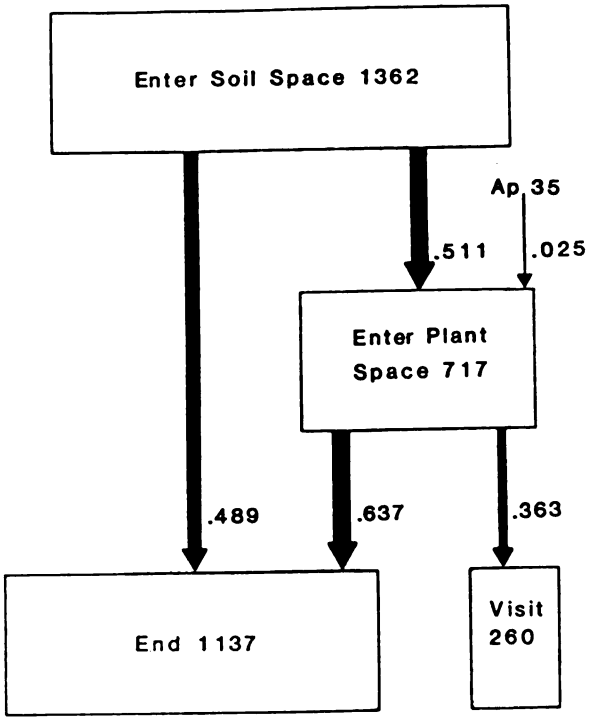
COMPARISON V : BROCCOLI-TANSY

APPENDIX C

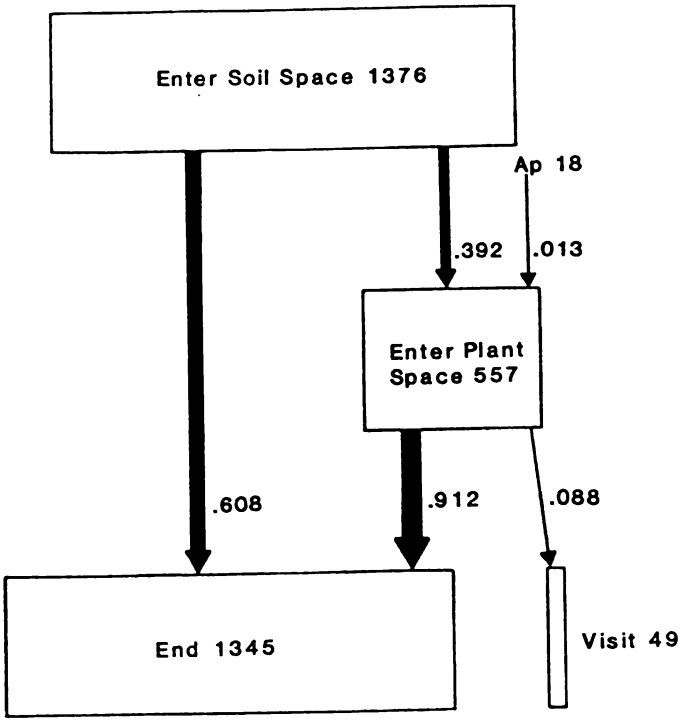
Number of butterflies performing the behaviors in the movement stage of oviposition for the plant species in each comparison.

The width of each box is proportional to the number of butterflies performing the behavior (given in or near the appropriate box). The width of each arrow is proportional to the transitional probability (given next to each arrow).

Appendix C

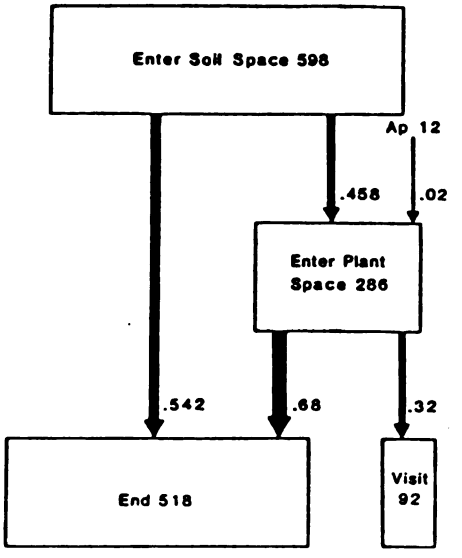


COMPARISON I : BROCCOLI

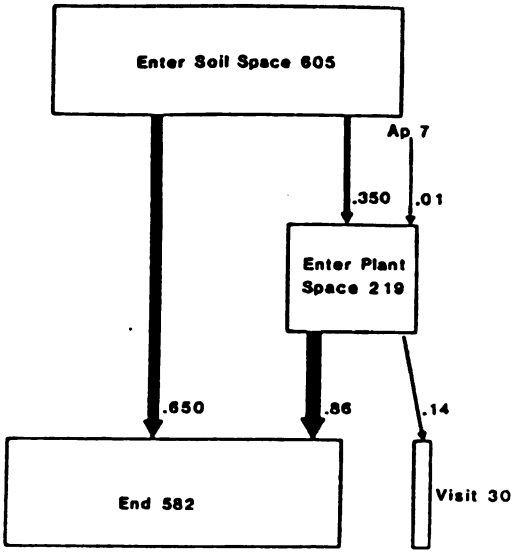


COMPARISON I : TANSY

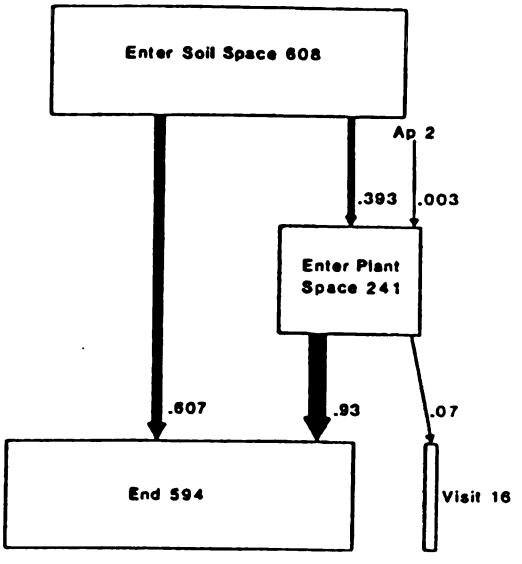
Appendix C (cont.)



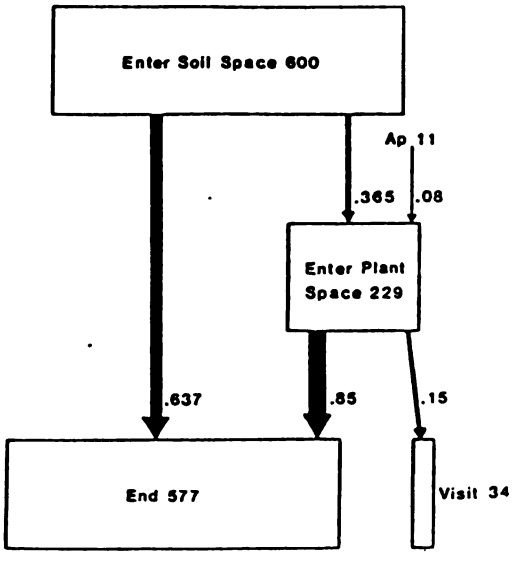
COMPARISON II : BROCCOLI



COMPARISON II : TANSY

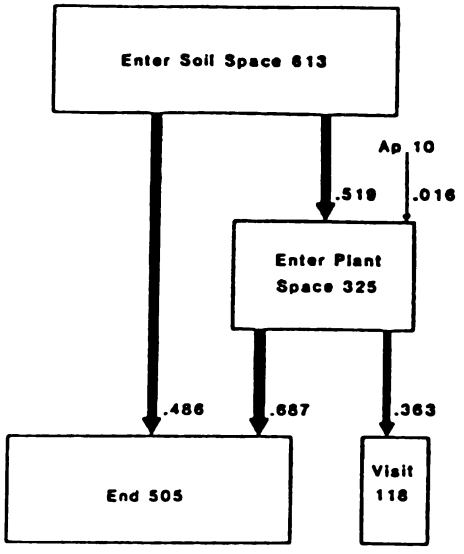


COMPARISON II : POT

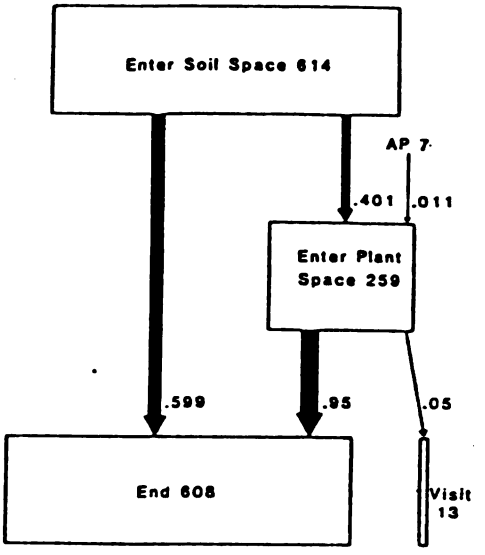


COMPARISON II : SAGE

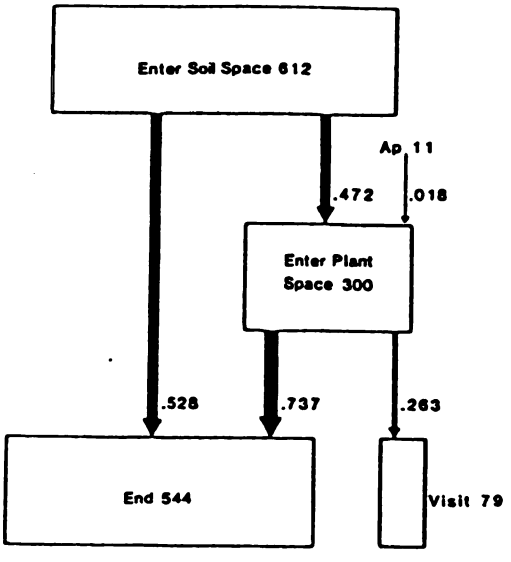
Appendix C (cont.)



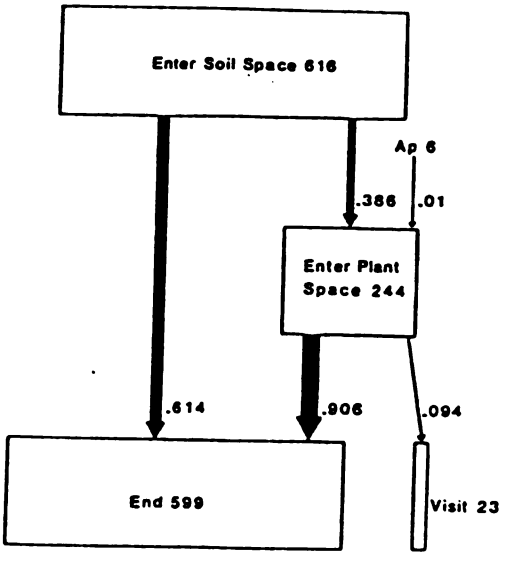
COMPARISON III : BROCCOLI



COMPARISON III : TANSY

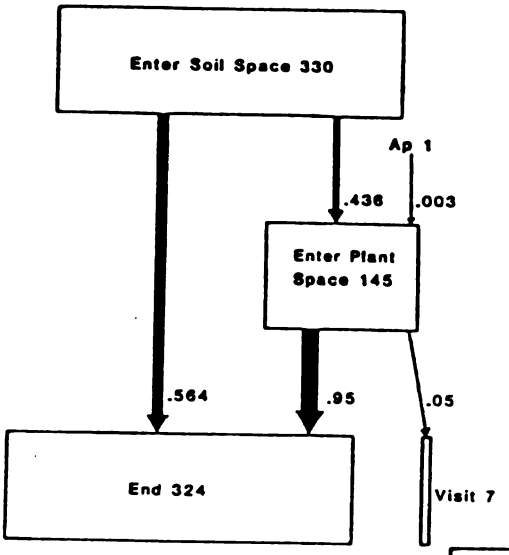


COMPARISON III : MUSTARD

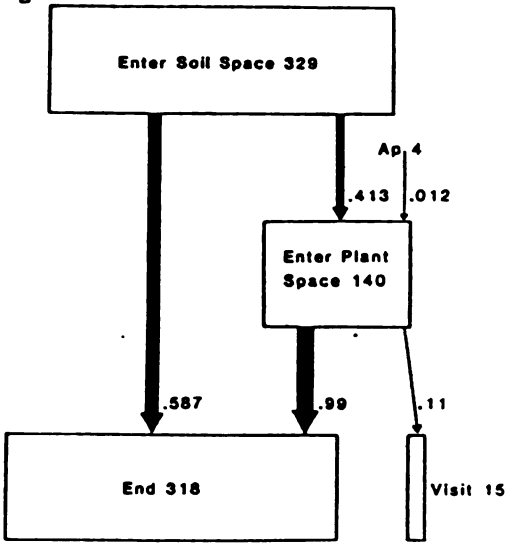


COMPARISON III : LETTUCE

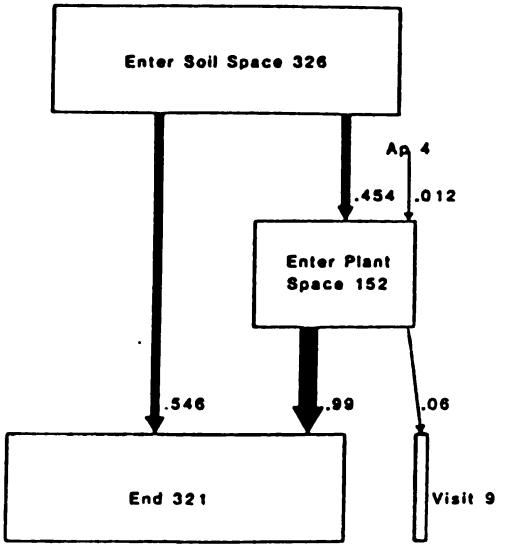
Appendix C (cont.)



COMPARISON IV : TANSY

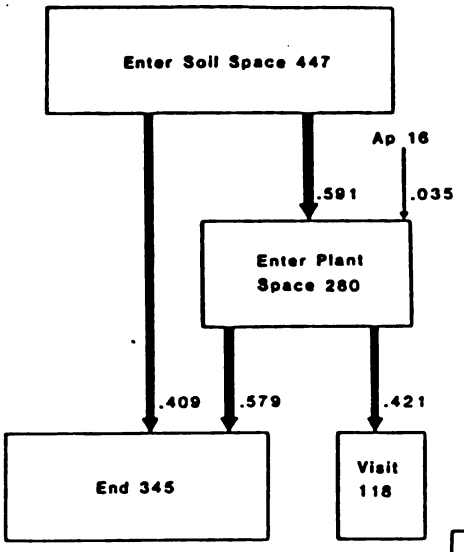


COMPARISON IV : LETTUCE

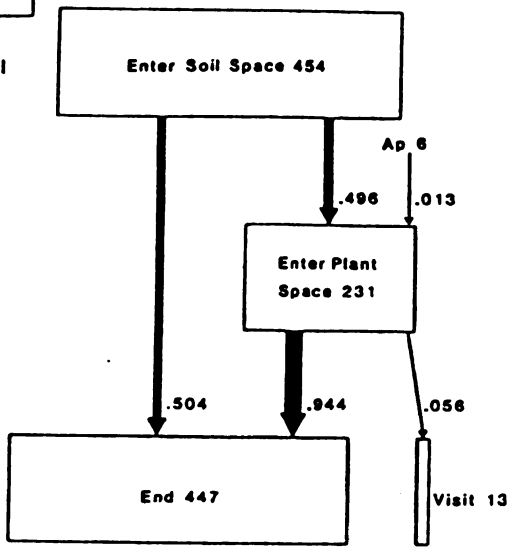


COMPARISON IV : SOYBEAN

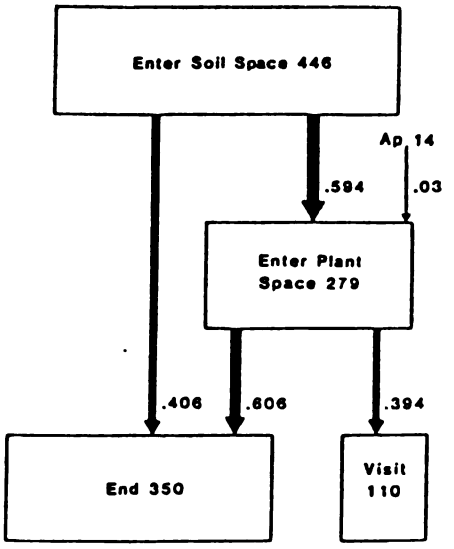
Appendix C (cont.)



COMPARISON V : BROCCOLI



COMPARISON V : TANSY



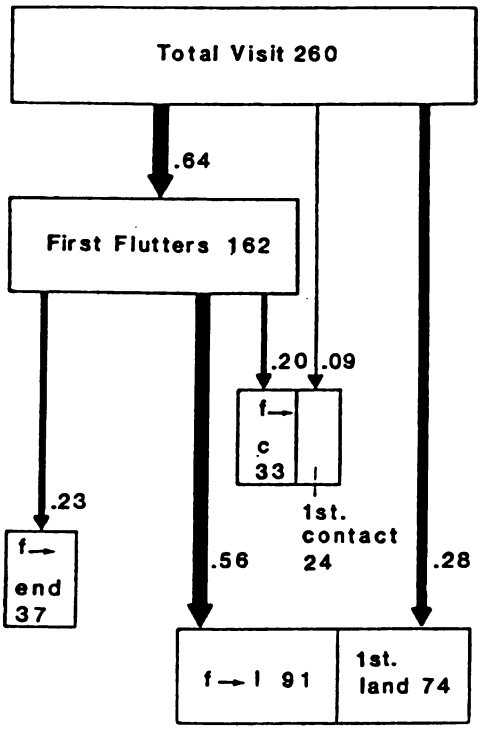
COMPARISON V : BROCCOLI-TANSY

APPENDIX D

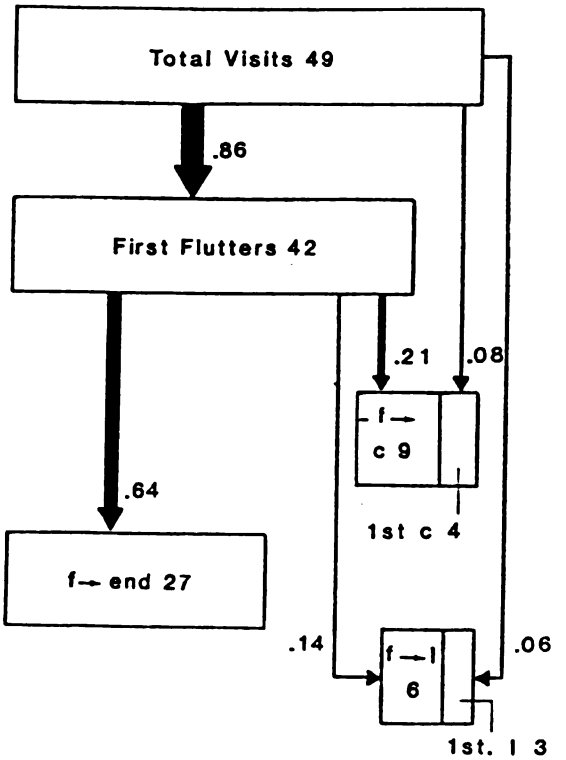
Number of butterflies fluttering, contacting, landing, and ending as the first two behaviors in visits to the plant species in each comparison.

The width of each box is proportional to the number of butterflies performing the behavior (given in or near the appropriate box). The width of each arrow is proportional to the transitional probability (given next to each arrow).

Appendix D

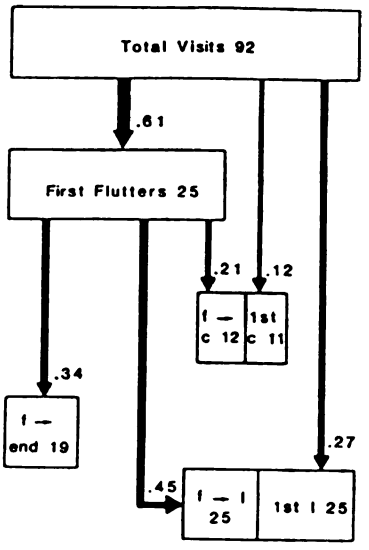


COMPARISON I : BROCCOLI

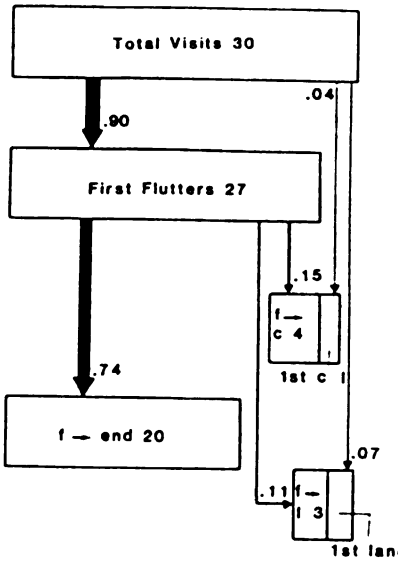


COMPARISON I :TANSY

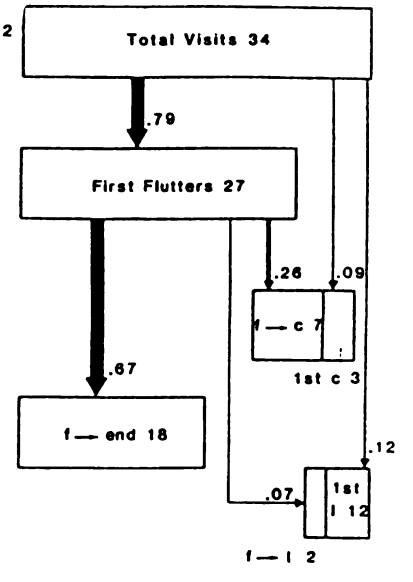
Appendix D (cont.)



COMPARISON II : BROCCOLI

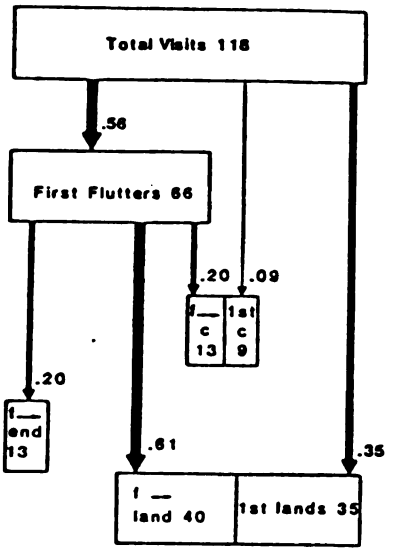


COMPARISON II : TANSY

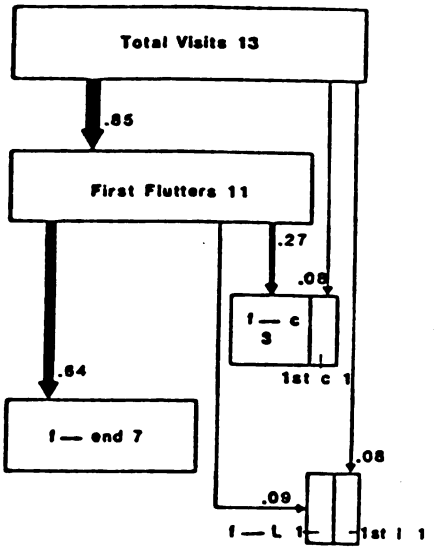


COMPARISON II : SAGE

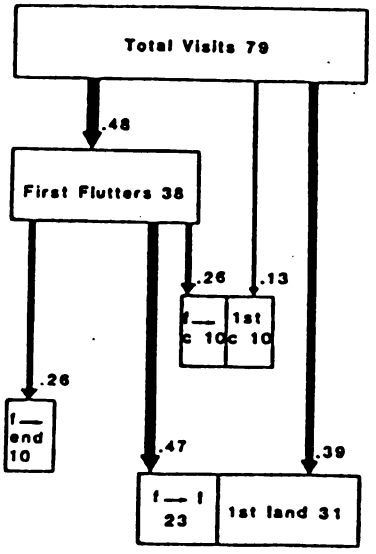
Appendix D (cont.)



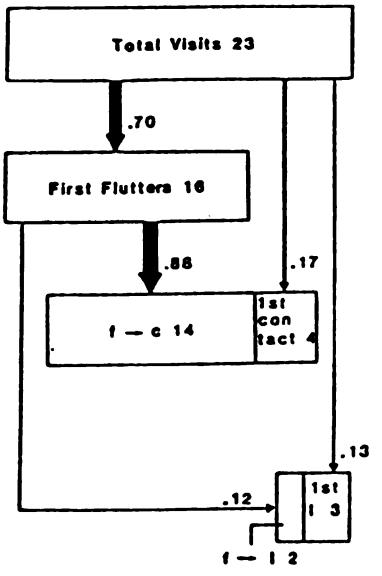
COMPARISON III : BROCCOLI



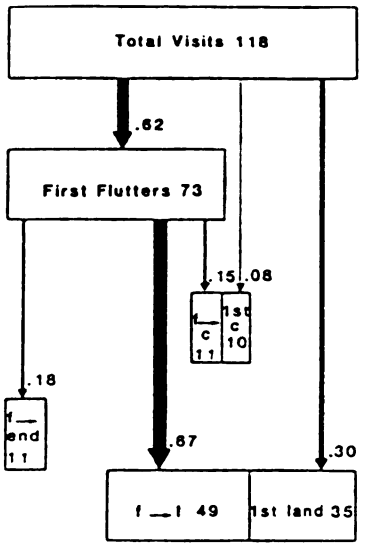
COMPARISON III : TANSY



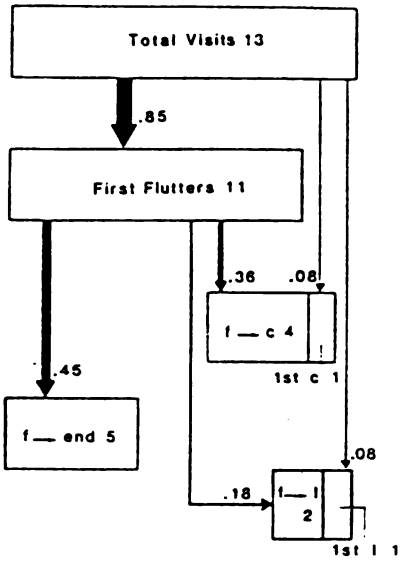
COMPARISON III : MUSTARD



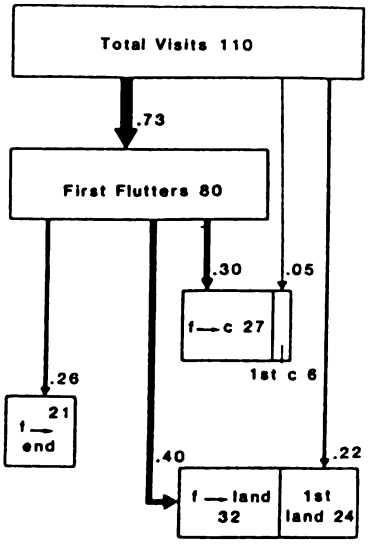
COMPARISON III : LETTUCE



COMPARISON V : BROCCOLI



COMPARISON V : TANSY



COMPARISON V : BROCCOLI-TANSY

MICHIGAN STATE UNIV. LIBRARIES
31293006759934