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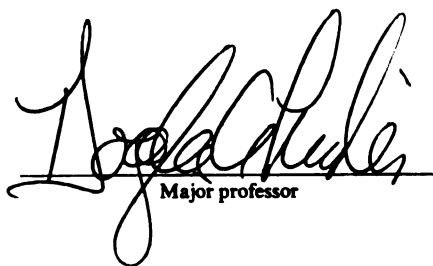
Non-crop Habitats and the Conservation of *Eriborus terebrans*
(Gravenhorst) (Hymenoptera: Ichneumonidae), a Parasitoid of the
European Corn Borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera:
Pyralidae)

presented by

Lawrence Evans Dyer

has been accepted towards fulfillment
of the requirements for

Doctor of Philosophy degree in Entomology



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**NON-CROP HABITATS AND THE CONSERVATION OF *ERIBORUS TEREBRANS*
(GRAVENHORST) (HYMENOPTERA: ICHNEUMONIDAE), A PARASITOID OF
THE EUROPEAN CORN BORER, *OSTRINIA NUBILALIS* (HÜBNER)
(LEPIDOPTERA: PYRALIDAE)**

by

Lawrence Evans Dyer

A DISSERTATION

**Submitted to
Michigan State University
in partial fulfillment of the requirements
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ABSTRACT

NON-CROP HABITATS AND THE CONSERVATION OF *ERIBORUS TEREBRANS* (GRAVENHORST) (HYMENOPTERA: ICHNEUMONIDAE), A PARASITOID OF THE EUROPEAN CORN BORER, *OSTRINIA NUBILALIS* (HÜBNER) (LEPIDOPTERA: PYRALIDAE)

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Eriborus terebrans (Gravenhorst) (Hymenoptera: Ichneumonidae) is the primary parasitoid of the European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Pyralidae), in Michigan. The within-field distribution of adult *E. terebrans* was sampled in 1991 and 1992, by placing malaise traps near a wooded edge, near an herbaceous edge, and in the field interior, in each of four corn fields. During the first generation of 1991 significantly more wasps were captured in the wooded-edge traps than in herbaceous edge or interior traps. In the first generation of 1992 more wasps were again captured in the wooded edge traps in two fields, while in the other two fields more wasps were captured in both the herbaceous edge and wooded edge traps than the interior trap. In the second generation of both years there was no consistent pattern of distribution among sites. The distribution of adult wasps was not consistently correlated with the distribution of *O. nubilalis* larvae. Further experiments demonstrated that *E. terebrans* longevity was greatly increased by access to sugar, and decreased by high temperatures. The microclimates of woodlots were more suitable for *E. terebrans* adults than early-season corn fields. In all habitats the longevity of adult wasps was enhanced by sugar.

Behavior of *E. terebrans* was observed in a greenhouse from before sunrise until after sunset, to assess diurnal patterns of behavior. From late afternoon until morning wasps assumed a quiet resting posture. The highest levels of activity, including walking, flying, and search for *O. nubilalis* larvae, were during the morning. Activity was low throughout the afternoon. Walking and flying by females increased in afternoons when

cages were hotter due to direct sunlight, which may indicate attempts to escape a stressful environment.

Eriborus terebrans needs habitats adjacent to corn fields for sources of sugar and a moderate microclimate unavailable in early-season corn. In annual agriculture, perennial habitats adjacent to crop fields may be necessary to provide the structure, stability and resources needed for the successful conservation of natural enemies, and effective biological control.

These pages, and the journey they represent are dedicated with love to my parents: to my father for the gift of love and curiosity for the natural world; to my mother for the gift of introspection and empathy, that I might seek to understand the hearts of others; to them both for teaching me to strive to live simply, honestly, and in accordance with my ideals.

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TABLE OF CONTENTS

LIST OF TABLES	viii
LIST OF FIGURES	x
KEY TO SYMBOLS AND ABBREVIATIONS	xiv
CHAPTER 1. Introduction to <i>Eriborus terebrans</i> and <i>Ostrinia nubilalis</i> in Michigan, and general overview	1
CHAPTER 2. The role of perennial non-crop habitats for successful conservation of biological control agents in annual agriculture	
Introduction	11
Attributes of perennial systems	15
Making annual cropping systems more amenable to biological control	16
Habitat diversity to provide perennial qualities in annual agroecosystems	19
Conclusions	23
CHAPTER 3. Distribution of <i>Eriborus terebrans</i> (Gravenhorst) (Hymenoptera: Ichneumonidae) in corn fields, with respect to adjacent non-crop habitats	
Introduction	24
Methods	26
1991 field season	26
1992 and 1993 field seasons	30
Results	33

Discussion	52
CHAPTER 4. Effects of habitat, temperature, and sugar availability on the longevity of <i>Eriborus terebrans</i> (Gravenhorst) (Hymenoptera: Ichneumonidae)	
Introduction	60
Methods	63
Growth chamber test of temperature, relative humidity, and provision effects	63
Greenhouse test of temperature and provision effects	67
Suitability of selected habitats	68
Results	70
Growth chamber test of temperature, relative humidity, and provision effects	70
Greenhouse test of temperature and provision effects	77
Suitability of selected habitats	82
Discussion	88
CHAPTER 5. Diurnal behavior of <i>Eriborus terebrans</i> (Gravenhorst) (Hymenoptera: Ichneumonidae) in a greenhouse	
Introduction	92
Methods	94
Results	102
Discussion	113
CHAPTER 6. Summary and conclusions	119
APPENDIX. Record of deposition of voucher specimens	131
LIST OF REFERENCES	134

LIST OF TABLES

Table 1.	Characteristics of fields sampled in 1991 and 1992.	27
Table 2.	Correlation of <i>E. terebrans</i> females with <i>O. nubilalis</i> larvae, and with % plants damaged by <i>O. nubilalis</i> , at the end of the first generations of 1991 and 1992, in corn fields in Michigan.	47
Table 3.	Differences in <i>O. nubilalis</i> infestation among sites within corn fields, in the first generation of 1991, and correlation of <i>E. terebrans</i> females with <i>O. nubilalis</i> infestation.	48
Table 4.	Parasitism of <i>O. nubilalis</i> larvae by <i>E. terebrans</i> , in corn fields in Michigan.	50
Table 5.	Relative humidities in cages in the growth chamber experiment, under combinations of salt solutions, temperatures and provision treatments.	65
Table 6.	ANOVA of <i>Eriborus terebrans</i> longevity in growth chambers: relative humidity and provision treatments nested within temperatures.	72
Table 7.	ANOVA of proportion of observations in which <i>Eriborus terebrans</i> were on wicks in growth chambers: relative humidity and provision treatments nested within temperatures.	76
Table 8.	ANOVA of <i>Eriborus terebrans</i> longevity in greenhouses: factorial of temperature and provision treatments.	79
Table 9.	ANOVA of proportion of observations in which <i>Eriborus terebrans</i> were on wicks in greenhouses: factorial of temperature and provision treatments.	81
Table 10.	ANOVA of <i>Eriborus terebrans</i> longevity in the early-season habitat experiment: wasps randomly assigned to habitat and provision treatments within fields (blocks).	83

Table 11.	Categories of behaviors recorded during observation, abbreviations used in the text and figures, and a description of the behaviors.	96
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LIST OF FIGURES

- | | | |
|------------------|---|----|
| Figure 1. | Schematic diagram of placement of malaise traps to sample <i>E. terebrans</i> adults, and the location of corn rows sampled for <i>O. nubilalis</i> larvae. Edge and woodlot malaise traps were used only in 1991. Rows 80 m from edges were sampled only in 1991. | 29 |
| Figure 2. | <i>Eriborus terebrans</i> females captured in malaise traps in 1991, at three locations in corn fields: herbaceous edge, interior, and wooded edge. Values are the means of four fields. Bars indicate capture on each date. The line graph is cumulative capture (cum) over the first (JD 164-190), and second (JD 196-260) generations. | 34 |
| Figure 3. | Total malaise-trap capture of <i>Eriborus terebrans</i> females in the first generation of 1991, at three locations (herbaceous edge, interior, and wooded edge) in each of four corn fields. <i>P</i> -values indicate levels of significance, and different letters indicate significant differences within fields (log-likelihood ratio goodness of fit tests). | 35 |
| Figure 4. | Total malaise-trap capture of <i>Eriborus terebrans</i> females in the second generation of 1991, at three locations (herbaceous edge, interior, and wooded edge) in each of four corn fields. <i>P</i> -values indicate levels of significance, and different letters indicate significant differences within fields (log-likelihood ratio goodness of fit tests). | 37 |
| Figure 5. | <i>Eriborus terebrans</i> females captured in malaise traps in 1992, at three locations in corn fields: herbaceous edge, interior, and wooded edge. Values are the means of four fields. Bars indicate capture on each date. The line graph is cumulative capture (cum) over the first (JD 155-208), and second (JD 212-274) generations. | 38 |

Figure 6.	Total malaise-trap capture of <i>Eriborus terebrans</i> females in the first generation of 1992, at three locations (herbaceous edge, interior, and wooded edge) in each of four corn fields. <i>P</i> -values indicate levels of significance, and different letters indicate significant differences within fields (log-likelihood ratio goodness of fit tests).	39
Figure 7.	Total malaise-trap capture of <i>Eriborus terebrans</i> females in the second generation of 1992, at three locations (herbaceous edge, interior, and wooded edge) in each of four corn fields. <i>P</i> -values indicate levels of significance, and different letters indicate significant differences within fields (log-likelihood ratio goodness of fit tests).	40
Figure 8.	Capture of <i>Eriborus terebrans</i> males and females in malaise traps at ground level (low) and at the top of the corn canopy (high), in three locations (herbaceous edge, interior, and wooded edge) in one corn field, in the second generation of 1991.	42
Figure 9.	<i>Eriborus terebrans</i> males captured in malaise traps in 1992, at three locations in corn fields: herbaceous edge, interior, and wooded edge. Values are the means of four fields. Bars indicate capture on each date. The line graph is cumulative capture (cum) over the first (JD 155-208), and second (JD 212-274) generations.	43
Figure 10.	Total malaise-trap capture of <i>Eriborus terebrans</i> males in the first generation of 1992, at three locations (herbaceous edge, interior, and wooded edge) in each of four fields. <i>P</i> -values indicate levels of significance, and different letters indicate significant differences within fields (log-likelihood ratio goodness of fit tests).	44
Figure 11.	Total capture of <i>Eriborus terebrans</i> males and females, in the first and second generations of 1993, in one malaise trap in a corn field, and four malaise traps elevated to different heights along an adjacent woodlot canopy.	46
Figure 12.	Daily maximum temperatures for May through August of 1991 and 1992, in E. Lansing Michigan.	57

Figure 13.	Mean longevity ($\pm$ standard error) of <i>Eriborus terebrans</i> females in growth chambers at two temperatures (25°C, 35°C, $P<0.058$), two relative humidities (low, high, $P<0.0016$), and three provision treatments (dry, water, sugar, $P<0.0001$). $n=4$ per treatment, except 35°C-low-sugar $n=3$.	73
Figure 14.	Mean longevity ($\pm$ standard error) of <i>Eriborus terebrans</i> males in growth chambers ($n=4$ per treatment), at two temperatures (25°C, 35°C, $P<0.0239$), two relative humidities (low, high, $P<0.8159$), and three provision treatments (dry, water, sugar, $P<0.0001$). $n=4$ per treatment, except 25°C-low-dry, 25°C-high-water, and 35°C-high-water $n=3$.	74
Figure 15.	Mean longevity ($\pm$ standard error) of <i>Eriborus terebrans</i> in greenhouses, at two temperatures (25°C, 35°C, female $P<0.0007$, male $P<0.0205$), and three provision treatments (dry, water, sugar, female $P<0.0001$, male $P<0.0010$). $n=4$ per treatment, except 35°C-sugar-female, 25°C-dry-male, 25°C-sugar-male, and 35°C-sugar-male $n=5$, and 35°C-water-female, 35°C-dry-male $n=3$.	80
Figure 16.	Mean longevity ($\pm$ standard error) of <i>Eriborus terebrans</i> females early in the growing season, in four habitats ($P<0.1285$), with two provision treatments ($P<0.0218$). $n=5$, except herbaceous-water, corn-sugar, and fencerow-sugar $n=4$.	84
Figure 17.	Mean longevity ($\pm$ standard error) of <i>Eriborus terebrans</i> males early in the growing season, in four habitats ($P<0.0504$), with two provision treatments ($P<0.005$). $n=5$, except herbaceous-water, corn-sugar, and fencerow-sugar $n=4$.	85
Figure 18.	Mean longevity ($\pm$ standard error) of <i>Eriborus terebrans</i> females late in the growing season, in four habitats with two provision treatments. $n=4$, except corn-water $n=5$.	86
Figure 19.	Mean longevity ($\pm$ standard error) of <i>Eriborus terebrans</i> males late in the growing season, in four habitats with two provision treatments. $n=4$, except corn-water $n=5$.	87

Figure 20.	Proportions of total observed behaviors, for <i>E. terebrans</i> females. Numbers are proportions for the corresponding behavior. Abbreviations are defined in Table 11. Dr here includes both drinking and sugar-feeding. Other = copulation + oviposition + other undefined behaviors.	98
Figure 21.	Proportions of total observed behaviors, for <i>E. terebrans</i> males. Numbers are proportions for the corresponding behavior. Abbreviations are defined in Table 11. Dr here includes both drinking and sugar-feeding. Other = courtship + copulation + other undefined behaviors.	99
Figure 22.	Day means for <i>E. terebrans</i> females, for inactive rest ($P<0.19$), combined walking and flying ($P<0.001$), and search for <i>O. nubilalis</i> larvae ($P<0.359$).	103
Figure 23.	Hour means for <i>E. terebrans</i> females, for inactive rest ($P<0.0001$), and combined walking and flying ($P<0.0001$). Asterisks indicate an hour mean is significantly different from the overall mean ($P<0.05$).	104
Figure 24.	Day means for <i>E. terebrans</i> males, for inactive rest ($P<0.07$), and combined walking and flying ($P<0.0001$).	105
Figure 25.	Hour means for <i>E. terebrans</i> males, for inactive rest ($P<0.0001$), and combined walking and flying ($P<0.0001$). Asterisks indicate an hour mean is significantly different from the overall mean ($P<0.05$).	106
Figure 26.	Contrasts between days 2 and 3 of each week (1300, 1400, and 1500 hours combined), for walking and flying by <i>E. terebrans</i> females: week one $P<0.5$, week two $P<0.025$, and week three $P>0.75$.	109
Figure 27.	Hour means of search for <i>O. nubilalis</i> larvae by <i>E. terebrans</i> females ($P<0.1098$). Asterisks indicate an hour mean is significantly different from the overall mean ($P<0.05$).	111
Figure 28.	Drinking by <i>E. terebrans</i> females and males: drinking from water wick, sugar wick, plant and cage surfaces combined.	112

KEY TO SYMBOLS AND ABBREVIATIONS

ANOVA	analysis of variance
cm	centimeters
df	degrees of freedom
ft	feet
ha	hectares
in.	inches
JD	Julian date
m	meters
m²	meters squared
ml	milliliters
mm	millimeters
N	experiment-wide sample size
n	treatment sample size
°C	degrees centigrade
oz	ounces
<i>P</i>	probabiilty of a type I error
r	correlation coefficient
s	seconds

CHAPTER 1

Introduction to *Eriborus terebrans* and *Ostrinia nubilalis* in Michigan, and general overview

Eriborus terebrans (Gravenhorst) (Hymenoptera: Ichneumonidae) was introduced into North America earlier in this century, as a biological control agent of *Ostrinia nubilalis* (Hübner) (Lepidoptera: Pyralidae), the European corn borer. Since then there has been no intentional management of *E. terebrans* as a biological control agent, but it is currently the primary parasitoid of *O. nubilalis* in Michigan (Landis and Haas 1992). Corn is the crop to which the greatest acreage is planted in Michigan, amounting to 2.5 million acres in 1993, at a value exceeding \$627 million (Fedewa and Pscodna 1994). *Ostrinia nubilalis* is one of the most important pests of corn. Though 80% of Michigan corn growers reported economic injury from *O. nubilalis* in the 10 year period from 1982 to 1992, few manage for it (Landis and Swinton 1994). In the paragraphs to follow I will argue that infestation of field corn by *O. nubilalis* is a situation that may best be managed by conservation of natural enemies, and that *E. terebrans*, as the primary parasitoid of *O. nubilalis* in Michigan, should be among the objects of conservation management. The studies that follow investigate the role of non-crop habitats for the conservation of *E. terebrans*.

Ostrinia nubilalis was first reported in Michigan in 1921 in Monroe County, along the shore of Lake Erie (Caffrey and Worthley 1927). Early surveys from Ohio and Michigan, reported a single generation (Poos 1926), but by the late 1930's a second generation of *O. nubilalis* was becoming increasingly common in the North Central

States (Vance 1942). Three ecotypes of *O. nubilalis* are now recognized in North America: a northern univoltine, a central multivoltine, and a southern multivoltine ecotype (Brindley et al. 1975). *Ostrinia nubilalis* in southern Michigan is multivoltine, having two generations in most years, and a third generation in very warm years.

Ostrinia nubilalis overwinter as fifth (final) instar larvae inside tunnels in host plants. After emergence from corn stubble in the spring, the majority of *O. nubilalis* must disperse to new fields in search of their hosts. In Michigan, 49.7% of corn fields are rotated annually, an additional 20.7% every two years, and 29.6% after three or more years (Landis and Swinton 1994). When first-generation *O. nubilalis* females emerge in the spring they move to stands of tall grass, termed action sites, where mating occurs (Showers et al. 1976). The availability of water, such as dew or raindrops is necessary to initiate the release of pheromone by females to attract males (DeRozari et al. 1977). Females then seek the tallest corn plants available for oviposition (Showers et al. 1989). Egg masses can vary greatly in size, but average from 15 to 20 eggs (Caffrey and Worthley 1927). Egg masses are distributed randomly throughout corn fields in the first generation (Chiang and Hodson 1959). Egg masses are generally laid on the underside of leaves, near the mid-rib. Early instar *O. nubilalis* larvae feed in the whorl of the corn plant, third and fourth instars feed mostly in leaf sheaths and midribs, then fifth instars tunnel into the stalk where they continue to feed (Brindley and Dicke 1963). Most pupation occurs within tunnels in corn stalks.

In Michigan, the second generation usually begins in late July. Second-generation *O. nubilalis* again move to action sites for mating (Showers et al. 1976). Females then preferentially seek recently tasseled, or silking corn plants (Showers et al. 1989). Egg masses are again distributed randomly throughout the corn field (Calvin et al. 1986). Early instars feed most heavily in the leaf axils where pollen accumulates, and in developing ears and tassels; later instars tunnel into ears and stalks (Brindley and

Dicke 1963, Showers et al. 1989). Fifth instar larvae enter diapause and overwinter in tunnels in corn stalks.

Twenty-one species of parasitoids were released in North America between 1920 and 1940, 13 of which were released in Michigan, in a classical biological control effort to suppress *O. nubilalis* (Baker et al. 1949). Of the seven species reported to have been established and in maintenance status in North America in 1949, four were reported to have established in Michigan: *E. terebrans*, *Lydella thompsoni* (Herting) (Diptera: Tachinidae), *Macrocentrus grandii* (Goidanich) (Hymenoptera: Braconidae), and *Sympiesis viridula* (Thomson) (Hymenoptera: Eulophidae). *Eriborus terebrans* was introduced into 12 counties in southeastern Michigan on 19 occasions between 1926 and 1937, with material that originated in Europe or Massachusetts, where populations had established from earlier introductions from Europe and Asia (Baker et al. 1949).

The relative success of species introduced for biological control has been highly variable, both among regions, and over the years since introduction. In Connecticut, *E. terebrans* was the most widespread and abundant parasitoid in the first years of surveys from 1939 to 1951, but its numbers gradually declined as the numbers of *M. grandii* increased (Arbuthnot 1955). By 1980, *E. terebrans* was recovered from only one site in Connecticut, with 0.4% parasitism, while *M. grandii* was still widespread with parasitism ranging from 2.7 to 18.4% (Andreadis 1982). In Massachusetts as well, *E. terebrans* and *S. viridula* were both recovered at very low levels, while *M. grandii* was responsible for over 92% of the parasitism of *O. nubilalis* (Pears and Lilly 1975). *Macrocentrus grandii* was also the most abundant parasitoid in Pennsylvania in 1990; average parasitism was 17.4%, while *L. thompsoni*, and *E. terebrans* were both present, but at less than 3% parasitism (Losey et al. 1992). In Ohio, *L. thompsoni* was the most important parasitoid in samples conducted between 1948 and 1955, though *E. terebrans* was widespread, and may have been more important in certain localities (Rolston et al. 1958). *Lydella thompsoni* was also the most abundant parasitoid in Iowa until 1962, but

then declined, and has not been recovered since 1966 (Lewis 1982). Between 1951 and 1980, *E. terebrans* remained widespread in Iowa, but with low levels of parasitism, while *M. grandii* was responsible for the highest percent parasitism (Lewis 1982). In Nebraska, *L. thompsoni* was last reported in 1965 (Hill et al. 1978), and *E. terebrans* has remained at low levels (Godfrey et al. 1991). *Lydella thompsoni*, *S. viridula*, and *E. terebrans* all have been reported in low numbers in Ontario (Wressell and Wishart 1959, Wressell 1973). In a more recent survey from 1987 to 1990, (Wendel and Wood 1991), *M. grandii* and *L. thompsoni* were the predominant parasitoids in eastern states, with a high for *M. grandii* of 4.36% parasitism in Pennsylvania, and for *L. thompsoni* of 10.36% in N. Carolina, whereas *E. terebrans* was more abundant in the north central region, with a high value of 2.2% in Michigan. Minnesota and Kansas were the only states in the north central region (IL, IN, IA, KS, MI, MN, MO, NE, ND, OH, SD, WI) where parasitism by *M. grandii* (MN=1.41, KS=0.04%) was higher than that of *E. terebrans* (MN=1.12, KS=0.0%) (Wendel and Wood 1991). *Lydella thompsoni* had all but disappeared from the north central region, having been detected only in Ohio (0.88%), where it may have reestablished due to dispersal from a more recent reintroduction in Delaware (Mason et al. 1994).

In 1989 and 1990, *E. terebrans* accounted for 92.2 to 99.2% of the total parasitism of *O. nubilalis* in fields sampled in Michigan (Landis and Haas 1992). In 1991, *E. terebrans* was responsible for 83.3 to 97.4 %, and in 1992 for 97.3 to 100 % of the parasitism of *O. nubilalis* in fields in Michigan (Dyer, unpublished data). Though parasitism of *O. nubilalis* by *E. terebrans* has generally been low throughout North America, parasitism rates are highly variable. Statewide averages of parasitism by *E. terebrans* ranged from 0.04 to 8.93% in Iowa, from 1951 to 1980 (Lewis 1982); 0.0 to 9.2% in Nebraska, from its release in 1950 until 1976 (Hill et al. 1978); and 0.27 to 5.4% in Ohio, between 1948 and 1955 (Rolston et al. 1958). In these same surveys, averages for counties ranged from 0.0 to 14.9% in Nebraska (Hill et al. 1978), and 0.0 to 24.4% in

Ohio (Rolston et al. 1958). At the field level, the highest percent parasitism reported for *E. terebrans* was 55.8% in 1938, in a field near Boston, MA (Baker et al. 1949). In Michigan, Landis and Haas (1992) report field averages ranging from 1.4 to 37.4% in 1990. Field averages reported in Chapter 3 range from 2.5 to 22.87% in 1991, and 4.6 to 44.7% in 1992. Though highly variable, percent parasitism by *E. terebrans* is generally higher in Michigan than elsewhere.

Eriborus terebrans has two generations per year in Michigan, corresponding to the generations of *O. nubilalis*. Baker et al. (1949), and Arbuthnot (1955) reported higher parasitism by *E. terebrans* in the first generation than the second. Winnie and Chiang (1982) reported that parasitism by *E. terebrans* was more closely synchronized with *O. nubilalis* flight and larval populations in the first generation. They found the development time of diapausing *E. terebrans* larvae to be very similar to that of diapausing fifth instar *O. nubilalis* larvae, therefore they emerged in reasonable synchrony in the spring. Second generation emergence in their study was less synchronous; adult *E. terebrans* emerged nearly four weeks ahead of peak larval abundance. The relationship, however, is not a simple one, because Landis and Haas (1992) found higher second-generation parasitism in 1989, but higher first-generation parasitism in 1990. In 1991 in this study, parasitism was higher in the first generation in two fields, but higher in the second generation in the third field (Chapter 3).

The generally low levels of parasitism of *O. nubilalis* by *E. terebrans* do not strongly recommend it as a biological control agent, yet some of the high values reported, particularly those in Michigan, are encouraging. The range of percent parasitism among years, fields, and generations indicates conditions for *E. terebrans* are variable, and suggests potential for improved management upon greater understanding of the needs of this parasitoid. Landis and Haas (1992) report differences in parasitism among locations within fields; parasitism was higher near edges, especially wooded edges, in the first generation, but did not differ among locations within fields in the

second generation. This spatial pattern suggests an important role for habitats adjacent to corn fields, and points the way for further studies of the biology of *E. terebrans*.

Most of what is known about the natural history of *E. terebrans* is presented by Baker et al. (1949): *Eriborus terebrans* females oviposit directly into second, third and fourth instar ECB larvae, but seem to prefer third instars; they appear to have difficulty penetrating the cuticle of fifth (final) instar *O. nubilalis* larvae; eggs hatch within 32 hours at 27°C and 70% relative humidity; wasp larvae remain in the first instar until their host is in the fifth instar, then complete development of all three larval instars; *Eriborus terebrans* larvae devour all but the head capsule and cuticle of their host, then spin a cocoon of silk in which to pupate; *Eriborus terebrans* overwinter as first instar larvae inside fifth instar *O. nubilalis* larvae; mating generally occurs shortly after emergence on the first day; females generally mate only once, but males will attempt to mate throughout their life. Older wasps have been observed to mate in our laboratory colony; in one case, the wasps were aged 15 to 23 days, and in another case the male was aged four days, and the female 37 to 52 days. Therefore, some remating by females can occur, but it is probably not common. The crowded conditions of the laboratory colony may not represent what occurs in nature.

Eriborus terebrans is a specialist parasitoid of *O. nubilalis*, though there are some reports of potential alternate hosts. Baker et al. (1949) report that *E. terebrans* oviposited in *Ostrinia obumbratalis* (Lederer) and *O. penitalis* (Grote) larvae, but none survived to moth pupa or parasitoid cocoon, so it is not known if *E. terebrans* is able to complete development in these hosts. Larvae of *O. obumbratalis* are very small in comparison with *O. nubilalis*, and it seems an unlikely host for a parasitoid the size of *E. terebrans*. Even if *E. terebrans* can use *O. obumbratalis* or *O. penitalis* as hosts, the abundance of these insects in an agricultural landscape, relative to that of *O. nubilalis* is probably so low as to make them inconsequential for populations of *E. terebrans*. There is one report of *E. terebrans* reared from European pine shoot moth, *Rhyacionia buoliana* (Denis and

Schifferrmüller) (Lepidoptera: Tortricidae) (Krombein et al. 1979). There are several reports of *E. terebrans* reared from *Chilo suppressalis* (Walker) (Lepidoptera: Pyralidae) from rice, in Japan (Katayama 1971, She 1988), and from *Sesamia inferens* (Walker) (Lepidoptera: Noctuidae) from sugar cane, in Japan (Nagatomi, et al. 1972). *Eriborus terebrans* appears to have no likely alternate hosts in Michigan.

By itself *E. terebrans* has not been a highly effective control agent, but it is one of the natural controls acting upon *O. nubilalis*, which in most years and in most fields, together work to maintain *O. nubilalis* populations below the economic threshold. The percentage of corn fields in which *O. nubilalis* populations reach economic threshold levels varies greatly from year to year, and from field to field. In the period from 1988 to 1992, *O. nubilalis* was a widespread pest in Michigan only in 1991, when nearly 70% of fields exceeded threshold; from 1988 to 1990 between 10 and 30% of fields exceeded threshold, and in 1992 significant damage by *O. nubilalis* was nearly absent (D. A. Landis, personal communication).

One of the most important natural controls of *O. nubilalis* is weather. Heavy rain when first instar larvae are feeding in the whorl of the corn plant can cause high mortality due to drowning (Showers et al. 1989). Cold nighttime temperatures can limit the flight of females, and thereby reduce larval populations. Predators, especially Anthocoridae, Coccinellidae, Chrysopidae, and spiders can also reduce *O. nubilalis* populations (Sparks et al. 1966, Godfrey et al. 1991, Andow 1990). Several native parasitoids also attack *O. nubilalis* larvae (Godfrey et al. 1991, Landis and Haas 1992). Sparks et al. (1966) concluded that predators can significantly reduce larval survival, but not consistently from year to year. The effectiveness of each species as an agent of biological control will vary uniquely with the changing environmental conditions from year to year. A diverse assemblage of natural enemies, including predators, parasitoids and pathogens, both generalists and specialists, will be more likely to provide agents of

control under varying conditions. *Eriborus terebrans*, being the most important parasitoid of *O. nubilalis* in Michigan, may be among the important natural controls.

Management of *O. nubilalis* is a case in which conservation of natural enemies may be a practical strategy. Though *O. nubilalis* can cause significant economic damage, corn growers in Michigan seldom attempt to manage it (Landis and Swinton 1994). The infrequency of economic levels of infestation makes growers reluctant to invest in the effort and cost of scouting, which in most years appears to afford no benefit. Control of the European corn borer by chemical means is difficult because of the hidden feeding sites of the insect (Showers et al. 1989). *Ostrinia nubilalis* might be most effectively controlled by designing the agricultural ecosystem to utilize natural controls to prevent economic levels of infestation, rather than responding to infestation with chemical controls. Weather, of course, is beyond the grower's control, however, habitat manipulation for conservation of natural enemies offers some potential.

Biological control through conservation of natural enemies is an approach to pest management very different from conventional strategies. Conservation entails management to prevent pest outbreaks, rather than reaction to them. Because of its mode of action, *E. terebrans* could never be employed in response to an outbreak, through inundative release. *Eriborus terebrans* allows its host larva to attain its maximum size before killing it, so the parasitoid does not reduce feeding damage by the pest. Control exerted by *E. terebrans* must be considered part of a long-term control strategy aimed at preventing outbreak levels of *O. nubilalis*. While some biological control agents can be utilized as biological pesticides through inundative releases (Stinner 1977), such as control of *O. nubilalis* with the egg parasitoid *Trichogramma nubilale* (Ertle & Davis) (Hymenoptera: Trichogrammatidae) (Prokrym et al. 1992), these strategies are often too costly for field crops such as grain corn. Conservation of natural enemies should prove to be a cost effective, low-investment, low-input pest management strategy.

The environment around agricultural fields can be managed to enhance natural enemies by providing shelter, alternate prey, overwintering sites, and resources such as flowers to provide nectar and pollen, that can serve as alternate food for some predators, and adult food for some parasitoids (van Emden 1990). Findings of Landis and Haas (1992) indicate habitats at field edges may be important for the success of *E. terebrans*. The studies reported here address the needs of *E. terebrans*, and the role of non-crop habitats in meeting those needs.

In Chapter 2 relevant literature is reviewed concerning conservation of natural enemies. Qualities of ecosystems are explored that promote successful biological control, and the relationship of those qualities to perenniality is investigated. It will be argued that many of those qualities can be incorporated into annual agricultural systems by managing perennial, non-crop habitats in the agricultural landscape.

The distribution of *E. terebrans* adults in corn fields with respect to edge types is addressed in Chapter 3. These studies were designed to assess whether the distribution of adult females could account for the previously observed pattern of parasitism, and to investigate factors that affect the adult distribution. A greater abundance of adults near edges could be a consequence of wasps dispersing from overwintering sites and having their flight arrested at edges of corn fields. Alternatively, their distribution could reflect that of their larval hosts, which might occur in greater abundance near edges. Thirdly, adult *E. terebrans* could aggregate near edges because of favorable qualities of edge habitats.

Habitat quality is addressed in Chapter 4, by studying the microclimate and adult food resource needs of adult *E. terebrans*. Temperature tolerance, and the need for sugar were investigated in growth chamber and greenhouse studies. The suitability of corn fields, woodlots, herbaceous vegetation, and wooded fencerows was then tested by caging wasps in those environments, with and without sugar.

The final study, Chapter 5, describes diurnal patterns of behavior of *E. terebrans* adults caged on corn plants infested with *O. nubilalis* larvae, in a greenhouse. It offers insight into the ways *E. terebrans* might respond to different environmental conditions, notably changes in temperature, and ways individuals might use resources available to them in nature.

Throughout these studies the case will be made that the well-being of *E. terebrans*, and its effectiveness as a biological control agent of *O. nubilalis*, depends upon resources and shelter provided by non-crop habitats. *Eriborus terebrans* is probably not unique among biological control agents in this respect. Conservation of natural enemies should be considered a primary strategy in the management of insect pests. These studies of *E. terebrans* will serve to illustrate the point that management of perennial habitats, in a diverse agricultural landscape is fundamental to successful biological control by conservation of natural enemies.

CHAPTER 2

The role of perennial non-crop habitats for successful conservation of biological control agents in annual agriculture

Introduction

In an ecologically based agriculture, many operations including pest control could be managed as ecosystem functions, controlled primarily by biotic components of the system. Management by the producer would be to promote desirable interactions among biotic elements of the system, and avoid perturbation of ecosystem structure and function. One goal of an ecologically based agriculture is reduced susceptibility to outbreak levels of pests, due to natural controls incorporated as elements of the agricultural ecosystem. Biological control would be the basis for ecosystem resistance to agricultural pests. Biological control is generally thought to be more successful in perennial than annual agricultural systems, due to the greater species diversity, structural diversity and stability of perennial systems (Batra 1982, Stehr 1975). The objective of this review is to examine the qualities of perennial systems that make them more amenable to biological control, then look at ways by which those qualities can be incorporated into annual systems.

Some ecosystem attributes of perennial systems that favor biological control have to do with perenniality itself, with the persistence of ecosystem components, the intervals between disturbances, and the magnitude and duration of disturbance. Temporal stability of the ecosystem allows the development of more stable relationships between biological

control agents and their hosts or prey. Annual agriculture will necessarily have greater levels of disturbance than perennial agriculture or natural ecosystems, which may limit species interactions that could control pest populations. It will be argued here that many of those limitations can be overcome by incorporating perennial components into annual agricultural systems.

Perennial ecosystems, such as woodlots, hedgerows, streamside vegetation and old fields have always been part of the agricultural landscape, and have provided services to agriculture, including erosion control, windbreaks, forage for animals, restoration of soil quality, as well as habitat for biological control agents. In recent decades, under modern agricultural practices many of these perennial elements have been disappearing from the landscape. The task at hand is to understand how perennial non-crop habitat can be maintained or restored to the agricultural landscape, and incorporated into modern agricultural systems. This review will investigate the role of perennial non-crop habitats in the success of biological control, in an agriculture predominantly of annual crops.

Three generally recognized approaches to biological control are: importation and release of exotic natural enemies, and the subsequent establishment of naturalized populations; augmentation of natural enemy populations by mass rearing and release; and conservation of natural enemies through management of the environment (DeBach and Rosen 1991). A goal of importation and conservation is the maintenance and enhancement of natural enemies, and the long-term control of pest populations at densities below economic thresholds. This is consistent with a goal of agricultural systems that are less susceptible to pest problems, in which pests are controlled by ecosystem processes, without direct human intervention into the population dynamics of pests and natural enemies. Augmentation is employed in response to, or anticipation of pest problems. This approach is inherently disruptive to pest and natural enemy populations. Augmentation can be a useful tool for controlling pests after they have exceeded threshold, but it interferes with the long-term stability of pest and natural

enemy dynamics in the ecosystem. Importation of natural enemies is also potentially disruptive of existing natural enemy populations, and this impact should be considered in planning classical biological control programs. But once imported natural enemies have been established, importation does not involve direct human intervention into their population dynamics. While augmentation should be available as one of the tools of pest management, it should not be a primary strategy. The more preventive approaches of importation and conservation of natural enemies should be the foundation of pest management in an ecologically based agricultural.

The different approaches to biological control entail different ecological considerations with regard to qualities of the natural enemies and the environment into which they are released (Batra 1982). For importation, natural enemies are generally sought that have a high degree of host specificity, or host preference for the pest, high reproductive rate relative to their host, such that they are able to respond numerically to pest population increase, adaptation to a broad range of environmental and climatic conditions in the geographical range of the pest, and good searching ability (DeBach and Rosen 1991, Huffaker et al. 1971). Host specificity should include phenological synchrony, so there will be little lag time in the numeric response of natural enemies to their hosts (Huffaker et al. 1971). Broad environmental tolerance should include the ability to persist during times of very low pest population density (Huffaker et al. 1971), which might include being able to utilize alternate hosts or food sources at those times (van den Bosch et al. 1982).

Of primary concern for augmentation of natural enemies is their ability to cause high mortality rapidly during the course of a growing season (DeBach and Rosen 1991), which may also include rapid reproductive rate during the season (Batra 1982). Generalist predators are often selected for augmentation (DeBach and Rosen 1991, Batra 1982). One advantage of generalist predators for use in augmentative release, is they immediately kill their prey. Larval parasitoids, which may be more specialized and more

effective at long-term control at lower prey densities, do not immediately kill their host, which may continue to cause feeding damage to the plant. Egg parasites have also been used effectively in augmentation. Some of the climatic and environmental considerations of importation are unimportant in augmentation, since establishment of permanent populations of natural enemies is not a concern. Immediate conditions in the agricultural ecosystem, such as weather, and the stages of development of the crop and pest are of greater concern (Batra 1982). Conditions must be sufficiently favorable that natural enemies released into a crop field remain there, find favorable weather and microclimate, and find adequate prey or alternate food.

Conservation biological control, rather than selecting organisms for release into the environment, seeks to maintain and enhance existing populations of natural enemies, through environmental management (DeBach and Rosen 1991, Gross 1987).

Conservation is also the main task of importation biological control, during the stages of establishment and maintenance of imported natural enemies (DeBach and Rosen 1991). Augmentation requires attention to the conservation of natural enemies on a local scale and short time frame. Importation, and conservation of existing natural enemies must, in addition, address the long-term well-being of natural enemies. The needs of natural enemies include adequate availability of hosts or prey, alternate hosts or prey when the primary one is scarce, additional sources of food, shelter, overwintering sites, mates, and an attractive host habitat (van den Bosch and Telford 1964, Stehr 1975). The importance of an attractive host habitat should be emphasized, because if all the other needs of a natural enemy are provided in a habitat, it will still not encounter its host unless it searches there. Many natural enemies are habitat-specialists in addition to, or rather than being host-specialists (Townes 1972, Felland 1990).

Many of the needs of natural enemies can be provided directly by means of artificial shelter, alternate food sources, or even infestation of the field with the pest species prior to, or simultaneous with release of the natural enemy. These tactics seem

most appropriate for augmentation. For importation and conservation it is preferable to make those resources available as components of the agricultural ecosystem, for example, plants that provide nectar for adult parasitoids, host plants for alternate host or prey insects, and plants that provide shade or shelter. Classical biological control by importation is reported to have been generally more successful in perennial systems than annual ones (Batra 1982, Stehr 1975). Presumably perennial systems are better for meeting the needs of natural enemies. Of interest here is first to identify the qualities of perennial systems that may make them more amenable to biological control, then seek ways by which those qualities can be incorporated into annual cropping systems.

Attributes of perennial systems

Features of perennial systems thought to favor natural enemies and foster the success of biological control are greater species and structural diversity, and stability (van Emden and Williams 1974). Species diversity and structural diversity are closely related, as plant structural diversity contributes to potential insect species diversity (Lawton 1983). Southwood et al. (1979) found insect species diversity was highly correlated with plant species diversity in early stages of succession, but more closely related to plant structural diversity in later stages of succession. Annual agriculture has been described as an early stage of succession (Odum 1961). If we use natural succession as a model for agricultural ecosystem design, and think of perennial agricultural systems as later stages of succession, we would want to incorporate structural diversity as well as species diversity into the design.

Species diversity per se is not the key to maintenance of stable and smaller pest populations, but rather the establishment of certain species interactions made possible by increased diversity (van Emden and Williams 1974). Structural diversity will influence those species interactions. Structural complexity may provide refugia for prey, such that they are not completely eliminated from the system by a highly efficient predator or

parasitoid, thereby allowing more stable predator-prey relationships (Huffaker 1958, Lawton 1983). As in natural succession, structural complexity can develop with the maturity of a system. In a managed system some structural diversity can be provided artificially, for example, bands on peach trees provide shelter for a number of predatory insects (Tamaki and Halfhill 1968).

Species and structural diversity can provide resources for natural enemies. Understory cover crops in orchard systems may provide resources such as nectar for natural enemies (Leius 1967, van Emden 1963), or alternate hosts for predators (Altieri and Schmidt 1896). Alternate hosts for *Anagrus epos*, a parasitoid of the grape leafhopper are provided by the presence of blackberry (Doutt and Nakata 1973) or French prune in vineyards. The stature of perennial systems, and the shelter provided by architectural complexity are responsible for the creation of favorable microclimates, which is an important consideration for natural enemies (Cloudsley-Thompson 1962, Townes 1972).

Stability in perennial systems should allow for the establishment and maintenance of resident populations of natural enemies (Brown and Welker 1992). Temporal stability should allow species interactions to attain a degree of stability. There are, however, perturbations, even in perennial agricultural systems that make them more frequently disturbed than natural ecosystems. Especially the application of pesticides may disrupt the population dynamics of predators and prey (Brown 1993). If both pests and their natural enemies must repeatedly colonize the system the opportunity for stable relationships between species is lost.

Making annual cropping systems more amenable to biological control

Many ecosystem qualities desirable for agriculture are functions of species diversity, but others are functions of ecosystem longevity or permanence (Ewel 1986). Annual cropping systems are characterized by extremely high levels of disturbance, that

keep them in a managed, early successional state (Odum 1961). Levels of disturbance are considerably higher in annual agriculture than even early stages of succession in nature. The high primary productivity characteristic of early stages of succession (Odum 1961) makes them desirable for agriculture, however, the benefits of later stages of succession that are functions of permanence are sacrificed. Even ecosystem attributes due primarily to species diversity may require less frequent disturbance to allow stable species interactions to develop. Management by humans, which is also a component of agricultural ecosystems, can guide the development of community structure, and may accelerate the formation of particular species interactions. So some of the ecosystem attributes exhibited by perennial agricultural systems may be built into annual cropping systems, while some that depend on longevity or permanence may be unattainable.

Ecosystem attributes due to species diversity and specific species interactions, may be incorporated into annual systems by intentionally increasing species diversity (Andow 1991, Altieri et al. 1977, van Emden 1990). This can be accomplished by sowing crops in polyculture (Andow 1991), using cover crops (van Emden 1990), and by selectively managing weeds (Altieri et al. 1977, Altieri and Whitcomb 1980). Increased species diversity in annual cropping systems could be expected to result in fewer pest problems, either because it favors the natural enemies of pests, or because it directly affects the searching and feeding behavior of pests, by making their resource less concentrated and therefore less accessible (Root 1973, Tahvanainen and Root 1972). There have been a number of tests of these two hypotheses (Risch 1981, Risch et al. 1983, Andow 1991), with varying results, but they do not consistently support the hypothesis that control of pests by natural enemies will be favored in diverse cropping systems. Reasoning similar to the resource concentration hypothesis has been extended to the next trophic level, and specialist natural enemies, such as those often sought for biological control agents, are therefore predicted to perform more poorly in diverse vegetation (Sheehan 1986). However, predators and parasitoids may be more adapted to

searching for an unevenly distributed resource, because even in a crop monoculture prey will be distributed in patches (Price and Waldbauer 1975). The searching abilities of many natural enemies, parasitic hymenoptera in particular, may be more refined than those of most herbivorous insects (Vet and Dicke 1992).

Though certainly not always the case, diverse annual cropping systems often do favor parasitoids and predators (Russel 1989). When this is the case, the mechanisms proposed are generally similar to those offered for the success of natural enemies in perennial systems. Vertical structure aids in attracting *Orius tristicolor* to corn-squash-cowpea polyculture (Letourneau 1990). Structure may modify the microclimate making it more favorable for natural enemies (Tahvanainen and Root 1972). Cooler temperatures and higher moisture have been proposed to explain a preference for no-till systems by predatory mites (House and Brust 1989), and may be a factor in accumulating parasitic Hymenoptera in maize plantings (Letourneau 1987). Weeds can provide sources of nectar (van Emden 1963) and pollen (Leius 1963) for parasitic Hymenoptera. The availability of alternate prey has been proposed to explain a positive correlation between weed density and predatory carabid beetles (Speight and Lawton 1976).

In spite of these similarities, many attributes of perennial systems may be unattainable in annual systems because of their temporal instability. The structure that would attract or arrest natural enemies, and provide shelter and a favorable microclimate, must develop each growing season. Insects that are dependent on these features must colonize anew each growing season. There is no opportunity to establish resident populations of natural enemies, or their hosts within the crop field itself. It can, on the one hand be advantageous that resident populations of pest insects are unable to establish; crop rotation is the recommended management practice for some insects, such as the corn rootworm complex. On the other hand, highly mobile pests cannot be managed simply by crop rotation. In a highly disturbed habitat, the control of pests by natural enemies requires that the natural enemies be as adept at colonizing as the pests, and their rate of

population increase be as great. Pest insects generally have all the characteristics of early succession invaders, including great ability to colonize newly disturbed habitats, and rapidly increase their populations once established; predators and parasitoids more often have characteristics of later-succession species, are less adept at rapidly invading newly disturbed habitats, and have lower intrinsic rates of increase than their prey (Price and Waldbauer 1975). If there is a lapse of time between colonization by the prey species and colonization by the predator, it is unlikely population control will be satisfactory, from an agricultural point of view (DeBach and Rosen 1991). Maintenance of pest populations at agriculturally acceptable levels, without direct intervention on the part of the grower, requires that resident populations of pests and their natural enemies be allowed to persist, for more stable predator-prey relationships to develop. This probably necessitates more stable habitats than the frequent disturbance regime of annual agriculture.

Habitat diversity to provide perennial qualities in annual agroecosystems

Though annually disturbed crop fields may be inherently limited in their capacity to conserve natural enemies, perennial habitats adjacent to agricultural fields may provide many of the necessary qualities of perennial ecosystems. Hedges and permanent grasslands can support resident populations of natural enemies (Dennis and Fry 1992, Nazzi et al. 1989, Wratten and Thomas 1990). Adjacent non-crop habitats can provide the resources for natural enemies described previously for perennial systems, including resident populations of alternate hosts (Doutt and Nakata 1973, Maredia et al. 1992, alternate food resources (van Emden 1963, 1965a), and favorable shelter and microclimate (Dennis and Fry 1992). If natural enemies are present in these habitats it may minimize the time required for them to colonize the crop, and they may be able to prevent rapid population increase of the pests.

Simply having natural enemies residing in adjacent habitats will not ensure biological control of agricultural pests. Natural enemies must still colonize annually disturbed fields from these edge habitats, and they must be able to do so in sufficiently large numbers, and at the right time to be effective. Their ability to do so will depend on both the arrangement of these habitats in the landscape, and the perception and dispersal abilities of the natural enemies. The arrangement of the habitats can to some degree be managed for conservation, and this should be done with consideration for how natural enemies will use the landscape.

Most modern agricultural landscapes are fragmented, consisting of various landscape elements, including: agricultural fields, remnants of native ecosystems, features of human habitation, and disturbed ecosystems in various stages of recovery and varying degrees of human management. Many of the perennial ecosystems of the agricultural landscape fall into this last category, including fencerows, roadsides, abandoned pastures and agricultural fields, and degraded woodlots, stream margins and wetlands. The habitat of any given organism will consist of only one or a few of these landscape elements. If landscape elements of importance to an organism occur in discrete units, and are widely separated relative to the dispersal ability of the organism, they can be thought of as islands in the landscape matrix (MacArthur and Wilson 1967). However, if a landscape is diverse, and elements are small relative to the dispersal capability of an organism, landscape elements may be perceived as patches in their habitat, rather than habitat islands. These different perceptions of landscape entail different management considerations for natural enemy conservation.

If crop and non-crop habitats are perceived as islands in a landscape matrix, factors that would minimize extinction and facilitate colonization of those islands should be considered. Island size is one factor involved in the risk of extinction. If the island under consideration is the crop field, size is probably not a problem, but if the island is a

non-crop habitat that a beneficial insect occupies during part of its life cycle, then maintaining islands sufficiently large to support a population may be a concern.

The structure of most agricultural landscapes is such that crop fields are very large islands, in close proximity to sources of colonization, with few barriers to dispersal. In general, pests tend to have superior abilities as island colonists (Simberloff 1981). Annual crops have a planned extinction of the primary producers each year, leaving them constantly in the early stages of island colonization. Natural enemies will generally lag behind in colonization, and for the reasons discussed earlier with regard to crop fields as early stages of succession, will be unlikely to control pest populations. One mitigating factor is that many predators and parasitoids need more than a single habitat type during their life history, and the close association of these habitats may allow the rapid colonization of crop fields by significant numbers of natural enemies whose populations increased in the other habitat.

A management strategy would be to provide stable non-crop habitat in close proximity to the crops (Wratten and Thomas 1990, Dennis and Fry 1992), to allow resident populations of natural enemies to exist, and grow to adequate numbers prior to colonization of the crop habitat. The crop field could then be modified to facilitate colonization, perhaps with strips as corridors (Speight and Lawton 1976), windbreaks that arrest flying insects, or vertical structure in the cropping system to induce predators to aggregate (Letourneau 1990). A crop environment could be created that would reduce emigration, and maintain natural enemies.

In a diverse landscape, if landscape elements are small relative to the dispersal capability of an organism, they may be perceived by the organism as patches in their habitat, rather than habitat islands. Parasitic Hymenoptera and Diptera tend to be very mobile organisms, and probably perceive a complex landscape to be a patchy environment. The movement and foraging behavior of individual parasitoids or predators is an important factor in their success as biological control agents (Luck 1990,

Karieva 1987, Lewis et al. 1990, Vet et al. 1990), and the importance of the influence of spatial heterogeneity on that search has been stressed (Karieva 1987, 1990). Generally the aspects of behavior that have been investigated have been search for prey (Karieva 1987, 1990), host selection (Luck 1990), and use of environmental cues and learning in the search for hosts (Vet et al. 1990, Lewis et al. 1990). It should also be kept in mind that natural enemies search for resources in addition to hosts or prey. If an adult parasitic wasp is dependent on a sugar source found primarily in perennial habitats bordering crop fields, the extent to which they exploit the crop field in search of hosts could be limited. Pest insects tend to be less limited by resources in annual crop fields than their natural enemies (Price 1976). While the availability of resources in field margins may also benefit pests (Showers et al. 1976, DeRozari et al. 1977), it is more likely to benefit natural enemies and enhance biological control.

The scale of landscape heterogeneity is clearly of primary concern for resource use by natural enemies. Whether they serve as corridors to facilitate colonization, sources of colonists, or patches of an essential resource, perennial landscape elements that decrease the effective size of crop fields should allow natural enemies to more fully colonize and exploit resources in the field interior.

The amount of non-crop habitat, or ratio of crop to non-crop habitat in a landscape is also important. Sufficient habitat for natural enemies must be maintained so they will not be overwhelmed numerically by their prey: a token hedgerow will not be sufficient. Landscape diversity on a regional scale can influence the composition of the insect fauna; diverse landscapes in Poland and Romania were found to have greater insect biomass, greater proportions of predator and parasitoid biomass, and higher correlations of predator and parasitoid biomass to herbivore and saprovores biomass, than uniform landscapes (Ryzkowski and Karg 1991, Ryzkowski et al. 1993). Marino and Landis (in press) sampled fields in two townships in Michigan, and found parasitism of *Pseudaletia unipuncta* (Haworth) (Lepidoptera: Noctuidae) to be higher in the diverse

landscape than the simple one. Habitat diversity over more extensive landscapes will support larger populations or metapopulations of natural enemies, and more sources for recolonization after local extinctions of populations.

How much perennial habitat is necessary to maintain adequate populations of natural enemies, is a very difficult question, that will not have a single answer. It is also a difficult question to address for management purposes. An individual grower can make decisions about management of his or her farm, but cannot control the diversity of neighboring farms. The place to begin is probably at the scale of farm or field, and create, preserve or modify habitat there, that is favorable for natural enemies. Much of the research needed to develop management plans for conservation of natural enemies will clearly need to be done on farms, because the scale and arrangement of crop fields and non-crop habitats is so critical to their use by natural enemies.

Conclusions

To make annual agriculture more amenable to biological control, it is desirable to incorporate qualities of perennial systems into annual agricultural systems. We wish to give annual systems the temporal stability that permits the development of stable relationships between pest insects and their natural enemies. To do so we must provide infrequently disturbed habitat, and a variety of resources for natural enemies that are more readily provided by structurally diverse, more mature vegetation. The crop fields themselves will be frequently disturbed, but the qualities and resources of perennial systems can be provided by non-crop habitats in the landscape. Annual agriculture is conducted in a perennial landscape, and if the farming system is thought to include adjacent non-crop habitats it can be made more favorable to biological control through conservation of natural enemies.

CHAPTER 3

Distribution of *Eriborus terebrans* (Gravenhorst)(Hymenoptera: Ichneumonidae) in corn fields, with respect to adjacent non-crop habitats

Introduction

Conservation of natural enemies is one of the three main biological control strategies (DeBach and Rosen 1991), however, it has recieved less attention than either importation, or augmentation of natural enemies. As agricultural technologies are sought that are less environmentally hazardous, and that rely less on costly purchased inputs, conservation should become a more prominent component of pest management practice. For conservation biological control to be effective, agricultural ecosystems must provide for the needs of natural enemies throughout their life histories, which might include reliable sources of alternate prey, alternate food sources for different life stages, such as prey for predaceous larvae, and nectar or pollen for adults, overwintering sites, shelter, and locations to find mates (van den Bosch and Telford 1964, Stehr 1975). In annual cropping systems, many of these resources may be provided by non-crop habitats within the agricultural landscape. The importance of non-crop habitats for the success of biological control agents is illustrated by the relationship between woodlots adjacent to corn fields and the distribution of adult *Eriborus terebrans* (Gravenhorst) (Hymenoptera: Ichneumonidae), and their parasitism of the European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Pyralidae).

Ostrinia nubilalis is an important pest of corn in Michigan. ~~Eighty percent of Michigan corn growers surveyed reported economic injury levels by *O. nubilalis*, in at~~

least 1% of their fields between 1982 and 1992 (Landis and Swinton 1994). *Ostrinia nubilalis* has two generations per year in southern Michigan. When first-generation *O. nubilalis* emerge in late May or early June, they move to grassy borders of corn fields and waterways to mate (Showers et al. 1976). Females then seek the largest corn plants available for oviposition (Showers et al. 1989). Early instar larvae feed in the whorl, then later instars tunnel into the stalk, where they continue to feed and eventually pupate. In the second generation, which begins in late July, females seek tasseling corn plants for oviposition (Showers et al. 1989). Early instar larvae feed on tassels and ears, and later instars tunnel into stalks and ears, which results in yield loss due to feeding damage, stalk lodging and ear drop (Showers et al. 1989, Brindley and Dicke 1963). *Ostrinia nubilalis* overwinters as fifth instar larvae in tunnels in corn stalks.

Eriborus terebrans is the primary parasitoid of *O. nubilalis* in Michigan. It was introduced in 12 counties in southeastern Michigan on 19 occasions between 1926 and 1937 (Baker et al. 1949), and has since become naturalized. Since then there has been no intentional management of *E. terebrans* as a biological control agent. *Eriborus terebrans* has two generations in Michigan, corresponding to the generations of its host. First generation emergence of *E. terebrans* is synchronous with that of *O. nubilalis*, but second generation is less so (Winnie and Chiang 1982). *Eriborus terebrans* females oviposit directly into second through fourth *O. nubilalis* larvae (Baker et al. 1949). A single wasp larvae completes development when its host is in the fifth and final instar; it devours as but the head capsule and cuticle of its host, then spins a cocoon of silk in which to pupate (Baker et al. 1949). *Eriborus terebrans* overwinters as a first instar inside its fifth instar host.

Eriborus terebrans accounts for 92.2 to 99.2% of the total larval parasitism of *O. nubilalis* in Michigan, with average parasitism in corn fields ranging from 1.4 to 37.4% (Landis and Haas 1992). Landis and Haas (1992) observed a pattern in the spatial distribution of parasitism within fields, in which first generation parasitism was higher

near edges, especially near wooded edges, but second generation parasitism did not differ among locations within fields. This spatial pattern suggests habitats adjacent to corn fields may be important for *E. terebrans*. Studies reported here were designed to identify patterns of distribution of adult *E. terebrans* with respect to field edges. Objectives of the studies were to determine if the distribution of adult *E. terebrans* could form the basis for the pattern of parasitism identified by Landis and Haas (1992), and uncover mechanisms driving the adult distribution.

Methods

The distribution within corn fields of *E. terebrans* adults, *O. nubilalis* larvae, and parasitism of *O. nubilalis* larvae by *E. terebrans* was studied during the 1991 and 1992 field seasons. In 1992 *E. terebrans* was also sampled in woodlots and woodlot edges. In 1993 adult *E. terebrans* were sampled in a corn field, and along an adjacent woodlot canopy.

1991 field season

Four corn fields (Allen, Diehl, Cheney and Emmons) were sampled, in Ingham County, Michigan (Table 1). Each field had a woodlot at one end, and a narrow strip of herbaceous vegetation at the other. The distances between the wooded and herbaceous edges ranged from 600 to 1000 m. In two fields the woodlot was at the north end of the field, in one it was at the west end and in one it was at the south end. Only one field (Cheney) had been planted with corn the previous year. Larvae were sampled along transects in Cheney in 1990 (Landis and Haas 1992); *Ostrinia nubilalis* larvae were present in all sites, and average parasitism by *E. terebrans* was 7.8%. Populations of *O. nubilalis* and *E. terebrans* in 1991 could, therefore, have arisen from resident populations in Cheney, but insects in the other three fields must have dispersed from the residue of other 1990 corn fields.

Table 1. Characteristics of fields sampled in 1991 and 1992.

Year & field name	Area in ha (acres)	Length in meters	Woodlot location	Previous crop	Primary tillage	Secondary tillage	No. cult. ^a	Herbicide	Insecticide
1991									
Allen	22.7(56)	770	north end	soybean	chisel plow	soil	1	pre ^b : Bicep	none
Diehl	68.0(168)	1190	north end	soybean	none	finisher soil finisher	1	pre: Dual post C: Attac, Tandem	none
Cheney	18.6(46)	600	west end	corn	chisel plow	soil finisher	0	pre: extrazine, Dual	Dyfonate, at planting
Emmons	10.5(26)	600	south end	wheat	chisel plow	disk	0	pre: extrazine	none
1992									
Allen	40.5(100)	635	east end	soybean	chisel plow	soil finisher	1	pre: Dual, atrazine	none
Hamlin	65.6(162)	630	west end	soybean	chisel plow	soil finisher	1	pre: Bicep	none
Lawson	40.5(100)	430	south end	corn	chisel plow	disk	1	pre: Dual post: Marksman	Counter, at planting
Steve's	87.8(217)	595	south end	corn	chisel plow	disk	0	pre: Dual post: Marksman	Counter, at planting

^a cultivations^b preemergence: herbicide application before crop emergence.^c postemergence: herbicide application after crop emergence.

Adult *E. terebrans* were sampled in each field by placing one malaise trap 20 m from a wooded edge, another 20 m from an herbaceous edge, and a third trap approximately midway between the herbaceous and wooded edges (Figure 1). The malaise traps (BioQuip Products model 2875B) were oriented such that one vane ran parallel, and the other perpendicular to the corn rows. Traps were 2.13 m (7 ft) tall; the portion of the vanes where flying insects would be intercepted extending from ground level to 1.07 meters (42 in.). Trap collecting heads contained 3x3 cm pieces of Shell Biostrip (2,2-dichlorovinyl dimethyl phosphate) as a killing agent. The contents of the trap heads were collected every fourth day during the first generation from 4 June to 17 July (Julian dates (JD) 155 to 198), and every seventh day during the second generation, from 24 July to 27 September (JD 205 to 270). Samples were taken to the lab and inspected for adult *E. terebrans*, and numbers of males and females were recorded.

At the beginning of the first generation the capture zone of the malaise traps encompassed the entire corn canopy, but during the season the corn grew above the malaise traps. In the second generation, an additional set of malaise traps was placed in one field (Allen), to investigate effects of the changing height relationship between the traps and corn. This second set of traps was placed such that the capture zone (150-257 cm) of the traps was at the top of the corn canopy (mean=241.17 cm, standard error=4.33, n=60 plants, height measured to the tip of the longest leaf).

Infestation by *O. nubilalis* was sampled at five locations in each field: one near each malaise trap, and in two additional locations, 80 m from the herbaceous edge and 80 m from the wooded edge. At each sampling date three rows were selected randomly from the 48 rows surrounding the malaise trap. All plants (typically 15 to 20) in 4 m of each selected row were counted and examined for *O. nubilalis* egg masses and feeding damage. If a row had fewer than 15 plants in 4 m it was considered an inadequate sample and another row was selected. The first and last plants in the row that showed signs of feeding damage were checked for *O. nubilalis* larvae. The youngest leaves were

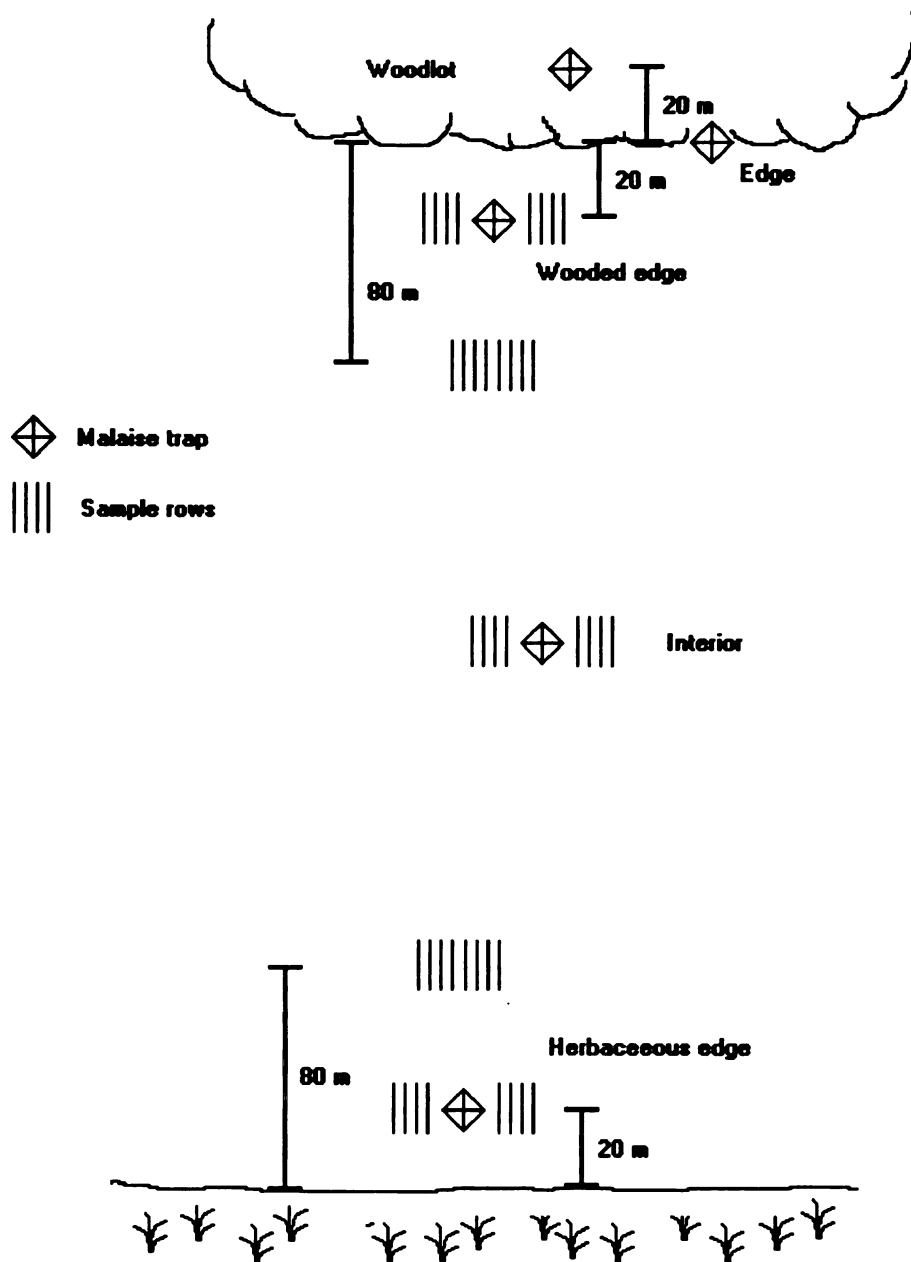


Figure 1. Schematic diagram of placement of malaise traps to sample *E. terebrans* adults, and the location of corn rows sampled for *O. nubilalis* larvae. Edge and woodlot malaise traps were used only in 1991. Rows 80 m from edges were sampled only in 1991.

pulled from the whorl of the plant and unfolded, and live larvae were counted and staged. Once sampled, a row was removed from the pool of possible rows for future sampling. During the first generation, larvae were sampled each time the malaise traps were sampled, from 4 to 30 June (JD 155-181). During the second generation larvae were sampled twice, on 6 and 20 August (JD 218, 232).

At the end of each generation *O. nubilalis* larvae were sampled. Three samples of 40 larvae were collected near each malaise trap (120 larvae per site, field total = 360 larvae). Twenty plants in a randomly selected row were sampled, then additional rows on either side were sampled until 40 larvae were collected. To ensure the three samples did not overlap, rows were chosen in a stratified random fashion; one row was selected from each 16 row subset of the total 48 rows. In each row, 20 plants were inspected for damage, then damaged plants were searched for larvae by removing all leaves and splitting the stalk from base to tassel. Plants were left standing such that no gaps greater than 40 cm occurred between plants in a row, thus, not all damaged plants were sampled. Sampling continued until 40 larvae had been collected, or until all 16 rows had been sampled. Each larva was placed in a 1 oz cup with artificial diet (Bio-Serve Resultstm Brand), and reared at 27°C and constant light. Larvae were checked for emerged adults every 2 to 4 days, and the species of moth or parasitoid, and sex of parasitoids was recorded. First generation sampling was conducted from 10 to 17 July (JD 191-198). First generation sampling was not done in Emmons field because *O. nubilalis* infestation was too low to expect reasonable sample sizes. Second generation sampling was conducted in all four fields, from 6 to 19 September (JD 249-262).

1992 and 1993 Field seasons

The four corn fields, Allen, Hamlin, Lawson and Steve's were, as in 1991, in Ingham County, Michigan (Table 1). The distances between the wooded and herbaceous edges ranged from 430 m to 640 m. In one field the woodlot was at the east end of the

field, in one it was at the west end, and in two fields it was at the south end. In 1992, to test the hypothesis that the pattern of adult distribution was a consequence of dispersal from overwintering sites to host habitats, two of the fields selected (Allen and Hamlin) were first year corn fields, and the other two fields (Lawson and Steve's) were second year fields. *Ostrinia nubilalis* and *E. terebrans* populations from the 1991 second generation were sampled in Steve's by collecting larvae from the corn residue. Three samples, each of 40 larvae were collected on 6 May 1992 (JD 126). Samples were located by randomly selecting coordinates on a grid in the field interior, at least 200 m from either the wooded or herbaceous edge. Lawson was not sampled for 1991 populations of *O. nubilalis* and *E. terebrans*, nevertheless, resident populations of these insects were most likely present because most corn fields in Ingham county were moderately to heavily infested with *O. nubilalis* in 1991, and all *O. nubilalis* populations sampled in this study in 1991 had some level of parasitism by *E. terebrans*.

Malaise traps were located in corn fields as in 1991. Samples were collected every fourth day from 4 June to 29 July (JD 155-210), then every seventh day until 7 October (JD 280).

Larvae of *O. nubilalis* were sampled near the three malaise trap locations in each corn field, but the locations 80 m into the fields were not sampled in 1992. The number of rows in the pool to be sampled was increased from 48 to 60. Sampling of larvae was conducted as in 1991 except that rather than sampling the plants in 4 m along a row we sampled 20 plants in a row, then measured the distance from plants 1 to 20.

Larvae were collected for parasitism sampling at the end of the first generation, from 4 to 17 August (JD 216-229). Because of generally lower *O. nubilalis* infestation, sample sizes obtained were smaller. In the field with highest infestation sampling was conducted as in 1991, using an upper limit of 20 rows per sample rather than 16. In five out of nine samples, all 20 rows were sampled and fewer than 40 larvae were collected. In the other three fields, three seven-row samples were collected near each malaise trap.

As in 1991, each larva was placed in a 1 oz cup with artificial diet, but the diet used in 1992 was prepared in our lab (recipe of T. Leahy, personal communication, after Guthrie et al. 1974, Reed et al. 1972).

In 1992, to determine if *E. terebrans* adults were present in the woodlot, two additional malaise traps were placed in each field: one 20 m into the woodlot, and one at the edge of the corn field and the woodlot. Both traps were placed with the capture zone from 0-1.07 m, like the traps in the corn field. These were first sampled on 3 July (JD 184), and sampled at the same time as other traps until 7 October (JD 280). This aspect of the study was continued in 1993 by placing four malaise traps elevated to different heights along the edge of a woodlot and corn field, in one site. One trap was placed at ground level, corresponding with the edge traps of 1992. The other four were elevated such that the capture zone of each consecutively higher trap began where the last ended (ground level=0-107 cm, low=107-214 cm, medium=214-321 cm, and high=321-428 cm). One malaise trap was also placed in the corn field, at ground level, 20 m from the edge of the woodlot. Traps were sampled every 2-7 days from 18 June until 7 October (JD 169-280).

The totals of wasps captured in malaise traps, during each of the first and second generations were analyzed with goodness of fit tests for differences among sites within fields, and heterogeneity tests for differences among fields (Zar 1984). Differences in parasitism among sites were analyzed in contingency tables, and differences among fields with heterogeneity tests (Zar 1984). Log-likelihood ratio (G-tests) were used for goodness of fit tests, contingency tables and heterogeneity tests (Zar 1984). Calculations were done in a spreadsheet (Microsoft Excel for Windows 3.0).

Correlation coefficients (r) were calculated (LINEST function in Microsoft Excel for Windows 3.0) for correlations between *E. terebrans* females and *O. nubilalis* larvae per m², and between *E. terebrans* females and the percentage of corn plants with *O. nubilalis* feeding damage, at sites within fields. Correlations were made for the first

generations of 1991 and 1992. This analysis was not conducted for the second generation of 1991, because there was no way to distinguish first generation from second generation feeding damage; only damaged plants were sampled, so without a measure of percent damaged plants there was no way to estimate overall larvae per unit area.

Differences in *O. nubilalis* infestation among wooded edge, interior and herbaceous edge sites within each corn field, were examined for the first five sampling dates (JD 164, 167, 171, 175, 179) of the first generation of 1991, using analysis of variance (SAS Institute 1988). In addition, for each sampling date when five or more *E. terebrans* females were captured in a field, correlation coefficients were calculated as described above, for correlations of larva infestation and *E. terebrans* females. These analyses were not done for Emmons field in 1991, or any field in 1992, because of insufficient infestation rates.

Results

During the first generation of 1991, considerably more *E. terebrans* females were captured in wooded-edge traps than in other traps, whereas in the second generation similar numbers were captured in wooded edge and interior traps, with fewer in herbaceous edge traps (Figure 2). Only five wasps were captured in one field (Emmons) in the first generation, so it was omitted from the analysis. Goodness of fit tests in individual fields showed significant differences among sites in the remaining three fields ($P < 0.001$) (Figure 3). Heterogeneity tests showed these fields to be from the same sample population (Zar 1984), so they were combined for a comparison among sites. The wooded edge trap capture was significantly higher than the herbaceous edge and interior traps combined ($P < 0.001$). In one of these fields (Diehl) there were only seven wasps captured. This also could be considered an insufficient capture for analysis. With this field removed from the analysis, within-site comparisons in the remaining two fields yielded the same conclusions ($P < 0.001$).

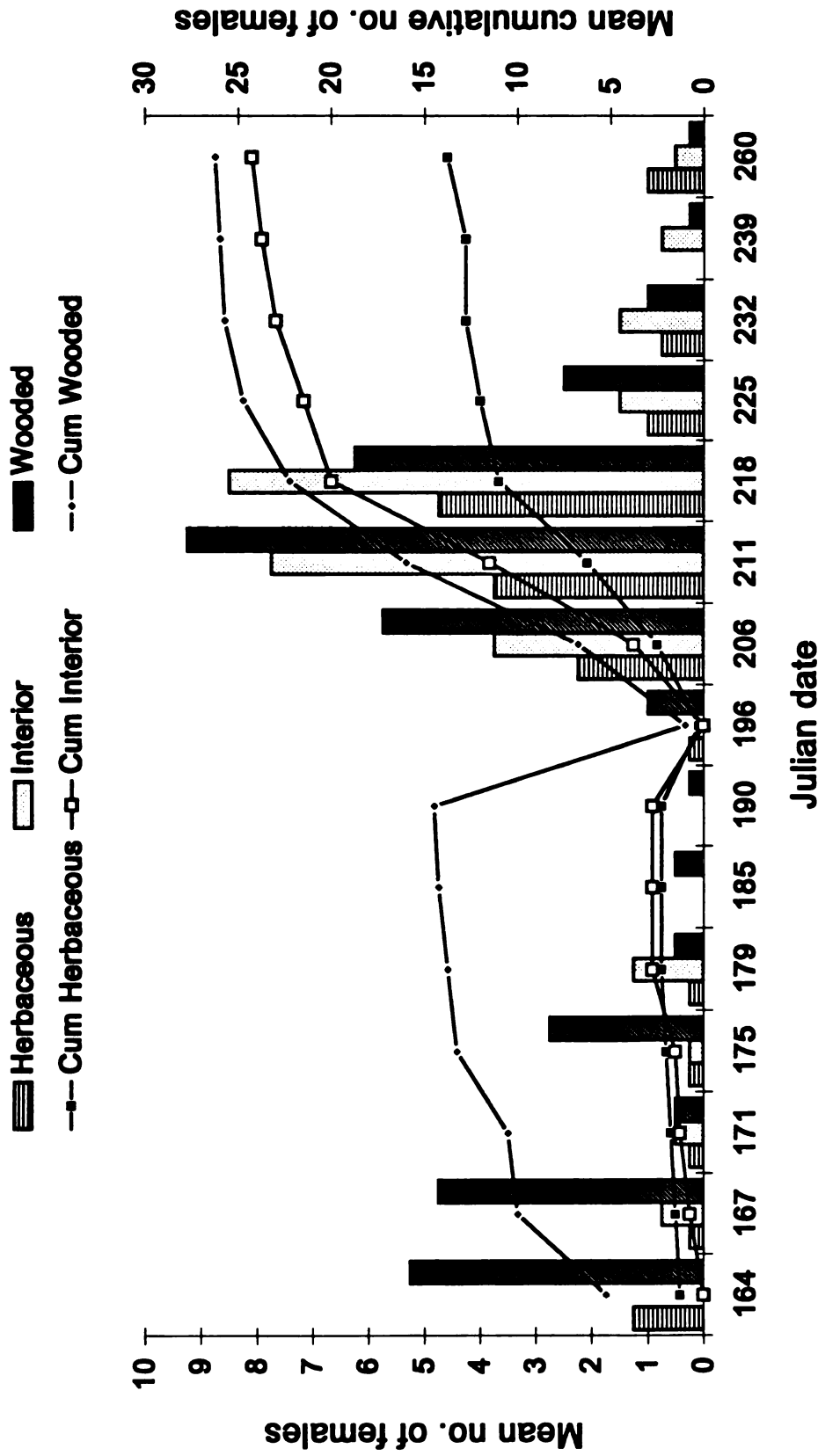


Figure 2. *Eriborus terebrans* females captured in malaise traps in 1991, at three locations in corn fields: herbaceous edge, interior, and wooded edge. Values are the means of four fields. Bars indicate capture on each date. The line graph is cumulative capture (cum) over the first (JD 164-190), and second (JD 196-260) generations.

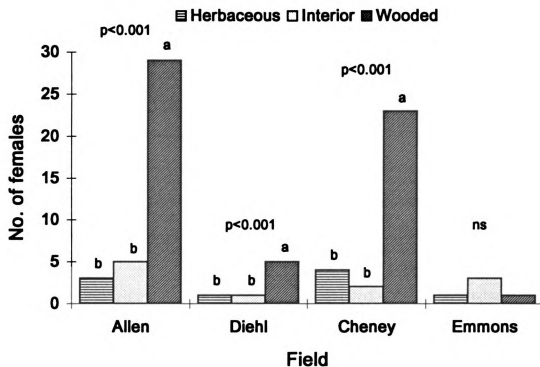


Figure 3. Total malaise-trap capture of *Eriborus terebrans* females in the first generation of 1991, at three locations (herbaceous edge, interior, and wooded edge) in each of four corn fields. *P*-values indicate levels of significance, and different letters indicate significant differences within fields (log-likelihood ratio goodness of fit tests).

In the second generation the distribution of females differed among fields (heterogeneity test, $P < 0.001$) (Figure 4). In one field (Cheney) significantly more females were captured in the wooded edge trap than either the herbaceous edge ($P < 0.05$) or interior trap ($P < 0.005$). In another field (Diehl) fewer females were captured in the herbaceous edge trap ($P < 0.001$). In the remaining two fields there were no differences among sites. While there was a pronounced preference of females for wooded edges in the first generation, there was no consistent pattern, and no consistent preference for edges in the second generation.

In the first generation of 1992, wasp capture was again higher in edge traps than interior traps, but in contrast to 1991, capture was high in herbaceous edge traps in some fields, as well as wooded edge traps (Figure 5). Heterogeneity testing showed significant differences among the four fields. Two pairs of fields could be distinguished that were homogenous in their distribution of females. In one pair (Hamlin and Steve's) the pattern was similar to 1991; significantly more wasps were captured at the wooded edge, and there was no difference between the herbaceous edge and the interior ($P < 0.001$) (Figure 6). In the other pair (Allen and Lawson) significantly fewer wasps were captured in the interior ($P < 0.001$), but there was no difference between the herbaceous edge and the wooded edge. If in all four fields the herbaceous edge and the wooded edge were combined for comparison with the interior, the four fields were then homogeneous, and the edge traps had significantly greater capture than the interior trap ($P < 0.001$). Thus, similarly to the results from 1991, there was a preference for edges in the first generation of 1992, but in two fields that included herbaceous edges as well as wooded edges.

In the second generation of 1992 the fields were again heterogeneous ($P < 0.001$) (Figure 7). In one field (Allen), significantly more wasps were captured at the wooded edge than either the interior or herbaceous edge ($P < 0.001$). In another field (Hamlin), the herbaceous and wooded edges had significantly higher captures than the interior ($P < 0.05$). The distributions in these fields follow the two patterns identified in the first

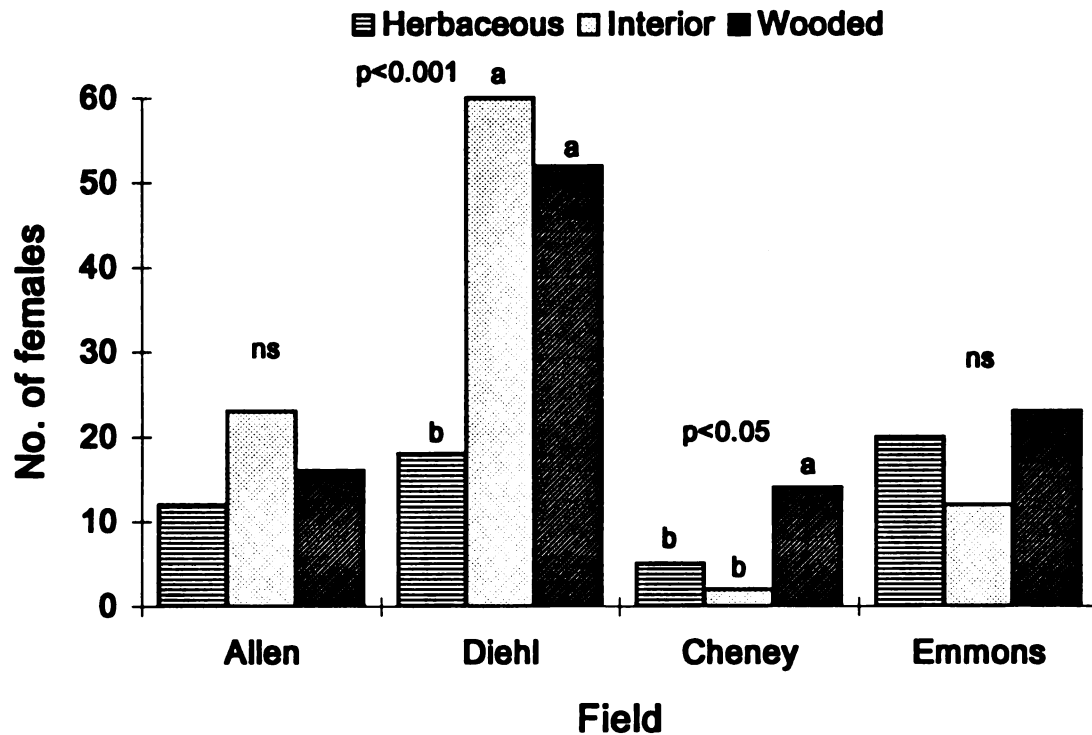


Figure 4. Total malaise-trap capture of *Eriborus terebrans* females in the second generation of 1991, at three locations (herbaceous edge, interior, and wooded edge) in each of four corn fields. *P*-values indicate levels of significance, and different letters indicate significant differences within fields (log-likelihood ratio goodness of fit tests).

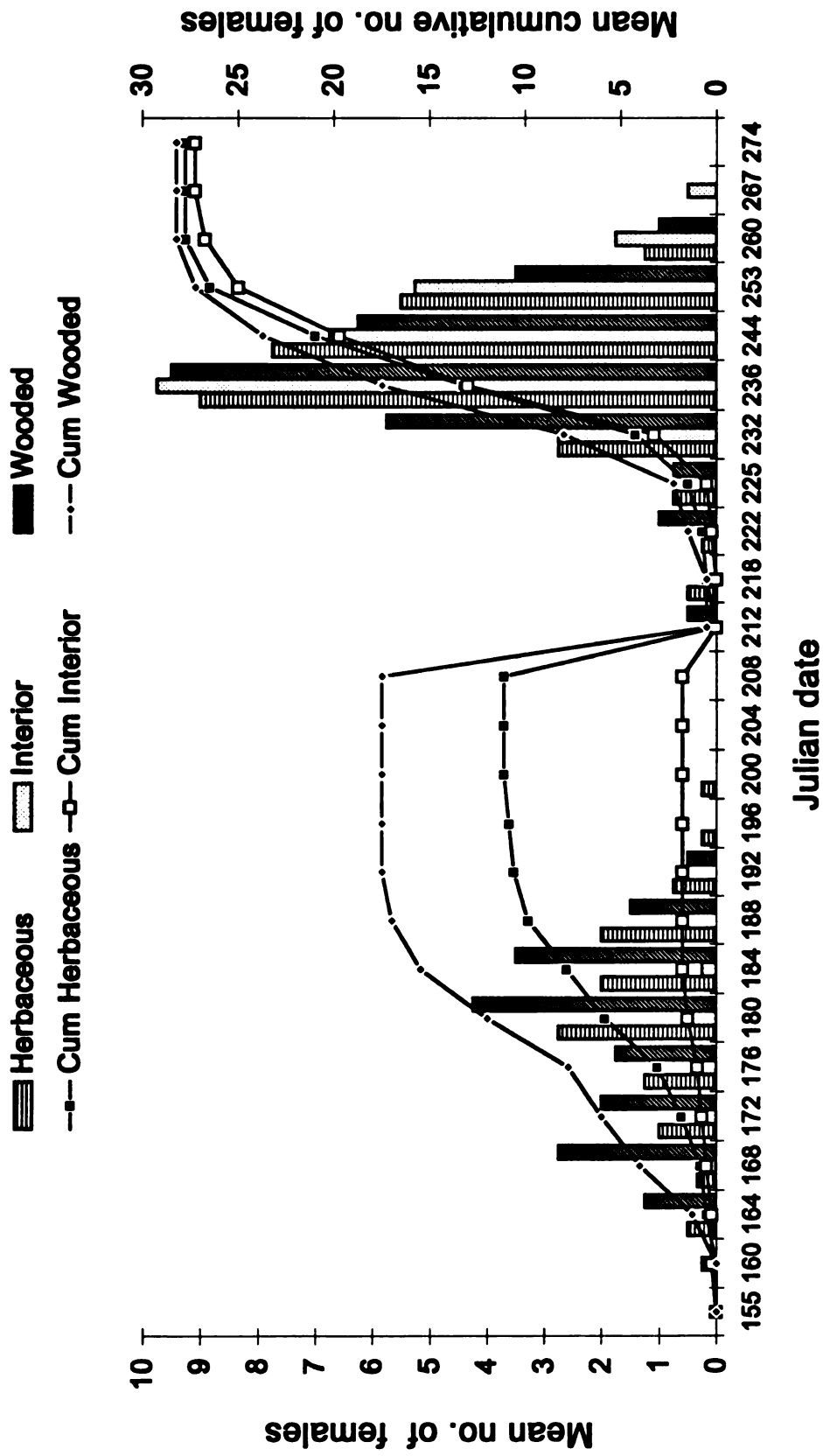


Figure 5. *Eriborus terebrans* females captured in malaise traps in 1992, at three locations in corn fields: herbaceous edge, interior, and wooded edge. Values are the means of four fields. Bars indicate capture on each date. The line graph is cumulative capture (cum) over the first (JD 155-208), and second (JD 212-274) generations.

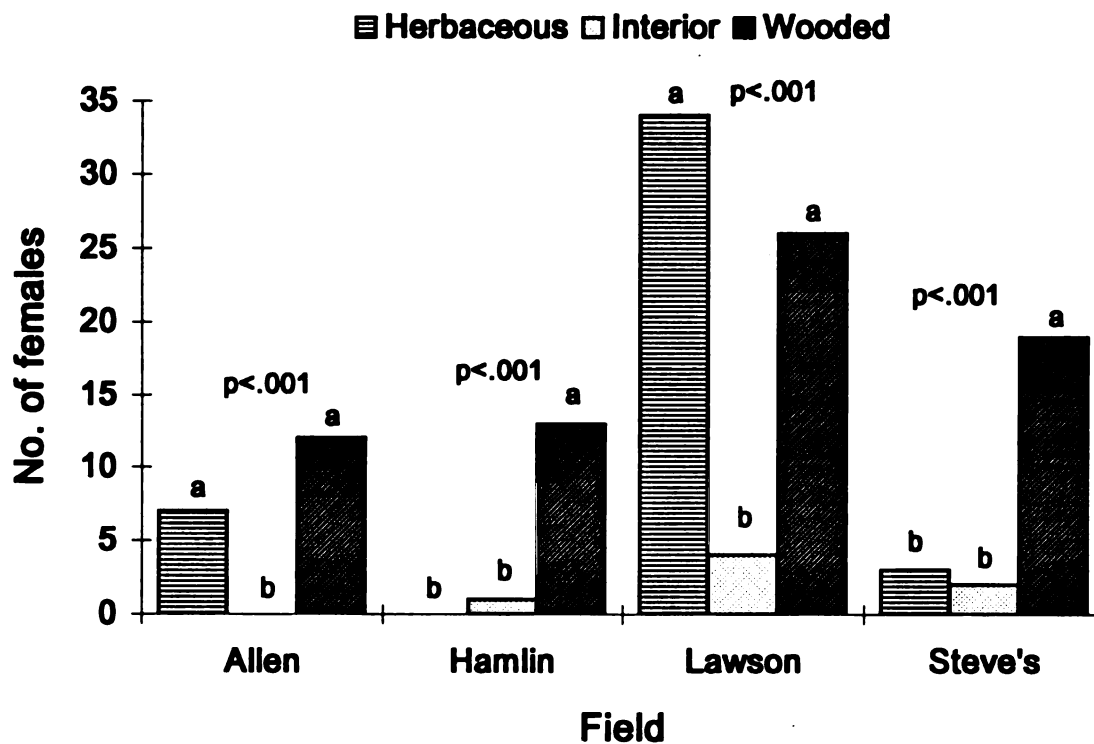


Figure 6. Total malaise-trap capture of *Eriborus terebrans* females in the first generation of 1992, at three locations (herbaceous edge, interior, and wooded edge) in each of four corn fields. *P*-values indicate levels of significance, and different letters indicate significant differences within fields (log-likelihood ratio goodness of fit tests).

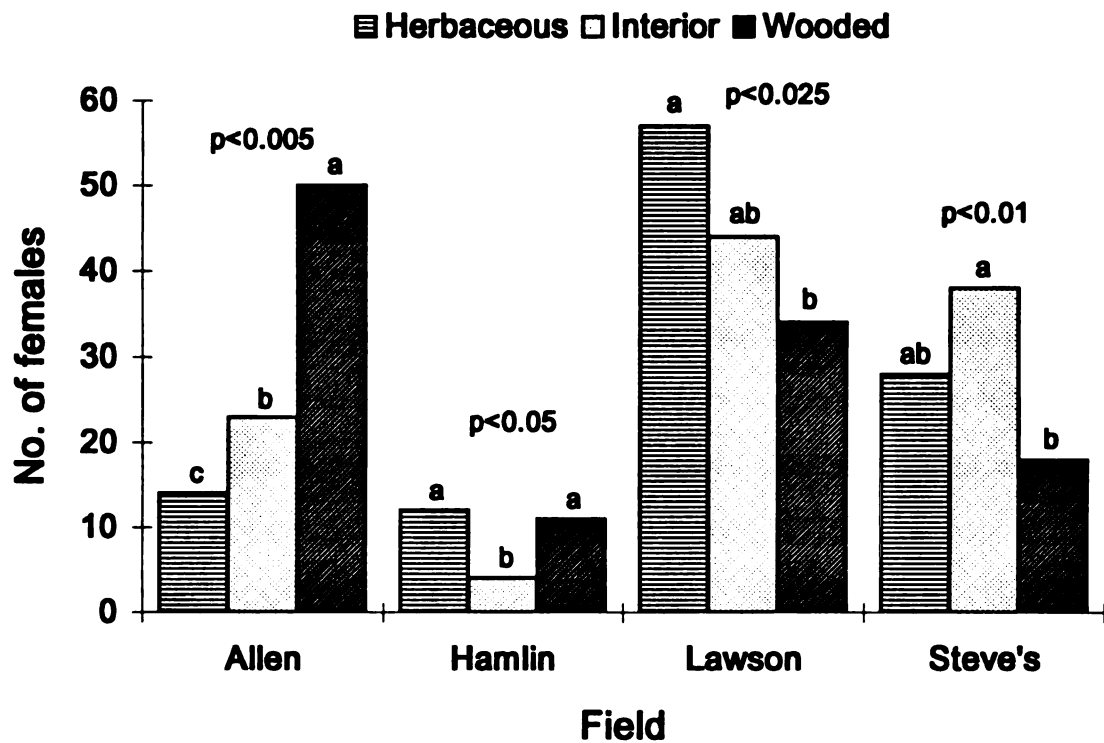


Figure 7. Total malaise-trap capture of *Eriborus terebrans* females in the second generation of 1992, at three locations (herbaceous edge, interior, and wooded edge) in each of four corn fields. *P*-values indicate levels of significance, and different letters indicate significant differences within fields (log-likelihood ratio goodness of fit tests).

generation, though in both fields the pattern changed between first and second generation. In a third field (Lawson), more wasps were captured at the herbaceous edge than the wooded edge ($P < 0.025$), while the interior trap fell between, but did not differ significantly from the two edge traps. In Steve's field the highest capture was in the interior trap, which was significantly greater than the wooded edge ($P < 0.01$), but not significantly greater than the herbaceous edge. Results from 1992 were similar to those of 1991; in the first generation wasps showed a preference for edges, but in the second generation there was no clear pattern of wasp distribution.

Very few male *E. terebrans* were captured in 1991. In the first generation, there were only three males, compared to 78 females. These three were all captured in the wooded edge trap in the field that had been planted to corn the previous year (Cheney). In the second generation 11 males were captured, compared with 257 females, and these males were distributed throughout the fields (herbaceous=6, interior=2, wooded=3). More males were captured, however, in the traps placed at the top of the corn canopy in Allen field, in the second generation (Figure 8). Male *E. terebrans* were flying at the top of the canopy in the second generation. This must not have been the case in the first generation, because they would have been captured in the traps at ground level, which encompassed the corn canopy in the first generation. In contrast, in the first generation of 1992, more males were captured in the corn field (Figure 9). The two fields with large captures of males in 1992 were both second-year corn fields (Figure 10). Male capture fell to very low numbers in the second generation (Figure 9), presumably because they were flying at the top of the canopy, and in the second generation the canopy was above the traps.

Malaise traps placed at ground level in woodlots in 1992 captured no wasps, and those at the edges captured a total of six wasps. One female was captured on 24 August (JD 236) in Allen field, and one female and four males were captured on 1 September (JD 244) in Lawson field. More wasps were captured in traps elevated above ground

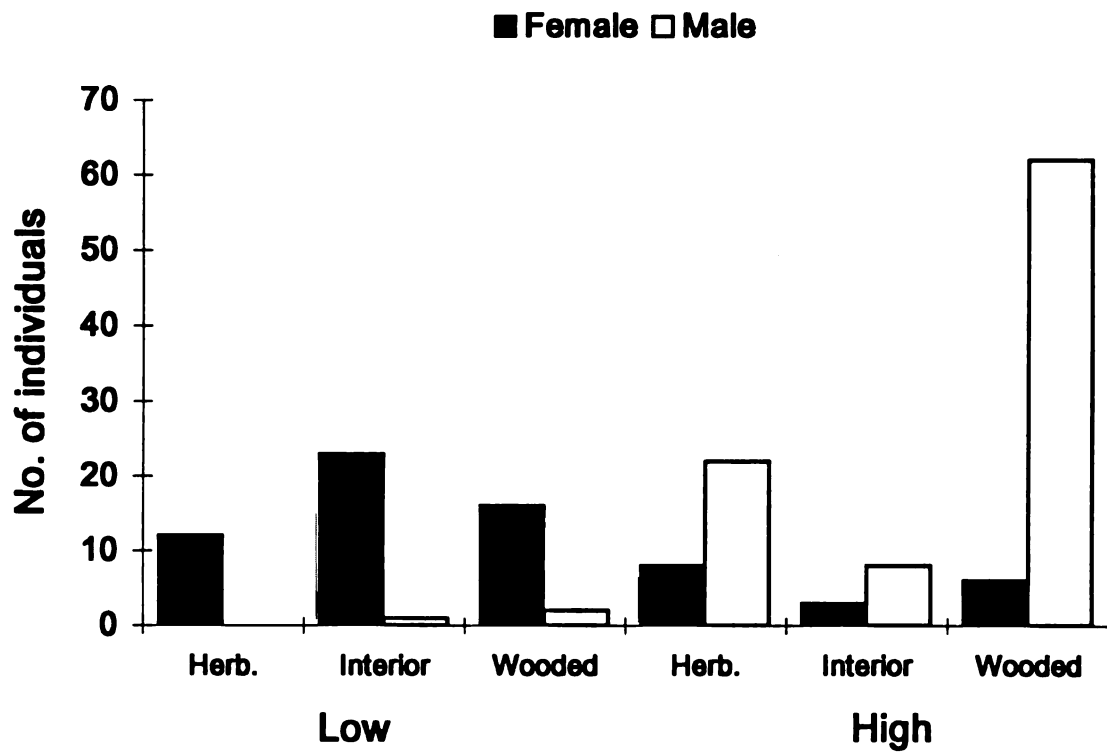


Figure 8. Capture of *Eriborus terebrans* males and females in malaise traps at ground level (low) and at the top of the corn canopy (high), in three locations (herbaceous edge, interior, and wooded edge) in one corn field, in the second generation of 1991.

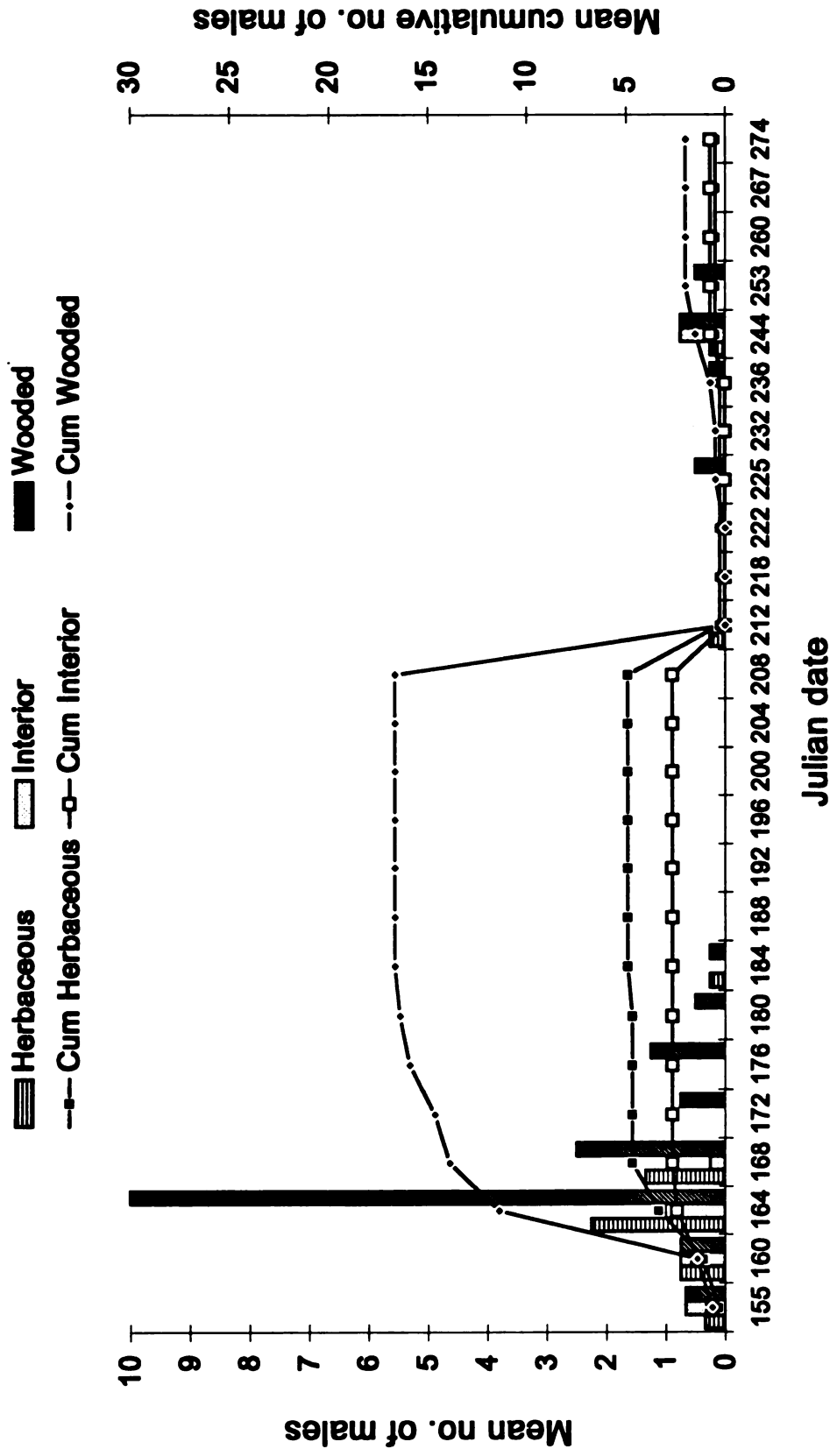


Figure 9. *Eriborus terebrans* males captured in malaise traps in 1992, at three locations in corn fields: herbaceous edge, interior, and wooded edge. Values are the means of four fields. Bars indicate capture on each date. The line graph is cumulative capture (cum) over the first (JD 155-208), and second (JD 212-274) generations.

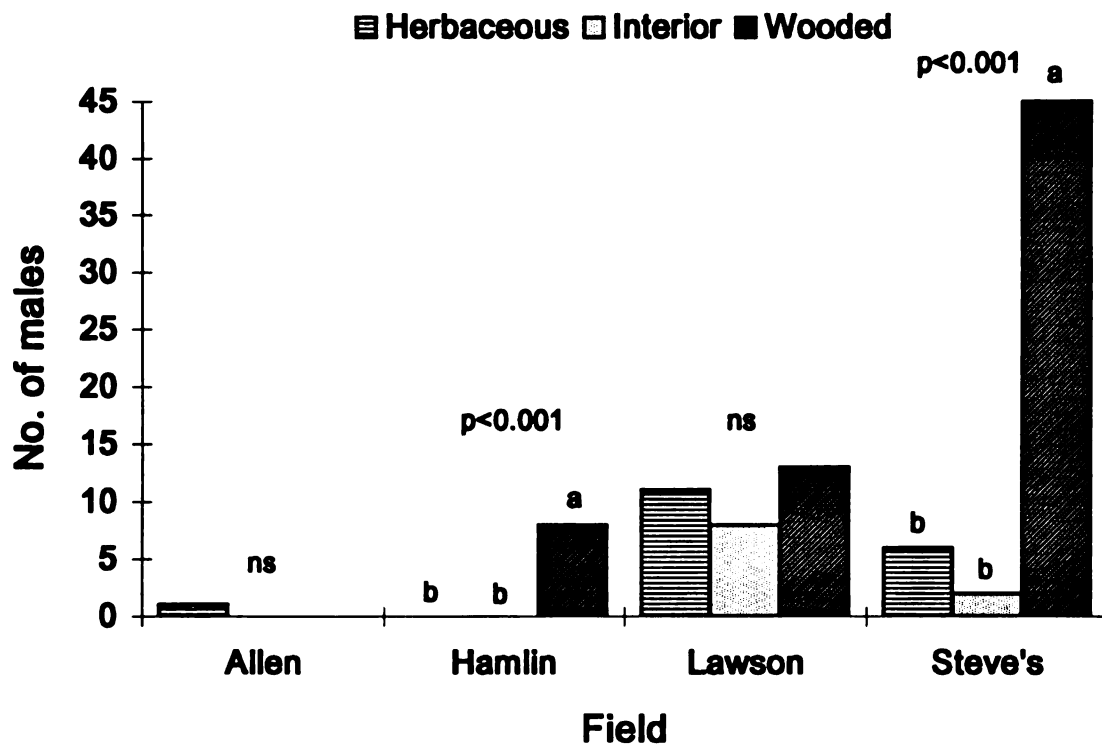


Figure 10. Total malaise-trap capture of *Eriborus terebrans* males in the first generation of 1992, at three locations (herbaceous edge, interior, and wooded edge) in each of four fields. *P*-values indicate levels of significance, and different letters indicate significant differences within fields (log-likelihood ratio goodness of fit tests).

level at the edge of a corn field, in 1993 (Figure 11). Consistent with the results of 1992, no wasps were captured in the edge trap at ground level in 1993. Apparently, wasps preferred to be higher in the canopy at the wooded edge. It is also interesting to note that males were captured in the corn field in the first generation in 1993, but none were captured there in the second generation.

The distribution of *E. terebrans* females was not strongly correlated with the distribution of *O. nubilalis* larvae, in the first generations of 1991 and 1992 (Table 2). Of the seven correlations calculated for *E. terebrans* females and *O. nubilalis* larvae, only one was significant (Lawson, $r=0.98$, $P<0.1$); three of these correlations had $r<0.8$, two of which were negative and one of which was positive. Similarly, of seven correlations calculated for *E. terebrans* females and percent plants damaged, one was significant (Cheney, $r=0.9$, $P<0.1$); three had $r<0.8$, one of which was negative and two of which were positive.

Ostrinia nubilalis larvae were not distributed in a consistent pattern within corn fields in the first generation of 1991 (Table 3). Analysis of five sampling dates in each of three fields, found five cases with significant differences among sites ($P<0.1$). Three of these cases were the first three dates in Allen, in which larval infestation increased from the herbaceous edge, to the interior, to the wooded edge; however, in the other two cases, the third and fourth dates in Cheney, the pattern of larval infestation varied, but in both cases the wooded-edge value was less than half the highest value. There were five cases in which *E. terebrans* females could be correlated with larval infestation. Four of these cases had $r<0.8$, and $P<0.2$, but two of these, in Allen, had positive slopes, and two, in Cheney, had negative slopes. In all of these cases *E. terebrans* females were more abundant at the wooded edge, regardless of *O. nubilalis* distribution.

The distribution of parasitism in the first generation of 1991 did not follow the pattern found for adult *E. terebrans* (Table 4). Only in Allen field was there a significant difference among locations within the field; parasitism was significantly lower at the

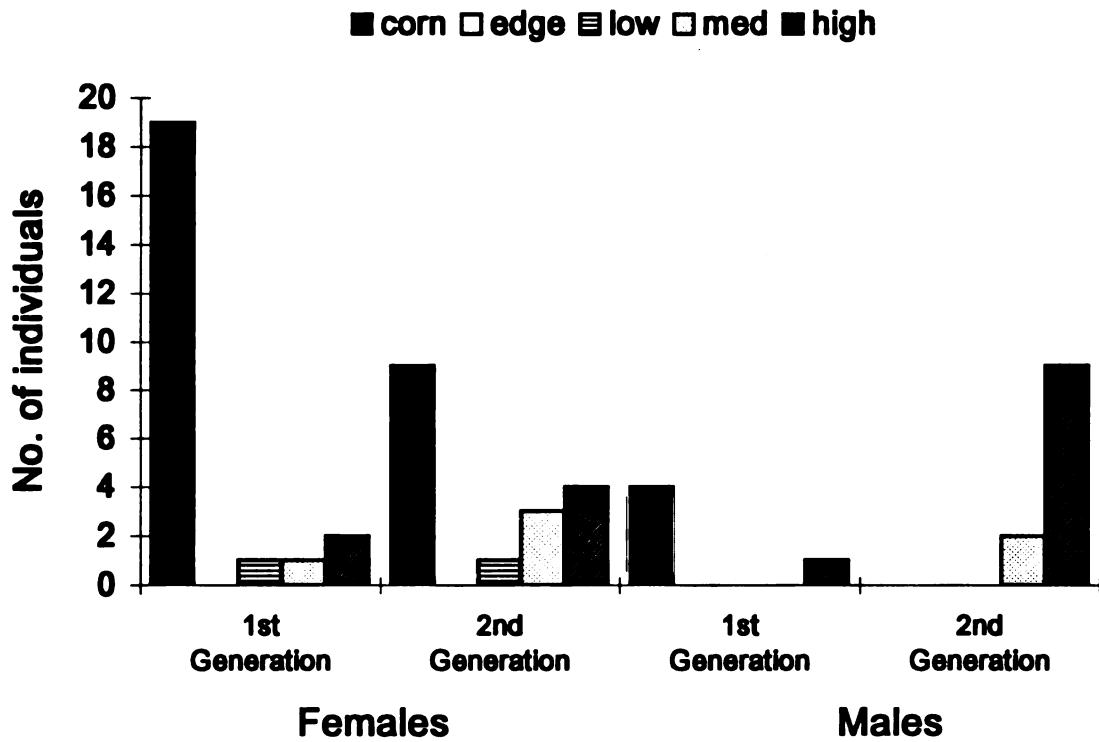


Figure 11. Total capture of *Eriborus terebrans* males and females, in the first and second generations of 1993, in one malaise trap in a corn field, and four malaise traps elevated to different heights along an adjacent woodlot canopy.

Table 2. Correlation of *E. terebrans* females with *O. nubilalis* larvae, and with % plants damaged by *O. nubilalis*, at the end of the first generations of 1991 and 1992, in corn fields in Michigan.

Field	Site ^a	<i>E. t. b</i> females	Larvae per m ²	r ^c	<i>P</i> <	% damaged	r	<i>P</i> <
1991								
Allen	H	3	1.89	-0.61	1.0	43.25	0.89	0.2
	I	5	2.52			37.97		
	W	29	1.73			51.30		
Diehl	H	1	4.97	-0.86	0.5	62.20	-0.86	0.5
	I	1	7.15			68.17		
	W	5	2.93			56.54		
Cheney	H	4	0.96	0.76	0.5	31.38	0.9	0.10
	I	2	1.17			31.89		
	W	23	1.31			41.17		
1992								
Allen	H	7	0.13	0.67	1.0	11.43	0.77	0.5
	I	1	0.40			13.10		
	W	12	1.33			30.71		
Hamlin	H	0	0.49	-0.92	0.5	22.86	-0.42	1.0
	I	1	0.28			17.38		
	W	13	0.04			18.33		
Lawson	H	34	2.91	0.98	0.1	72.02	0.97	0.2
	I	4	2.37			61.38		
	W	26	2.87			66.96		
Steve's	H	3	1.30	-0.1	1.0	46.43	-0.47	1.0
	I	2	1.56			69.05		
	W	19	1.42			48.33		

^a Sites within corn fields: H=herbaceous edge, I=field interior, W=wooded edge.

^b *Erioborus terebrans*.

^c Correlation coefficient, with 1 degree of freedom, in all correlations.

Table 3. Differences in *O. nubilalis* infestation among sites within corn fields, in the first generation of 1991, and correlation of *E. terebrans* females with *O. nubilalis* infestation.

Field	JD ^a	Site ^b	Larvae per plant ^c	F ^d	P<	<i>E. t.</i> ^e females	r ^f	P<
Allen	164	H	0.07±0.073	18.69	0.0026	2	0.85	0.2
		I	0.47±0.291			0		
		W	1.61±0.115			6		
	167	H	0.28±0.185	3.89	0.0824	0	0.96	0.1
		I	1.10±0.119			0		
		W	3.49±0.145			10		
	171	H	0.07±0.073	8.22	0.0191	0		
		I	1.03±0.360			1		
		W	1.78±0.362			2		
	175	H	0.67±0.344	1.61	0.2761	1	0.23	0.5
		I	1.37±0.311			0		
		W	1.22±0.204			9		
	179	H	0.71±0.410	0.31	0.7475	0		
		I	0.78±0.434			4		
		W	1.15±0.444			0		
Diehl	164	H	0.29±0.145	0.25	0.7833	0		
		I	0.17±0.167			0		
		W	0.32±0.158			1		
	167	H	0.17±0.090	2.05	0.2096	0		
		I	0.0±0.00			0		
		W	0.25±0.125			1		
	171	H	1.20±0.238	1.38	0.3208	0		
		I	2.09±0.844			0		
		W	0.89±0.280			0		
	175	H	0.89±0.241	0.79	0.4944	0		
		I	1.73±0.501			1		
		W	1.78±0.798			1		
	179	H	1.25±0.315	1.05	0.4079	1		
		I	0.84±0.220			0		
		W	0.66±0.333			1		

Table 3 (continued).

Cheney	164	H	0.15±0.149	1.15	0.3771	3	-0.91	0.2
		I	0.37±0.259			0		
		W	0.0±0.00			14		
	167	H	0.83±0.245	1.12	0.3874	1	-0.82	0.2
		I	0.42±0.231			2		
		W	0.30±0.302			7		
	171	H	1.26±0.233	3.82	0.0850	0		
		I	0.41±0.035			0		
		W	0.53±0.334			0		
	175	H	0.60±0.102	3.72	0.0888	0		
		I	1.39±0.278			0		
		W	0.58±0.292			1		
	179	H	1.29±0.621	1.68	0.2641	0		
		I	0.40±0.280			0		
		W	0.28±0.281			1		

^a Julian Date

^b Sites within corn fields: H=herbaceous edge, I=field interior, W=wooded edge.

^c *Ostrinia nubilalis* larvae per plant: Mean ± standard error.

^d F-statistics, with 2 degrees of freedom in the numerator, and 6 degrees of freedom in the denominator

^e *Eriborus terebrans*

^f Correlation coefficients, with 1 degree of freedom: capture of *E. terebrans* females sufficient for correlation occurred in five cases.

Table 4. Parasitism of *O. nubilalis* larvae by *E. terebrans*, in corn fields in Michigan.

Field	Site ^a	<i>E. t.</i> ^b females	<i>O. n.</i> ^c larvae collected		% Parasitism	<i>P</i> <	
			<i>E. t.</i> ^d	Total			
1991		First generation					
Allen	H	3	13	114	11.40	a ^e b b	0.001
	I	5	30	107	28.04		
	W	29	32	107	29.91		
Diehl	H	1	4	104	3.85		0.50
	I	1	9	113	7.96		
	W	5	7	100	7.00		
Cheney	H	4	6	51	11.76		0.75
	I	2	6	68	8.82		
	W	23	10	65	15.38		
		Second generation					
Allen	H	12	5	73	6.85		0.95
	I	23	5	81	6.17		
	W	16	7	92	7.61		
Diehl	H	18	7	68	10.29		0.975
	I	60	9	84	10.71		
	W	52	9	76	11.84		
Cheney	H	5	0	72	0.00		0.10
	I	2	4	75	5.33		
	W	14	1	53	1.89		
Emmons	H	20	5	69	7.25		0.90
	I	12	4	81	4.94		
	W	23	4	70	5.71		

Table 4 (continued).

1992		First generation					
Allen	H	7	0	2	0.00		0.25
	I	1	1	9	11.11		
	W	12	10	31	32.26		
Hamlin	H	0	1	15	6.67		0.75
	I	1	0	6	0.00		
	W	13	0	1	0.00		
Lawson	H	34	16	108	14.81	a	0.025
	I	4	4	88	4.55	b	
	W	26	16	95	16.84	a	
Steve's	H	3	5	14	35.71		0.50
	I	2	6	14	42.86		
	W	19	6	10	60.00		

^a Sites within corn fields: H=herbaceous edge, I=field interior, W=wooded edge.

^b *Eriborus terebrans*

^c *Ostrinia nubilalis*

^d No. of larvae parasitized by *E. terebrans*.

^e Letters indicate significant differences among sites within corn fields, determined by log-likelihood ratio goodness of fit tests.

herbaceous edge, and there was no difference between the interior and the wooded edge. In the second generation there were no significant differences among sites within any of the four fields. Parasitism was sampled only for the first generation of 1992. In one field, Lawson, there were significant differences among sites, and in this case they paralleled the pattern found for *E. terebrans* females; parasitism was higher at the herbaceous and wooded edges than in the interior. Though the results were not significant, in Allen and Steve's the pattern of parasitism also reflected the pattern of adult female abundance; the highest parasitism occurred at the wooded edge. Only one parasitized larva was found in Hamlin. Due to low *O. nubilalis* infestation in 1992, the intensity of sampling was lower in three of the four fields than in 1991. The sample in Lawson was comparable to samples in 1991, which may explain why the results were significant in Lawson, but not for the other three fields.

Discussion

During the first generation, *Eriborus terebrans* females were clearly documented to be more abundant near edges of corn fields, in particular wooded edges. In the second generation no consistent pattern was apparent. Three hypotheses will be considered to account for these observations: the pattern may be a consequence of wasps dispersing from overwintering sites to new host habitats, and stopping when they encounter an edge; alternatively, female wasps may be following the distribution of their larval hosts; thirdly, wasps may be choosing to be near edges because of some desirable edge qualities.

Eriborus terebrans overwinter as first instar larvae, inside fifth instar *O. nubilalis* larvae (Baker et al. 1949), which overwinter in tunnels in corn stalks. Early spring dispersal patterns have not been documented for *E. terebrans*, however, approximately 70% of Michigan corn fields are rotated to another crop each year (Landis and Swinton 1994), therefore, most *E. terebrans* and *O. nubilalis* must migrate from the field in which

they overwinter, to new fields in search of their hosts. If *E. terebrans* flight were arrested upon encountering an edge of a corn field, the result would be a greater abundance near edges. If this alone were responsible for the greater abundance of first-generation *E. terebrans* observed near edges, we would expect to see it regardless of edge type, yet in general a greater abundance was observed near wooded edges.

In the second generation *E. terebrans* females more fully colonize the field interior than in the first generation. When second-generation females emerge they find themselves in their host habitat, so rather than dispersing, they may remain in the field and more fully colonize the field interior. If the distribution of *E. terebrans* females throughout corn fields in the second generation were due to their emergence in corn fields, we would expect the same to be true for first-generation females that emerge in second-year corn fields. Cheney field in 1991 was a second year corn field, so *E. terebrans* emerging there would not have had to leave the field to find their host habitat. Nevertheless, the distribution of *E. terebrans* females was the same in Cheney as in the other fields. This hypothesis was tested further in 1992 by examining the distribution of *E. terebrans* in two first-year fields (Allen and Hamlin), and two second-year fields (Lawson and Steve's). There were two different patterns of distribution of *E. terebrans* females identified in these fields, but field history was not the basis of those differences. In Hamlin (first-year) and Steve's (second-year), females were more abundant near the wooded edge. In the Allen (first-year) and Lawson (second-year), females were more abundant near both the wooded and herbaceous edges than in the field interior. Thus, we conclude that the pattern of *E. terebrans* adult distribution is not simply a result of dispersal.

Alternatively, female *E. terebrans* may be more abundant in certain parts of fields because their hosts occur in greater abundance there. For the distribution of *E. terebrans* females to be explained by the distribution of their larval hosts, four conditions must be met: females must be able to detect the presence of their larval hosts, they must use that

information for habitat location, more *E. terebrans* must aggregate in areas of larger *O. nubilalis* infestation, and *O. nubilalis* larvae must be more abundant near edges of corn fields in the first generation, but not the second.

Many parasitoids orient to volatile chemicals from their host larvae, and damaged host plants (Vet and Dicke 1992). *Eriborus terebrans* will orient to odors from damaged corn plants, *O. nubilalis* larvae, and frass (Galeota 1981, Ma et al. 1992). To locate their hosts, parasitoids must first locate the host habitat, then locate the host; these two stages of host location may require different search modes (Vinson 1976). Though female parasitic wasps clearly orient to odors of plants and larval hosts (Vet and Dicke 1992), it is not certain individuals orient to those odors in a longer-range habitat search.

It is also not certain that greater numbers of parasitoids aggregate in areas of greater larval infestation. Baker et al. (1949) sampled parasitism by *E. terebrans* in two fields 200 yards apart, one infested with *O. nubilalis* larvae at a rate of 1372 larvae/100 stalks, and the other at a rate of 5120 larvae/100 stalks. Parasitism by *E. terebrans* was 4% in the field with low infestation, and 1% in the field with infestation four times higher, indicating the same number of parasitoids per 100 stalks. Landis and Haas (1992) also found no indication that *E. terebrans* parasitism was related to host infestation. Data from this study show no consistent effect of *O. nubilalis* larval distribution on *E. terebrans* female abundance or parasitism. In 1992, populations of *O. nubilalis* larvae were negligible, and though there were few larvae to influence the distribution of female wasps, a significant edge effect was observed.

Finally, there is no indication that *O. nubilalis* larvae occur in greater abundance near edges. *Ostrinia nubilalis* egg masses and larvae have been shown to be randomly distributed in field corn in the first generation (Chiang and Hodson 1959), and second generation (Calvin et al. 1986, Coll and Bottrell 1991), and in sweet corn (Shelton et al. 1986). Landis and Haas (1992) found no differences in larvae per damaged plant, among sites in corn fields. In this study, larvae in the first generation of 1991 were not

distributed in a consistent pattern. Thus, factors other than larval distribution appear to be responsible for the occurrence of greater numbers of *E. terebrans* females near the edges of corn fields.

Eriborus terebrans females may be more abundant near field edges because of qualities of those edges. This might be due to passive dispersal of insects by wind, as altered by the woodlot (Lewis 1965), or it might be due to choices of individuals seeking alternate hosts, adult food, or a favorable microclimate.

Among the fields surveyed in this study, the locations of woodlots relative to corn fields were such that each cardinal direction was represented by at least one field. Given this configuration, it is unlikely that a consistently greater abundance of wasps at wooded edges would result from the windbreak effect of woodlots.

Eriborus terebrans has no documented alternate host in Michigan. Baker et al. (1949) reported oviposition by *E. terebrans* into *Ostrinia obumbratalis* (Lederer) and *O. penitalis* (Grote) larvae, but none of the larvae survived to moth pupa or parasitoid cocoon, so it could not be determined if *E. terebrans* could complete development in these hosts. *Ostrinia obumbratalis* and *O. penitalis* use various species of *Polygonum* as hosts, which are common plants, so *O. obumbratalis* and *O. penitalis* could be widely distributed. However, the abundance of *Polygonum* sp. and of *O. obumbratalis* and *O. penitalis* must be low, relative to that of corn and *O. nubilalis*. Even if *E. terebrans* can use *O. obumbratalis* and *O. penitalis* as hosts they are unlikely to be major factors influencing the observed distribution of *E. terebrans*.

Adult food and microclimate present the most likely explanations for the observed distribution of adult *E. terebrans*. The longevity of adult *E. terebrans* is greatly enhanced by a sugar source, and significantly reduced by high temperatures (Chapter 4). Adult *E. terebrans* are probably unable to find sources of food in the corn field early in the season, and the high temperatures and low relative humidities that can occur in corn fields during the first generation make them less suitable habitats for *E. terebrans* than

woodlots (Chapter 4). Wasps may seek the cooler, more humid microclimate of the forest, where they may also find food resources, such as floral and extrafloral nectar, dripping sap from broken branches, or homopteran honeydew. If this explains why wasps are more abundant near woodlots in the first generation, then conditions must change to make the corn field more attractive in the second generation. Once the corn canopy has closed, temperatures are probably lower and relative humidities higher in the corn field. In addition, aphids on the corn plants, primarily the corn leaf aphid *Rhopalosiphum maidis* (Fitch) (Homoptera: Aphidae) and weeds flowering in the fields may provide food for the wasps. Landis and Marino (in press) have shown the longevity of *E. terebrans* females to be enhanced by availability of certain flowers, most notably wild carrot, *Daucus carota* (Umbelliferae), and by lambsquarters, *Chenopodium* sp. (Chenopodiaceae), infested with aphids.

Differences in the observed distribution of *E. terebrans* females between 1991 and 1992 may be explained by the weather. During the first generation of 1992 temperatures rose above 30°C only once, whereas in 1991 higher temperatures were common (Figure 12). If wasps need only food resources from the edge, an herbaceous edge may suffice, whereas, if they need a moderate microclimate they may be forced to seek the shelter of the forest.

Differences in the distribution of male *E. terebrans* between 1991 and 1992 may also be explained by temperature differences between those years. Males appear to be, in general less tolerant of stressful condition than females (Chapter 4). In the first generation of 1991, when it was hotter, very few males were captured in the corn field, whereas in 1992 considerable numbers of males were captured in two of the fields. Male distribution was more closely related to the wooded edge in the first generation of 1992 than that of females. That males were observed in the second generation of 1991 in traps at the top of the corn canopy, is likely a result of males searching for females in the corn fields. It is also interesting that the two fields with sizable male capture in the first

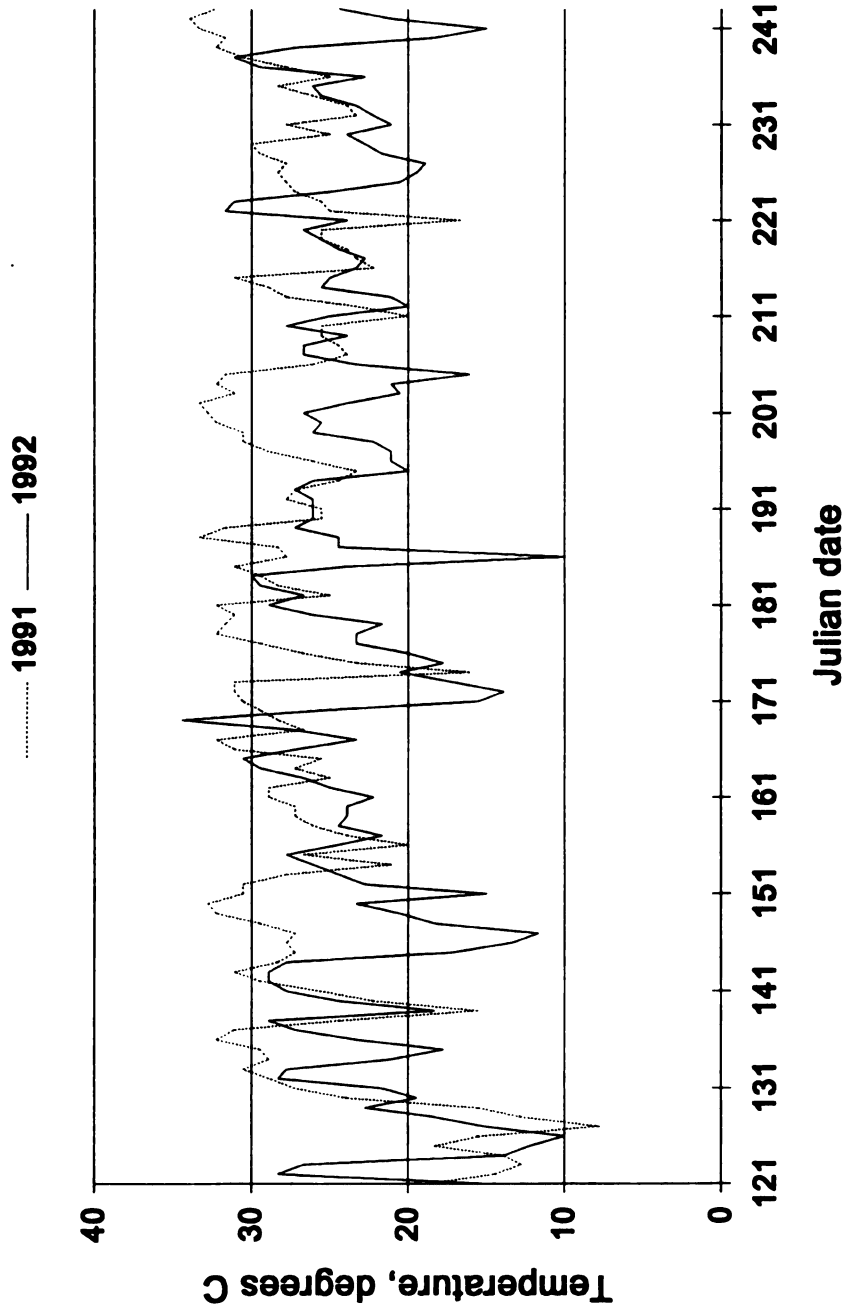


Figure 12. Daily maximum temperatures for May through August of 1991 and 1992, in East Lansing, Michigan.

generation of 1992, and the only field with any male capture in the first generation of 1991, were all second-year corn fields. It may be that males do not migrate far from the field in which they emerge, but remain there searching for females. This suggests the possibility that woodlots and other adjacent non-crop habitats may also provide sites to encounter mates.

The constraints on the distribution of *E. terebrans* of adult food requirements, microclimate, and encounter of mates, may have important consequences for the biological control of *O. nubilalis*. Conservation of natural enemies may be an effective strategy for management of *O. nubilalis*, because of the difficulty of conventional management strategies. Though *O. nubilalis* can cause significant economic damage, few corn growers in Michigan manage for it (Landis and Swinton 1994). The infrequent occurrence of economic levels of infestation makes growers reluctant to invest the effort in scouting, which in most years appears to afford no benefit. In the period from 1988 to 1992, *O. nubilalis* was a widespread pest only in 1991, when upwards of 70% of fields exceeded threshold; from 1988 to 1990 between 10 and 30% of fields exceeded thresholds, and in 1992 significant damage by *O. nubilalis* was nearly absent (D. A. Landis, personal communication). Control of the European corn borer by chemical means is difficult, because of the hidden feeding sites of the insects (Showers et al. 1989). *Ostrinia nubilalis* might be more effectively controlled by managing the agricultural ecosystem to utilize natural controls to prevent economic levels of infestation, rather than responding to them with chemical controls after they occur.

Variation in *O. nubilalis* infestation from year to year indicates that in most years, in most fields, natural controls work to maintain *O. nubilalis* populations below economic threshold levels. One of the most important natural controls may be weather, which is, of course, beyond the grower's control. Heavy rain when first instar larvae are feeding in the whorl of the corn plant can cause high mortality due to drowning (Showers

et al 1989). Cold nighttime temperatures can limit the flight of females, and thereby reduce larval populations.

Predators and parasitoids can also affect population levels (Sparks et al. 1966, Godfrey et al. 1991), and there may be potential to manage the effectiveness of these by habitat manipulation. *Eriborus terebrans*, being the most important parasitoid of *O. nubilalis* in Michigan, may be among the important natural controls. The success of *E. terebrans* appears to be strongly influenced by shelter and resources provided by woodlots. A need for resources provided by non-crop habitats is not unique to *E. terebrans* (van Emden 1965, 1990, Dennis and Fry 1992). Perennial habitats adjacent to agricultural fields can provide temporally stable resources for natural enemies. The structure of annual agricultural ecosystems must develop each season, creating a delay in the availability of sources of food and favorable microclimates. Management of perennial non-crop habitats may be key to conservation of natural enemies for biological control.

CHAPTER 4

Effects of habitat, temperature, and sugar availability on the longevity of

Eriborus terebrans (Gravenhorst)(Hymenoptera: Ichneumonidae)

Introduction

The success of conservation and classical biological control of agricultural pests depends on the ability of natural enemies to establish populations in the landscape where the pest occurs. Pest populations generally provide ample supplies of hosts or prey, but natural enemies have additional needs, including overwintering sites, adult food sources, alternate hosts, mating sites, and shelter (van den Bosch and Telford 1964, Stehr 1975). Habitats other than the host habitat may be necessary to meet some of those needs. For *Eriborus terebrans*, a parasitoid of the European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Pyralidae), the presence of habitats other than corn fields appears to influence the distribution of *E. terebrans* adults (Chapter 3) and parasitism (Landis and Haas 1992). If the resources needed by *E. terebrans*, and the role of non-crop habitats in providing those resources can be better understood, our ability to conserve *E. terebrans* as a biological control agent may be enhanced.

Eriborus terebrans is responsible for 92.2 to 99.2% of the parasitism of *O. nubilalis* in Michigan (Landis and Haas 1992). *Eriborus terebrans* was introduced into Michigan from Europe and Asia during the 1920's and 1930's, as part of an effort to control *O. nubilalis* in North America (Baker et al. 1949). *Ostrinia nubilalis* is a pest of great economic concern in Michigan; it is one of the most serious pests of corn, and corn

is Michigan's largest crop. Control of *O. nubilalis* by conventional means is problematic. It is a sporadic pest in Michigan, making it difficult to determine when to apply chemical controls, and the hidden feeding sites of the insect limit the effectiveness of chemical controls. Conservation of *E. terebrans* and other natural enemies may provide opportunity for improved control of *O. nubilalis*.

Eriborus terebrans is a solitary larval endoparasitoid of *O. nubilalis*. Female *E. terebrans* oviposit into second through fourth instar larvae; an *E. terebrans* larva completes its development while its host is in the fifth and final instar, then spins a cocoon of silk in which to pupate (Baker et al. 1949). *Eriborus terebrans* has two generations per year, in Michigan, that coincide with the two generations of *O. nubilalis*. The first generation usually begins in June, when corn plants are small. The second generation begins in late July, generally about the time corn plants are silking or tasseling. Second-generation *O. nubilalis* larvae enter diapause inside tunnels in corn stalks. Second-generation *E. terebrans* overwinter as larvae within their host larvae.

Landis and Haas (1992) examined spatial patterns in percent parasitism by sampling *O. nubilalis* larvae along transects through corn fields, during both first and second generations. They found first-generation parasitism to be higher near edges of corn fields, particularly those adjacent to woodlots. Second generation parasitism did not differ significantly among the sites sampled within fields. The distribution of adult *E. terebrans* within corn fields, in relation to edges was investigated in 1991 and 1992, by placing malaise traps near a wooded edge, near an herbaceous edge, and in the field interior, in each of four corn fields (Chapter 3). During the first generation of 1991 significantly more wasps were captured in the wooded-edge traps than either the herbaceous-edge or interior traps. In the first generation of 1992 capture was again highest in wooded-edge traps, but significantly more wasps were also captured near herbaceous edges than in the interior. In the second generation of both years there was no consistent pattern of distribution. The distribution of *O. nubilalis* larvae was not

sufficient to explain the distribution of adult wasps in either year. In Chapter 3 it was argued that *E. terebrans* was more abundant near edges in the first generation because of resources obtained at those edges, particularly sources of sugar, and cool microclimates.

Preliminary observations in the greenhouse suggest *E. terebrans* is very sensitive to temperatures above 30°C, becoming unable to fly in less than half an hour, and eventually dying if temperature is not reduced. The longevity of adult wasps is also greatly enhanced by a sugar source (Baker et al. 1949). Longevity of female *E. terebrans* caged in the field on Queen Anne's lace, *Daucus carota*, (mean=13.4 d), and on common lambsquarters, *Chenopodium album*, with aphids and honeydew (mean=13.6 d) was significantly longer than wasps provided only with water (mean=1.2 d) (Landis and Marino, in press). Early in the growing season a corn field is a very open, hot, dry, windy environment, largely devoid of sugar sources. Later in the season, increased populations of aphids and flowering weeds in corn fields may provide sugar sources, and closure of the corn canopy creates a more shaded and humid microclimate. Based on these observations, it is proposed that early in the season *E. terebrans* must remain near the wooded edge because of their need for a food source and a moderate microclimate, but later in the season those needs can be met in the corn field, allowing them to venture further into the field interior. This raises a further question of whether other perennial, structurally complex habitats, such as fencerows with tall woody vegetation could also provide the microclimate and adult food needed by *E. terebrans*.

The experiments reported in this chapter were designed to test the hypotheses that: *Eriborus terebrans* longevity is decreased under high temperatures, their longevity under field conditions is greater in woodlots and wooded fencerows than in early-season corn fields, and in favorable microclimates their longevity is enhanced by the availability of sugar. Three experiments were conducted under conditions ranging from the controlled microclimates of growth chambers, to wasps caged on corn plants in

greenhouses, to a field test of wasps caged in selected habitats in the agricultural landscape.

Methods

In all three experiments, wasps were given one of three provision treatments: sugar solution and water (sugar), water only (water), or neither (dry). In the growth chamber and greenhouse experiments the sugar solution was a 50% dilution of honey with distilled water. Honey for all cages in both experiments was from the same container (bulk, raw Michigan honey, East Lansing Food Cooperative). In the habitat suitability experiment, a solution of sucrose, glucose, and fructose in a 1:1:1 ratio was used rather than honey, because it had less odor and therefore incurred less risk of detection and damage by raccoons and woodchucks. The nectar of most flowers contains glucose, fructose and sucrose, and floral nectars are characterized as hexose-rich, containing predominantly glucose and fructose, or sucrose-rich (Baker and Baker 1983). Bees and wasps tested by Baker and Baker (1983) tended to prefer sucrose-rich nectars, however, adult *E. terebrans* in our colony have performed well on a solution of honey and water, which consists of glucose and fructose (Gojmerac 1981). Provisions were supplied using Kimwipe[™] wicks, through 6 mm glass tubes, from 8 dram (30 ml) medicine vials containing distilled water. Dry treatments were provided with dry wicks. Sugar treatments had a portion of the moist wick dipped in the sugar solution.

Growth chamber test of temperature, relative humidity, and provision effects

This experiment simultaneously tested the effects of temperature, relative humidity and provisions on longevity of *E. terebrans*. Each cage housed one female and one male wasp, and provided an independent combination of relative humidity (RH) (high or low) and provision treatments. Cages were placed in growth chambers at 25 or 35°C. There were two growth chambers for each temperature.

Cages were constructed from clear plastic pint containers (Del-Pak™, diameter=11 cm, height=7.5 cm) with snap-fit lids, nested into clear plastic quart containers (Del-Pak™, diameter=11 cm, height=15 cm). A portion of the bottom of the pint container was replaced with 20 x 20 mesh nylon screen to allow air flow between the pint and quart containers. In the bottom of the quart container was a saturated salt solution to maintain constant relative humidity. Lithium chloride (LiCl) (low RH), and sodium chloride NaCl (high RH) were chosen because they maintain a fairly constant relative humidity over a wide range of temperatures; the solutions were expected to maintain relative humidities of 11.5-12.0% (LiCl), and 75.5% (NaCl) (Winston and Bates 1960). Actual relative humidities were close to expectations for the dry treatments, but in both the sugar and water treatments, where moist wicks were provided, relative humidities were much higher (Table 5). Provisions were supplied via a single glass tube with a wick, inserted through the bottom of the pint cup, from a vial suspended in the quart cup below. For sugar treatments, the end of the wick was dipped in the honey solution, so the end of the wick provided moistened honey, and the portion of the wick closest to the glass tube provided plain water.

The experiment was conducted as a nested design, with growth chambers nested within the temperature main plots, and the RH-provision combinations in sub-plots. Four pairs of wasps were exposed to each temperature-RH-provision combination (two pairs in each growth chamber), for a total of 48 females and 48 males. All wasps were from the same cohort of laboratory-reared *E. terebrans* (14-23 d). They were assigned to treatments in a stratified random fashion. The first 12 pairs captured from the colony cage were randomly assigned to the 12 treatment combinations. The next three sets of 12 were each handled in the same way. The sets of 12 pairs were then randomly assigned to growth chambers. This stratified randomization scheme was followed to minimize potential bias due to the order in which insects were captured.

Table 5. Relative humidities in cages in the growth chamber experiment, under combinations of salt solutions, temperatures and provision treatments.

Salt ^a & Temperature ^b	Dry ^c	Water ^d	Sugar ^e
LiCl			
25	13.41±0.28 (4) ^f	74.71±2.01 (4)	69.67±1.32 (4)
35	13.77±0.47 (4)	73.73±1.40 (3)	68.44±1.99 (3)
NaCl			
25	76.50±1.04 (4)	92.44±0.51 (4)	89.12±0.48 (4)
35	76.69±1.06 (4)	92.19±0.66 (3)	89.97±0.50 (3)

^a Saturated salt solutions

^b °C

^c Neither water nor sugar

^d Only water

^e Sugar and water

^f Mean ± standard error (sample size)

On the first day of the experiment wasps were observed every hour for nine hours (h), then were observed three times on the second day, twice daily for the next two days (d), and once daily until the last individual had died. Wasps that lived for fewer than 6 h on the first day were recorded as 0.25 d. The longevity of wasps that died within the first 4 d was recorded to the nearest half day, and for those that lived longer than 4 d, to the nearest day. The last live observation was considered to be the last half day of a wasp's life. In some cases wasps were observed in an incapacitated state, characterized by erect wings, curled antennae, and a failure to respond to tapping the side of the cage. No wasp observed in this state ever recovered, thus, incapacitated wasps were considered dead when recording their longevity. Longevity data were positively skewed, so data were transformed for analysis ($l' = \log_{10}(\text{longevity} + 1)$) (Zar 1984).

It was noted if wasps were observed resting on a wick. The proportion of observations in which a wasp rested on a wick was analyzed, to determine if wasps sought moisture more in stressful microclimates than favorable ones. The proportions of observations on a wick were transformed for analysis ($p' = 1/2[\arcsin((X/(n+1))^{1/2} + \arcsin((X+1)/(n+1))^{1/2}]$, where X =no. observations on wick, and n =total no. observations) (Zar 1984).

Analyses were done with a SAS general linear models (GLM) procedure, nested analysis of variance (SAS Institute 1988). Females and males were analyzed separately. There was one missing value from the female longevity data set, two from the male longevity data set, and one from the male wick observation data set. The female and one of the males missing from the longevity data sets lived long enough to provide observations on the wick before dying, possibly by drowning, after becoming wrapped in the wick. The female longevity missing value was estimated using a formula from Zar (1984). The other data sets with missing values were simply analyzed with missing values, using SAS GLM procedure. Planned multiple comparisons were done with Bonferroni's t-tests, which were calculated by hand (Gill 1978) using means and mean

squared errors from the SAS procedure, and compared to critical values of Student's *t*-distribution based on Sidak's multiplicative inequality (Rohlf and Sokal 1981). *P*-values for the analysis of variance are reported here with the accuracy of the SAS printout, and for the multiple comparisons with the accuracy of table values (alpha values of 0.01, 0.05, and 0.10). Results of the analysis of variance were used as preliminary tests to determine which planned comparisons were appropriate, considering the significance of interaction terms.

A priori predictions of the growth chamber experiment were that longevity of wasps at a moderate temperature and relative humidity would be enhanced by the availability of water, and further enhanced by the availability of both sugar and water. In contrast, the longevity of wasps at a stressful temperature and relative humidity was expected to be enhanced by the availability of water, which would help them tolerate heat and desiccation, but would not benefit further from sugar. It was also predicted that wasps would seek the moist wick as a refuge or oasis more in hot, dry conditions than in moderate ones.

Greenhouse test of temperature and provision effects

Pairs of wasps were caged on potted corn plants approximately 1 m tall, in greenhouses at 25 or 35°C, with three provision treatments. Cages in the greenhouse experiment consisted of 18 x 16 mesh aluminum screen wrapped in a cylinder around the corn plant, with the ends of the cylinder plugged with 2" thick foam. Provisions were supplied by wicks through glass tubes, inserted through slits in the cage foam. All cages received two wicks: in the sugar treatment one wick was dipped in the honey solution and the other wick provided water, in the water treatment both wicks provided water, and in the dry treatment both wicks were dry.

There were only two greenhouses, so the effects of temperature and the possible effects of greenhouse differences were confounded. Each temperature-provision

combination was replicated five times, for a total of 30 females and 30 males. The first three replications were from the same cohort of wasps (age 4-16 d) and were run simultaneously. Replications four and five were each from different cohorts, (age 15-27, and 17-29 d respectively) and were run at different times. Several wasps were lost during the experiment, leaving a total of 24 females and 26 males in the longevity data sets, and 27 males and 27 females in the wick observation data sets. Missing values were distributed fairly evenly across treatments, with the smallest sample size in any treatment combination being $n=3$. Within each replication, wasps were assigned randomly to the six possible temperature-provision treatment combinations.

Wasps were observed three times on the first day of the experiment, twice on the second day, and once every day thereafter. Longevity was recorded following the criteria of the growth chamber experiment; wasps that died within the first 2 d were recorded to the nearest half day, and for those that lived longer than 2 d, to the nearest day. The proportion of observations in which each wasp was on a wick was recorded as in the growth chamber experiment. Data were transformed for analysis, as in the growth chamber experiment. Analyses were conducted as a full factorial model, with missing values, analyzed with SAS GLM procedure (SAS Institute 1988). Multiple comparisons were conducted as in the growth chamber experiment. A priori predictions were identical to those of the growth chamber experiment.

Suitability of selected habitats

Corn fields, woodlots, herbaceous vegetation and wooded fencerows were selected to be tested for suitability as habitats for *E. terebrans*. Suitability was determined by observing the longevity of *E. terebrans* caged in those habitats at two periods during the growing season. The early-season experiment began in June, when the corn was small, to correspond with the first generation of *E. terebrans* in the field. The late-season experiment began in August, after corn canopy closure, during the

second generation. Cages and provision treatments were as in the greenhouse experiment, with each cage housing one female and one male wasp. The dry provision was later omitted from analysis, because rain and dew made maintenance of dry conditions inconsistent.

Both early-season and late-season experiments were replicated in five fields. Each field had one cage of each provision treatment, in each of the four habitats, for a total of twelve cages per field. Fields were set up on different days. Sites for cages in each habitat were chosen randomly. Cages were set up, and a pair of wasps was placed in them, in the evening of the day before observation. Wasps were assigned randomly to cages in the four habitats. At that time all three cages in each habitat were provided with sugar and water. The following morning, cages in each habitat were selected randomly to receive the provision treatments, and the wicks were changed. Cages were observed twice daily for the first 10 d, then once daily thereafter. Longevity was recorded to the nearest half day for wasps living less than 10 d, and to the nearest day for those living longer, following the criteria used in the greenhouse and growth chamber experiments.

Temperatures and relative humidities were measured six times in each habitat, in each field. Temperature was measured with thermometers, and relative humidity with a wet bulb-dry bulb hygrometer and a hand held hygrometer (Hana Instruments Stick Hygrometer, model HI 8565). Thermometers and hygrometers were placed in the shade and allowed to equilibrate while observations of the wasps were made. The wet bulb-dry bulb hygrometer was then fanned for one minute, then readings were taken of all thermometers. The stick hygrometer was observed for one minute, and the low and high readings during that period were recorded.

Fields were treated as blocks in a mixed model analysis of variance, treating habitat and provisions as fixed effects. There were four missing values for females in the early-season experiment, and three for males. In one case, a corn field-sugar treatment, the female lived for 9.5 d before disappearing. The male in that cage lived to 11 d. The

ratio of female to male longevity in sugar treatments in the other habitats of that field was used to estimate the female's longevity from that of the male. The other three missing values were distributed among treatment combinations, such that all habitat-provision combinations had $n=4$ or $n=5$, for total sample size (N) of 37, for both males and females. The same treatment combinations were missing for males and females. Males and females were analyzed separately. Longevity data were transformed for analysis, analyses were done using SAS GLM procedure, and multiple comparisons were performed as in the growth chamber and greenhouse experiments. Analysis of the late-season experiment was not possible because too many treatments were lost due to damage by vertebrates.

A priori predictions were, that in the early-season experiment longevity would be greater in woodlots and wooded fencerows than in corn fields or herbaceous vegetation, but in the late-season experiment, longevity should not differ among corn fields, woodlots, and fencerows; longevity in the herbaceous vegetation was not expected to differ between early and late-season experiments, because the vegetation structure, and therefore the microclimate would not have changed. Based on results from the growth chamber and greenhouse studies, it was expected that sugar would enhance longevity in all habitats.

Results

Growth chamber test of temperature, relative humidity, and provision effects

Longevity of females in the growth chambers was significantly influenced by the main effects of temperature ($P<0.0058$), RH ($P<0.0016$) and provisions ($P<0.0001$) (Table 6, Figure 13). Significant interactions occurred between temperature and provision ($P<0.0001$) and RH and provision ($P<0.0001$). There was no interaction between temperature and RH ($P<0.5269$).

Because of significant interactions, provision effects were explored within temperatures, and temperature effects within provisions (Figure 13). At 25°C, female longevity did not differ between the water and dry treatments, ($P>0.10$), but at 35°C water significantly enhanced longevity ($P<0.10$). Sugar significantly enhanced longevity relative to water ($P<0.01$) at both temperatures, however, the magnitude of the difference was greater at 25°C. Longevity was significantly less at 35°C than at 25°C for all three provision treatments (dry $P<0.01$, water $P<0.05$, sugar $P<0.01$); the magnitude of the difference was greater for sugar than for other treatments.

For provision treatments within levels of RH, female longevity was significantly lower in the dry treatment than the water treatment at low RH ($P<0.01$), but did not differ at high RH ($P>0.1$). The comparison of dry and water treatments at low RH was probably not a fair one, because the water and sugar treatments increased relative humidity as well; the dry-low RH combination experienced both a lack of water and lower relative humidity than the water-low RH combination. The same was true at the high RH, but the magnitude of the difference was less because the relative humidities were so high. Longevity was significantly greater in sugar than water treatments at both high and low RH ($P<0.01$), so the provision effect appeared to be unaffected by RH. Relative humidity significantly affected longevity for only those wasps in the sugar treatment ($P<0.01$); longevity was greater at low RH, so the effect was not of desiccation reducing longevity, but rather some negative effect of very high relative humidity.

Male longevity was significantly influenced by temperature ($P=0.0239$) and provision ($P=0.0001$), but not by RH ($P=0.8159$) (Table 6, Figure 14). The only significant interaction was temperature by provision ($P=0.0559$). Dry and water treatments were not significantly different at either 25°C or 35°C ($P>0.1$). Wasps in sugar treatments lived significantly longer than those in water treatments at 25°C ($P<0.01$), but not at 35°C ($P>0.1$). Longevity was significantly greater at 25°C than 35°C, only in the sugar treatment ($P<0.01$).

Table 6. ANOVA of *Eriborus terebrans* longevity^a in growth chambers: relative humidity and provision treatments nested within temperatures.

Source of variation	Female ^b			Male		
	df	Mean Square	P <	df	Mean Square	P <
Temperature (temp.) ^c	1	2.07493	0.0058	1	0.84302	0.0239
Error a ^d	2	0.01215		2	0.02087	
Relative humidity(RH) ^e	1	0.14120	0.0016	1	0.00213	0.8159
Provision ^f	2	2.98229	0.0001	2	1.04104	0.0001
RH* Provision	2	0.14640	0.0001	2	0.05689	0.2453
Temp.*RH	1	0.00490	0.5269	1	0.03753	0.3323
Temp.*Provision	2	0.44766	0.0001	2	0.12242	0.0559
Temp.*RH*Provision	2	0.01134	0.3987	2	0.00585	0.8604
Error b	34	0.01200		32	0.03873	

^a Transformed for analysis: longevity' = log₁₀(longevity + 1).

^b Female N=48, male N=46 (=48-2 missing values).

^c 25 and 35°C.

^d Temperature tested with error a (= temp.*growth chamber); all other factors tested with error b (=residual error).

^e High and low RH (values in Table 5).

^f Three treatments: sugar and water, only water, neither.

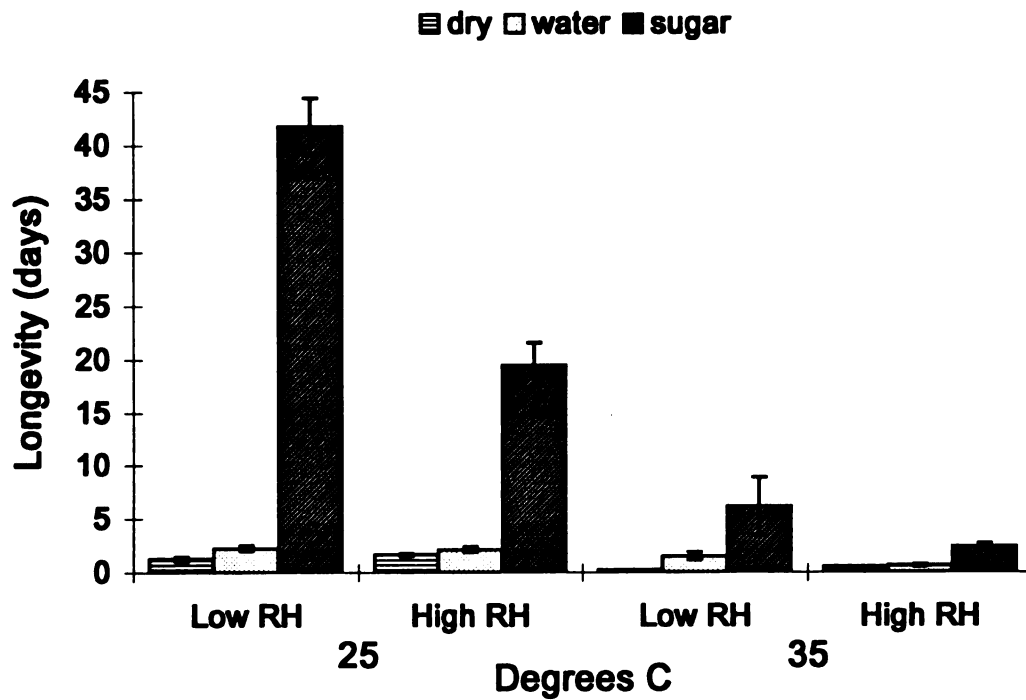


Figure 13. Mean longevity ($\pm$ standard error) of *Eriborus terebrans* females in growth chambers at two temperatures (25°C, 35°C, $P < 0.058$), two relative humidities (low, high, $P < 0.0016$), and three provision treatments (dry, water, sugar, $P < 0.0001$). $n = 4$ per treatment, except 35°C-low-sugar $n = 3$.

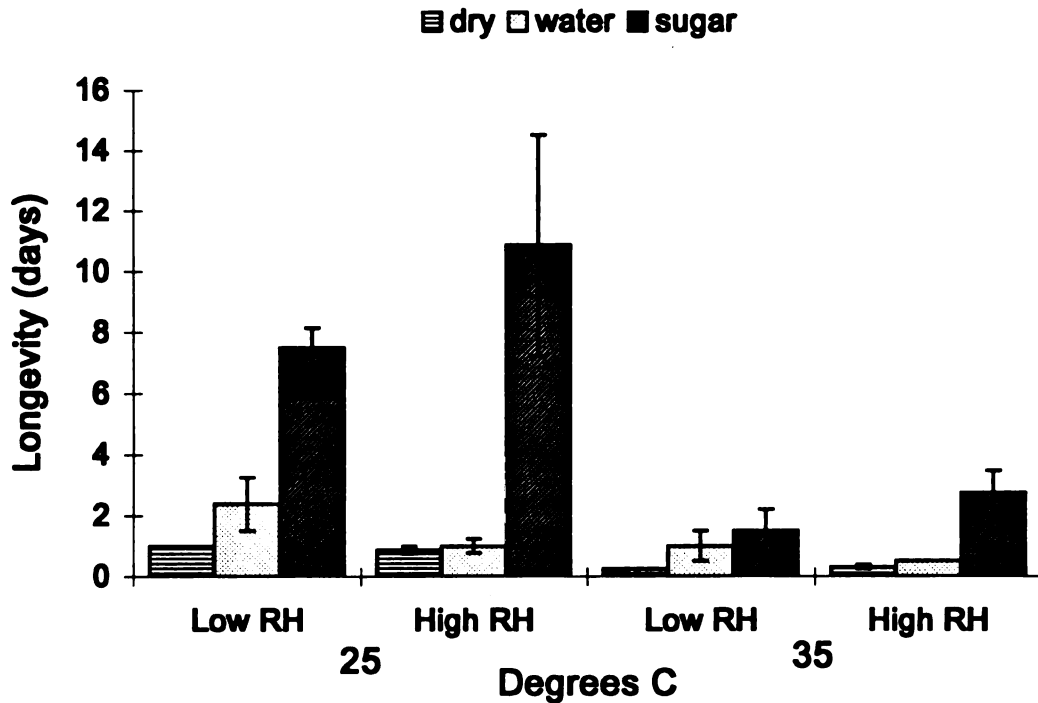


Figure 14. Mean longevity ($\pm$ standard error) of *Eriborus terebrans* males in growth chambers ($n=4$ per treatment), at two temperatures (25°C, 35°C, $P<0.0239$), two relative humidities (low, high, $P<0.8159$), and three provision treatments (dry, water, sugar, $P<0.0001$). $n=4$ per treatment, except 25°C-low-dry, 25°C-high-water, and 35°C-high-water $n=3$.

Frequencies of females on wicks were significantly different for temperature ($P<0.0022$), RH ($P<0.0148$), and provision treatments ($P<0.0001$) (Table 7). Significant interactions occurred between provision and temperature ($P<0.0001$), and temperature and RH ($P<0.0069$), but not between provision and RH ($P<0.4869$); the three-way interaction was significant enough to warrant consideration ($P<0.1821$). Dry treatments were compared, as a control, to combined water and sugar treatments, to ask if wasps were found on moist wicks more frequently under stressful environmental conditions. The difference between dry and moist wicks was significant at 35°C ($P<0.01$), but not at 25°C ($P>0.1$). There was no difference between water and sugar treatments at either 25°C or 35°C ($P>0.1$), thus wasps were more frequently found on wicks at the higher temperature because of moisture rather than sugar.

Further comparisons addressed whether wasps visited wicks more frequently at high temperatures and low relative humidities. Because of significant interactions, comparisons of temperature were made at both levels of RH, and of RH at both levels of temperature, under all three provision treatments. No comparisons of temperature or RH were significant for dry treatments ($P>0.1$), further emphasizing that wasps chose the wicks because of moisture. Under water treatments, wasps were observed on wicks more at low RH at 35°C ($P<0.01$), but not at 25°C ($P>0.1$). For wasps in sugar treatments there were no significant effects of RH at either temperature ($P>0.1$). Wasps in both water and sugar treatments were observed more frequently on wicks at 35°C than at 25°C for both high and low RH ($P<0.01$).

The proportion of observations of males on wicks differed significantly between temperatures ($P<0.0379$), and among provisions ($P<0.0002$), but not between RH treatments ($P<0.1431$) (Table 7). All interactions among these three main effects were significant. Dry treatments were compared to combined water and sugar treatments at all combinations of temperature and RH. As for females, there were no significant differences between dry and moist wicks at 25°C ($P>0.1$). Males were observed more

Table 7. ANOVA of proportion of observations in which *Eriborus terebrans* were on wicks^a in growth chambers: relative humidity and provision treatments nested within temperatures.

Source of variation	Female ^b			Male		
	df	Mean Square	P <	df	Mean Square	P <
Temperature ^c	1	2.59872	0.0022	1	1.93430	0.0379
Error a ^d	2	0.00570		2	0.07762	
Relative humidity(RH) ^e	1	0.14208	0.0148	1	0.07906	0.1431
Provision ^f	2	0.47857	0.0001	2	0.38136	0.0002
RH* Provision	2	0.01585	0.4869	2	0.19287	0.0087
Temp.*RH	1	0.17851	0.0069	1	0.11533	0.0791
Temp.*Provision	2	0.77076	0.0001	2	0.40303	0.0002
Temp.*RH*Provision	2	0.03862	0.1821	2	0.15665	0.0193
Error b	34	0.02156		33	0.03512	

^a Transformed for analysis: proportion' = $1/2[\arcsin((X/(n+1))^{1/2} + \arcsin((X+1)/(n+1))^{1/2}]$, where X=no. observations on wick, and n=total no. observations.

^b Female N=48, male N=47 (=48-1 missing values).

^c 25 and 35°C.

^d Temperature tested with error a (= temp.*growth chamber); all other factors tested with error b (=residual error).

^e High and low RH (values in Table 5).

^f Three treatments: sugar and water, only water, neither.

often on moist wicks at 35°C and low RH ($P<0.01$), but not at high RH ($P>0.1$). To confirm that males visited wicks because of moisture rather than sugar, water to sugar treatments were compared at all levels of temperature and RH; only at 35°C and low RH was there a significant difference ($P<0.01$), in which were males were on wicks more in the water than the sugar treatment.

To address whether males were more frequently on wicks under stressful environmental conditions, temperature and RH comparisons were made in each provision treatment. The effects of RH were significant only at 35°C in the water treatment ($P<0.01$), where males were on wicks more at low RH. Temperature was of greater consequence, as was the case with females; males were found more frequently on wicks at 35°C, at both low and high RH, in both the water and sugar treatments (low RH-water $P<0.01$, low RH-water $P<0.10$, high RH-water $P<0.10$, high RH-sugar $P<0.10$). There were no differences in the dry treatments, emphasizing that moisture was responsible for the observed differences in other treatments.

Greenhouse test of temperature and provision effects

Female longevity was significantly influenced by both temperature ($P<0.0007$) and provision ($P<0.0001$) treatments, and the interaction between the factors was significant ($P<0.0014$) (Table 8, Figure 15). Longevity was significantly greater at 25°C only for females in the sugar treatment ($P<0.01$). Female longevity did not differ significantly between dry and water treatments, at either 25 or 35°C ($P>0.1$). Sugar significantly enhanced longevity relative to water at 25°C ($P<0.01$), but not at 35°C ($P>0.1$).

These results are consistent with the growth chamber temperature results in that water did not enhance longevity at 25°C, but sugar did. Results of the two experiments differ in that both water and sugar enhanced longevity of females at 35°C in the growth chamber, but neither enhanced longevity at 35°C in the greenhouse. Apparently 35°C is

more stressful in the greenhouse than in the growth chamber. Also, female longevity was greater at 25°C for all provision treatments in the growth chamber, whereas in the greenhouse only sugar enhanced longevity at 25°C. This suggests that 25°C is also more stressful in the greenhouse than in the growth chamber, so unless sugar is available, female longevity is not significantly greater at 25 than at 35°C.

Results for male longevity were similar to those for females. Effects on longevity were significant for temperature ($P<0.0205$) and provision ($P<0.001$), and the interaction between temperature and provision was significant enough to be considered for multiple comparisons ($P<0.1113$) (Table 8, Figure 15). As for females, the effect of temperature was significant only for the sugar treatment ($P<0.05$), and sugar enhanced longevity only at 25°C ($P<0.05$).

Females in the greenhouse were observed more frequently on wicks at 35°C than at 25°C ($P<0.0003$) (Table 9). Provision treatments also significantly influenced the proportion of observations on wicks ($P<0.0011$), and the interaction between temperature and provisions was significant enough to warrant consideration in multiple comparisons ($P<0.0685$). To determine if moisture was responsible for wasps being on the wicks, dry wicks were compared to combined sugar and water treatments. For females there was no difference at 25°C ($P>0.1$), but they were observed less frequently on the dry wicks at 35°C ($P<0.01$). There was no difference between water and sugar treatments at either 25 or 35°C ($P>0.1$), so moisture rather than sugar is the important factor. Females were observed more frequently on wicks at 35°C than at 25°C for water treatments ($P<0.01$), and sugar treatments ($P<0.05$), but not for dry treatments ($P>0.10$).

For males also, the frequency of observations on wicks was significantly influenced by temperature ($P<0.0003$) and provision treatments ($P<0.0004$), and the interaction between temperature and provisions was significant ($P<0.0854$) (Table 9). Males were observed less frequently on the dry wicks at both 25°C ($P<0.05$), and 35°C ($P<0.01$). There was no difference between water and sugar treatments at either 25 or

Table 8. ANOVA of *Eriborus terebrans* longevity^a in greenhouses: factorial of temperature and provision treatments.

Source of variation	Female ^b			Male		
	df	Mean Square	<i>P</i> <	df	Mean Square	<i>P</i> <
Temperature ^c	1	0.73195	0.0007	1	0.38485	0.0205
Provision ^d	2	0.72570	0.0001	2	0.60994	0.0010
Temperature*Provision	2	0.43061	0.0014	2	0.14918	0.1113
Error (residual)	18	0.04423		20	0.06076	

^a Transformed for analysis: longevity' = log₁₀(longevity + 1).

^b Female N=24, male N=26.

^c 25 and 35°C; one greenhouse for each temperature.

^d Three treatments: sugar and water, only water, neither.

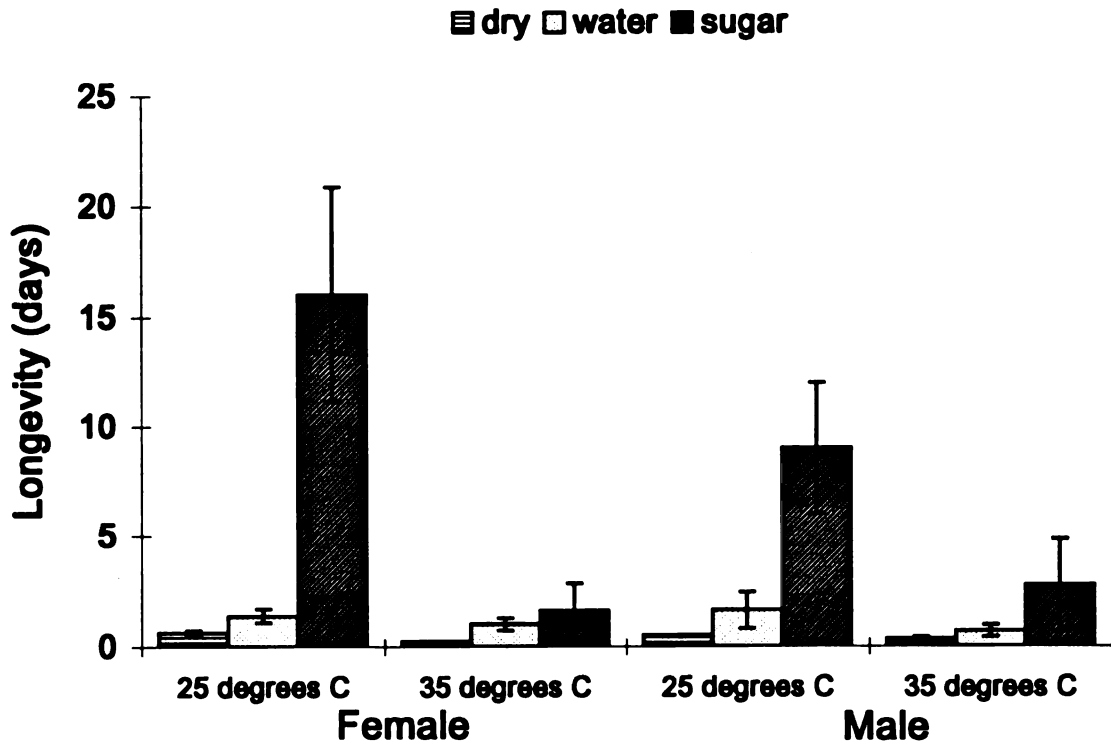


Figure 15. Mean longevity ($\pm$ standard error) of *Eriborus terebrans* in greenhouses, at two temperatures (25°C, 35°C, female $P < 0.0007$, male $P < 0.0205$), and three provision treatments (dry, water, sugar, female $P < 0.0001$, male $P < 0.0010$). $n = 4$ per treatment, except 35°C-sugar-female, 25°C-dry-male, 25°C-sugar-male, and 35°C-sugar-male $n = 5$, and 35°C-water-female, 35°C-dry-male $n = 3$.

Table 9. ANOVA of proportion of observations in which *Eriborus terebrans* were on wicks^a in greenhouses: factorial of temperature and provision treatments.

Source of variation	Female ^b			Male		
	df	Mean Square	P <	df	Mean Square	P <
Temperature ^c	1	0.96932	0.0003	1	0.86997	0.0002
Provision ^d	2	0.48557	0.0011	2	0.57053	0.0002
Temperature*Provision	2	0.15357	0.0685	2	0.11954	0.0854
Error (residual)	21	0.05027		21	0.04312	

^a Transformed for analysis: proportion' = $1/2[\arcsin((X/(n+1))^{1/2} + \arcsin((X+1)/(n+1))^{1/2}]$, where X=no. observations on wick, and n=total no. observations.

^b Female N=27, male N=27.

^c 25 and 35°C; one greenhouse for each temperature.

^d Three treatments: sugar and water, only water, neither.

35°C ($P>0.10$), so moisture rather than sugar is the determining factor. Males were observed more frequently on wicks at 35°C than at 25°C in water ($P<0.05$) and sugar treatments ($P<0.01$), but not in dry treatments ($P>0.1$).

Suitability of selected habitats

Females longevity in the early season habitat experiment increased from herbaceous vegetation, to corn field, to fencerow, to woodlot, but there were no significant differences among habitats ($P<0.1285$) (Table 10, Figure 16). The provision effect was significant ($P<0.0218$). Because there were only two provision treatments, and because there was no interaction between habitats and provisions ($P<0.6159$), it is safe to conclude sugar enhanced longevity in all habitats.

Longevity of males differed significantly among habitats ($P<0.0504$) (Table 10, Figure 17). Longevity was significantly greater in the woodlot than in the corn field ($P<0.1$) and the herbaceous vegetation ($P<0.1$). With the untransformed data (Figure 17), mean longevity was lower in the fencerow than the corn field or herbaceous vegetation, however, there was one value missing from the fencerow, from the field in which all other longevities were longest. Using the transformed values the impact of this missing value was not as great; longevity increased from herbaceous vegetation, to corn field, to fencerow, to woodlot. Sugar also enhanced the longevity of males in all habitats ($P<0.0632$). If the error term for provision is pooled with the residual error the p-value for provisions becomes $P<0.005$. Strictly speaking, the difference between the mean squared errors is too large to pool (Gill 1978), so the probability of type I error is increased, but with $P<0.005$ it is probably safe to conclude the effect of provision is significant.

The late season experiment could not be analyzed because of the number of missing values. Simply looking at the longevity data ($n=4$ in all treatments except corn-water $n=5$), longevity appears to be greater in the woodlot than the other habitats for both

Table 10. ANOVA of *Eriborus terebrans* longevity^a in the early-season habitat experiment: wasps randomly assigned to habitat and provision treatments within fields (blocks).

Source of variation	Female ^b			Male		
	df	Mean Square	P <	df	Mean Square	P <
Field	4	0.29389	0.0002	4	0.26176	0.0009
Habitat ^c	3	0.10842	0.1285	3	0.12237	0.0504
Error a ^d	12	0.04699		12	0.03516	
Provision ^e	1	0.84360	0.0218	1	0.54020	0.0632
Provision ^f	.	.	.	1	0.54020	0.0050
Error b ^g	4	0.06332		4	0.08296	
Habitat*Provision	3	0.00912	0.6159	3	0.03559	0.2290
Error c ^h	9	0.01454		9	0.02050	

^a Transformed for analysis: longevity' = log₁₀(longevity + 1).

^b Female and male N=37 (=40-3 missing values).

^c Habitats: herbaceous vegetation, corn field, wooded fencerow, woodlot.

^d =Field*Habitat: used to test habitat

^e provisions: sugar and water, or only water

^f provision tested with tested with pooled errors b and c: Mean Square=0.03972, df=13.

^g =Field*Provision: used to test provision

^h =residual error: used to test habitat*provision

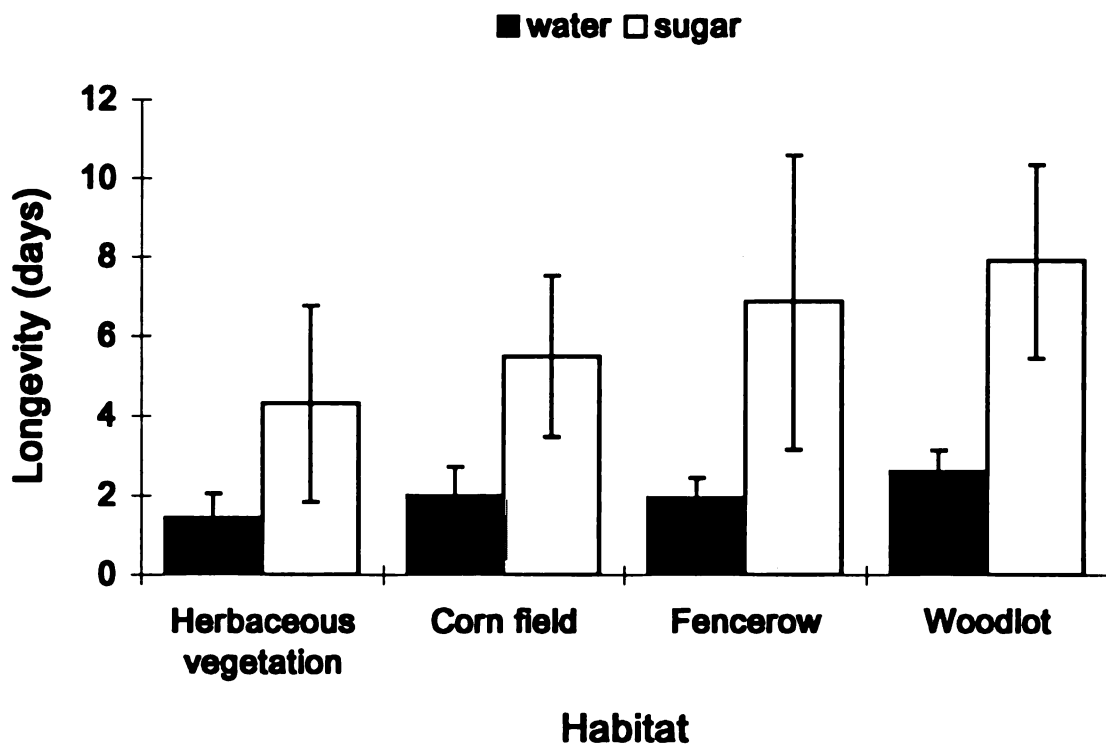


Figure 16. Mean longevity ($\pm$ standard error) of *Eriborus terebrans* females early in the growing season, in four habitats ($P < 0.1285$), with two provision treatments ($P < 0.0218$). $n=5$, except herbaceous-water, corn-sugar, and fencerow-sugar $n=4$.

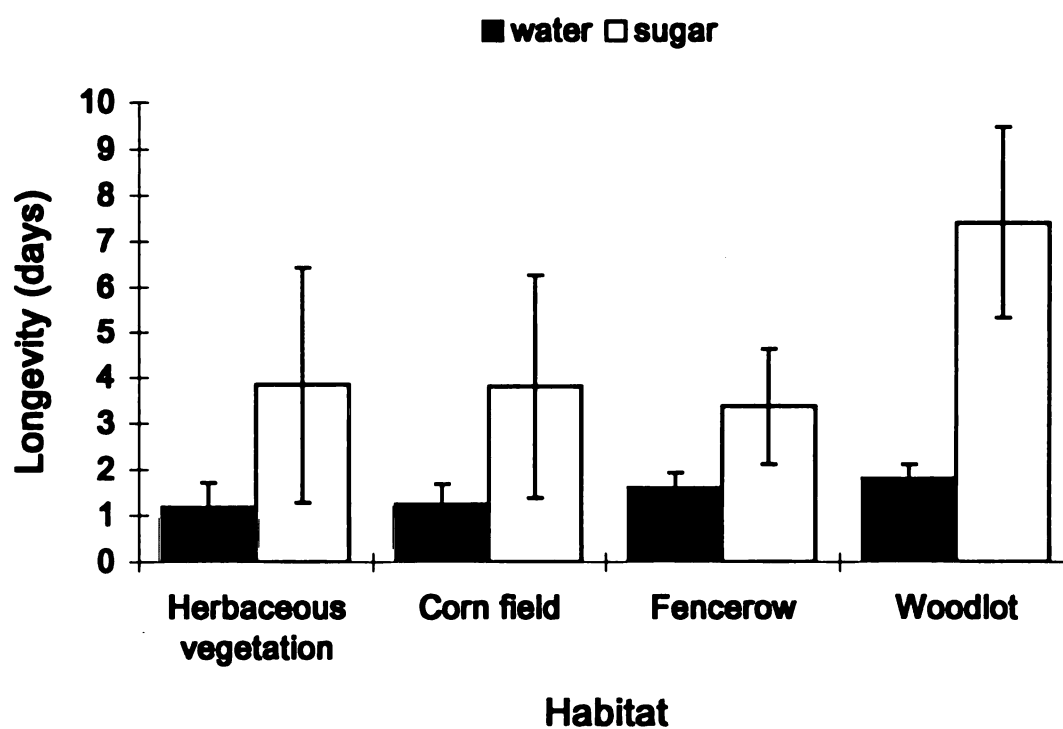


Figure 17. Mean longevity ($\pm$ standard error) of *Eriborus terebrans* males early in the growing season, in four habitats ($P < 0.0504$), with two provision treatments ($P < 0.005$). $n = 5$, except herbaceous-water, corn-sugar, and fencerow-sugar $n = 4$.

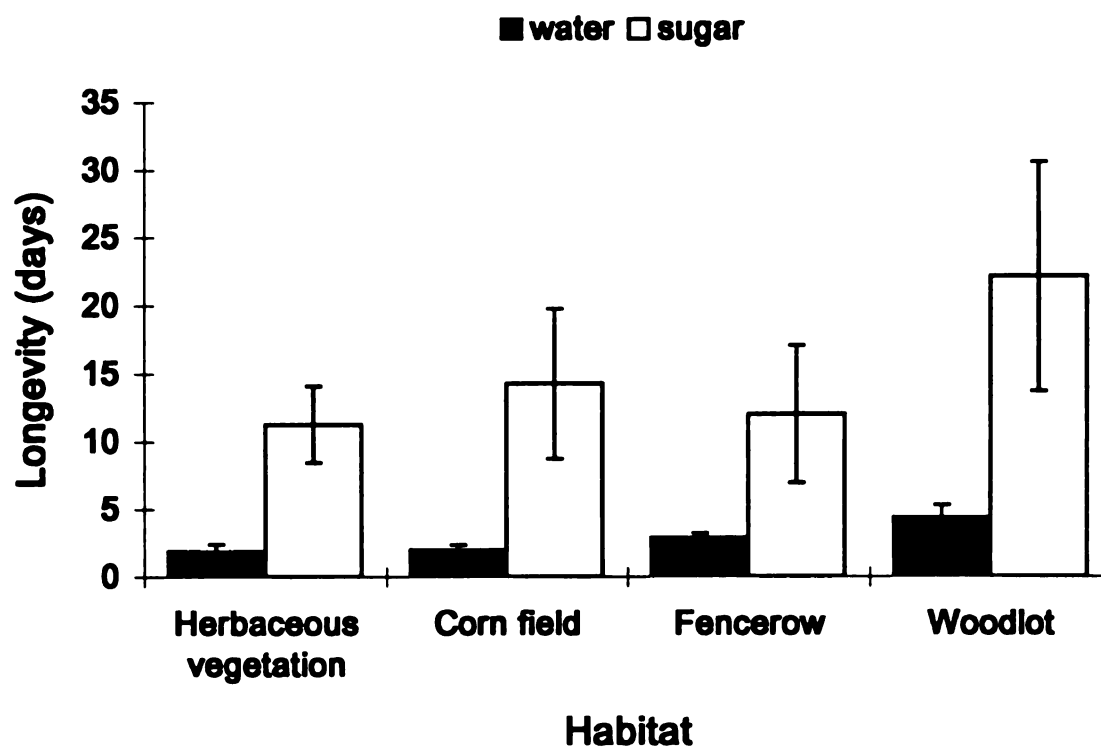


Figure 18. Mean longevity ($\pm$ standard error) of *Eriborus terebrans* females late in the growing season, in four habitats with two provision treatments. $n=4$, except corn-water $n=5$.

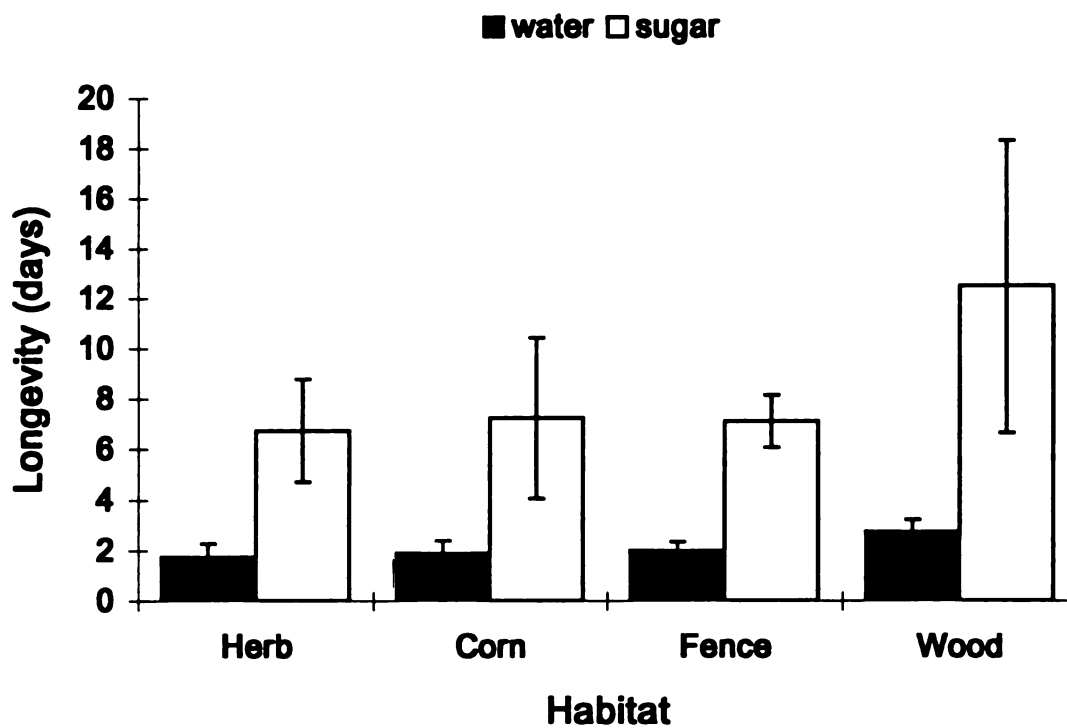


Figure 19. Mean longevity ($\pm$ standard error) of *Eriborus terebrans* males late in the growing season, in four habitats with two provision treatments. $n=4$, except corn-water $n=5$.

females (Figure 18) and males (Figure 19). It is worth noting that in all habitats longevity of was nearly three times greater for females and two times greater for males than during the early-season experiment.

Discussion

These experiments clearly demonstrate that availability of a source of sugar is an important factor affecting the longevity of *E. terebrans*. Sugar enhanced longevity of both males and females in all habitats, in both the early and late-season experiment. The prediction that water would better enable wasps to tolerate heat, but that sugar would not further enhance longevity, was found not to be true. For males in the growth chamber and both males and females in the greenhouse, neither sugar nor water enhanced longevity at 35°C, but under any circumstances where water enhanced longevity, sugar enhanced it further. Wasps benefit proportionately more from sugar at moderate temperatures, but sugar also appears to be essential to heat tolerance for *E. terebrans*.

The high temperatures used in the growth chamber and greenhouse experiments seriously reduced the longevity of *E. terebrans*. Females under all provision treatments in the growth chamber lived longer at 25°C than at 35°C. Males in the growth chamber and both males and females in the greenhouse with sugar lived longer at 25°C than at 35°C. But do these temperatures reflect anything wasps encounter in nature? Conditions in greenhouses appear to be more severe than growth chambers at the same temperatures. Conditions in the field are likely to be more so. In the greenhouse and in the field, wasps experience heat from direct solar radiation, which is probably more severe for a black-bodied insect than the warm air in the growth chamber. In addition, higher temperatures in the field and greenhouse are often accompanied by lower relative humidity, which increases the potential for water loss. Windy conditions in the field also increase desiccation potential. Daily maximum temperatures in southern Michigan seldom reach

35°C, but temperatures in the high 20's and low 30's are common, and these are probably stressful temperatures for *E. terebrans*.

Longevity data for females in the early-season habitat experiment, did not support the hypothesis that woodlots provide a more suitable microclimate than corn fields, however, they were not sufficient to solidly reject that hypothesis either. For early-season males, woodlots were more favorable habitats than either corn fields or herbaceous vegetation. Males were more sensitive to high temperature in the growth chamber and greenhouse experiments, so they may be more sensitive indicators of microclimate effects. The trend of increasing longevity from herbaceous edge, to corn field, to fencerow to woodlot was the same for males and females. It seems likely that the trend for females was a real one, but the test was not powerful enough to detect significance. These results suggest that, while microclimate in these habitats is not the only factor of importance, it probably exerts some influence on the distribution and performance of *E. terebrans* adults.

These results aid the interpretation of earlier observations, that percent parasitism of *O. nubilalis* larvae (Landis and Haas 1992), and numbers of *E. terebrans* females (Chapter 3) were greater near wooded edges of corn fields. Corn fields appear to be less suitable habitats for *E. terebrans* than woodlots, particularly if sugar sources are not available in corn fields, but are in woodlots. The microclimate may also be stressful for *E. terebrans*, but even if they are able to tolerate the microclimate, it is nearly certain that early in the growing season wasps must leave the corn field to find sugar.

Corn fields, however, are not lethal environments on a time frame of hours to a few days, therefore, *E. terebrans* is not excluded from them. Even if sugar is not available, wasps could survive for several days in the field interior, yet they were not encountered there in previous surveys (Chapter 3). There may be a behavioral component to the distribution of *E. terebrans*, in which they attempt to avoid stressful environments, causing them to leave corn fields in hot, dry weather. Observations in the

growth chamber and greenhouse studies show that *E. terebrans* will seek refuge on moist wicks at high temperatures. In greenhouse observations, when temperatures rose above 30°C wasps exhibited sustained, somewhat erratic flight, often flying directly against the sides of the cage for several seconds, as if they were trying to escape the stressful environment. At lower temperatures movement consisted of walking, and short bouts of hovering flight. In a more complete study of diurnal behavior (Chapter 5), *E. terebrans* females flew more in hot afternoons than cool ones. This could correspond to an escape behavior wasps might exhibit as temperatures rise in corn fields during the day. We can pose the hypothesis that wasps subjected to stressful temperatures in the corn field leave, and seek a more moderate microclimate in a woodlot.

Results of the late-season habitat experiment appeared to contradict the prediction that late-season corn fields would be as favorable to *E. terebrans* as woodlots, however, the longevities of wasps were greater in all habitats in the late-season experiment, than in the early-season experiment. A more favorable microclimate, combined with greater access to sugar due to increased populations of aphids and flowering weeds, would make corn fields more suitable for *E. terebrans* in the second generation. In other studies, *E. terebrans* were found throughout corn fields in the second generation, and there was no consistent relationship between field edges and the distribution of adult *E. terebrans* or parasitism (Chapter 3, Landis and Haas 1992).

During the first generation, the penetration of *E. terebrans* into the interior of corn fields appears to be limited by the lack of sugar sources, and by stressful temperatures and relative humidities in the corn field. Females probably venture into the corn field on a daily basis in search of *O. nubilalis* larvae, returning to the shelter of a woodlot during the heat of the day.

This study does not provide a clear answer to whether the microclimates provided by habitats such as woodlots and fencerows are essential for *E. terebrans*, but it suggests microclimate is an important factor, and sugar an essential one, affecting the spatial

distribution of *E. terebrans* in corn fields. During the course of the growing season the corn field habitat becomes more favorable, with increased relative humidity and decreased temperature after closure of the corn canopy, and increased populations of flowering weeds and aphids, especially the corn leaf aphid *Rhopalosiphum maidis* (Fitch), to provide sugar. But the annual agroecosystem is unable to provide those resources early in the season during the first generation of *E. terebrans*. Perennial non-crop habitats in the agricultural landscape are necessary to provide those resources. Perennial components of the agricultural landscape have the potential to provide the temporal stability to annual agricultural systems that has been lacking, and that has limited the success of biological control efforts in annual systems.

CHAPTER 5

Diurnal behavior of *Eriborus terebrans* (Gravenhorst)(Hymenoptera: Ichneumonidae), in a greenhouse

Introduction

The success of biological control agents is dependent on many behavioral attributes of the insects, such as host search, mating, and use of food resources. Understanding the behavior of beneficial insects can contribute their successful management in biological control (Luck 1990, Kareiva 1987). The behavior of parasitic Hymenoptera has been studied extensively with regard to host-finding behavior (Vet and Dicke 1992, Vinson 1976). The success of a biological control agents, however, depends on more than host-finding; beneficial insects have diverse needs, including alternate hosts, food resources, shelter, mates, and overwintering sites. Understanding aspects of parasitoid behavior in addition to host search could offer insight into how these resources are used, and may be important for developing biological control strategies. This study was undertaken to describe the diurnal behavior of *Eriborus terebrans* (Gravenhorst) (Hymenoptera: Ichneumonidae) is a parasitoid of the European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Pyralidae).

Most of what is known of the biology of *E. terebrans* was reported by Baker et al. (1949): *Eriborus terebrans* females oviposit directly into second through fourth instar *O. nubilalis* larvae, and the eggs hatch within 32 hours at 27°C and 70% relative humidity. The solitary wasp larvae remain in the first instar until their hosts are in the fifth and

final instar, then complete development of three larval instars. *Eriborus terebrans* larvae devour all but the head capsule and cuticle of their hosts, then spin cocoons of silk in which to pupate. Mating occurs shortly after emergence, usually on the first day; females generally mate only once, but males will attempt to mate throughout their life. *Eriborus terebrans* females have a very short, or no pre-oviposition period, and will search for *O. nubilalis* larvae and oviposit on the first day following eclosion. When searching for hosts, *E. terebrans* females have been shown to orient to odors from damaged corn plants, *O. nubilalis* larvae and frass (Galeota 1981, Ma et al. 1992).

Eriborus terebrans was introduced into Michigan during the 1920's and 1930's, as part of an effort to control *O. nubilalis*. *Eriborus terebrans* has two generations per year in Michigan, where its host *O. nubilalis* has two generations. The wasps overwinter as first instar larvae inside fifth instar *O. nubilalis* larvae, which diapause within tunnels in corn stalks. The development time of *E. terebrans* is nearly the same as that of *O. nubilalis* (Winnie and Chiang 1982), and they emerge in reasonable synchrony with their larval hosts in the spring, usually in late May or early June. The second generation usually begins sometime in late July.

Previous studies have demonstrated that parasitism by *E. terebrans* is higher (Landis and Haas 1992), and abundance of *E. terebrans* females is higher (Chapter 3) near wooded edges of corn fields, during the first generation. Lab and field studies demonstrated that adult *E. terebrans* are sensitive to high temperatures (35°C), and require sugar (Chapter 4); they can use aphid honeydew or plant nectar as sources of sugar (Landis and Marino in preparation). Early-season corn fields are less suitable habitats than woodlots, even with sugar provided (Chapter 3), however, this may not provide a full explanation of why few wasps are found in early-season corn fields. Though early-season corn fields, appear to be stressful environments, they are not lethal ones, at least on a scale of hours. *Eriborus terebrans* females could survive in field interiors for at least several days. Even on days when temperatures in corn fields rise to

stressful levels, females could be active during cooler hours, yet few were encountered in field interiors in previous studies (Chapter 3). The hypothesis is proposed that *E. terebrans* exhibits a behavioral response to stressful temperatures before they become lethal, and leave the stressful environment, seeking the shelter of a woodlot.

This greenhouse study was conducted to characterize the diurnal behavior of *E. terebrans* under semi-natural conditions. Temperature variation within the observation arenas was exploited to test the hypothesis that *E. terebrans* exhibits greater movement in response to high temperatures.

Methods

Individual wasps were observed hourly from 0600 until 1900 hours, for three consecutive days. Observations spanned a three week period; one cohort, consisting of 6 females and 6 males was observed during each week, for a total of 18 females and 18 males. Three additional observations were made during the night (1 November at 2400, 2 November at 2100, and 17 November at 0300 hours). During this period, from 1 November to 17 November 1994, sunrise ranged from 0712 to 0733 hours, and sunset ranged from 1731 to 1714 hours.

Greenhouse temperature was maintained between 18 and 27°C. Mean temperature in the cages varied through the day (hourly mean $\pm$ standard error) from 20.34°C $\pm$ 0.13 to 26.47°C $\pm$ 0.55. Over the course of the study, temperatures in the cages ranged from 18.25 to 36.5°C; high temperatures in the cages were due to sunlight.

Six observation cages each housed one female and one male. Cages were cylindrical (diameter=30 cm, height=106.5 cm), with sides of transparent plastic, top of black nylon tulle, and bottom of plywood. A hole in the cage bottom held a pot containing three corn plants, approximately 40-60 cm in height. Corn plants were infested with 10-20 second instar *O. nubilalis* larvae per plant. No subsequent effort was made to assess the level of infestation, but all plants used had *O. nubilalis* larvae and

feeding damage. Each cage was provided a moist dental wick soaked in sugar water (1:1:1 ratio, by weight of fructose, dextrose and sucrose), and a wick moistened with distilled water. Wicks were kept continually moist by being inserted in an 8 dram vial of distilled water, with 3 cm of wick available to the wasps. Wicks were changed each evening after observations had ended.

Wasps were from a colony initiated from *O. nubilalis* larvae collected on 30 September, and 5 and 14 October, 1993, in St. Joseph Co., Michigan. Adult *E. terebrans* emerged between 30 December 1993, and 14 March 1994, and subsequent generations were reared in the laboratory on *O. nubilalis*. Generation time is approximately 4 weeks, so by the beginning of the experiment the colony had been in the laboratory 8-12 generations.

All individuals were from one to three days old, and were unmated at the beginning of observations. Wasp pupae were held individually in one ounce cups, with agar in the bottom to maintain moisture, and cups were checked daily. As wasps emerged they were transferred to individual cages with access to water and moistened honey. On the evening before observation, one male and one female were placed in separate petri dishes in each observation cage. The following morning, one hour (h) before observation, the petri dish was opened. At this hour wasps were inactive, and in all but a few cases did not move when the petri dish was opened. Those that were disturbed quickly settled, and remained quiet until it became light.

Each cage was observed, in randomized order, every hour, for 13 h. In each cage, the female was observed first for three minutes (min), then the male for 3 min. Their behaviors were described as belonging to 13 categories (Table 11). A one-zero recording method was used (Martin and Bateson 1993); each 3 min observation period was divided into 15 second (s) intervals, and each behavior was recorded that occurred at least once, during each 15 s interval. The resulting measurement for each behavior was the proportion of all behaviors recorded during the 3 min observation. This recording

Table 11. Categories of behaviors recorded during observation, abbreviations used in the text and figures, and a description of the behaviors.

Inactive Rest	Ri	Posture prostrate, abdomen, head and thorax may be touching the substrate; antennae held low, near or touching the substrate, and close together, with little movement.
Rest	R	Resting that cannot be clearly placed in Ri or Ra; the sole purpose of this category was to better define the other two categories of rest, and was not used for analysis. It was often transitional between Ri and Ra.
Active Rest	Ra	Posture with head and thorax elevated; antennae up, apart and moving. A pause in other behaviors of greater than 2 seconds was required to be categorized as rest.
Preening	Pr	Cleaning or rubbing of antennae, legs, wings or body.
Circling	Cir	Several turning steps, often making a complete circle, or a few halting forward steps traveling less than 2 cm.
Walking	W	Walking
Flying	F	Flying
Drinking	Dr	Drinking at the water wick, or chewing on other surfaces of the plant or cage.
Sugar feeding	H	Drinking on the sugar wick.
Search	Cur	Antennating the surface with antennae curled so the dorsal surface of the antennae touch the surface.
Probing	Prb	Probing with the ovipositor.
Wing fanning	WF	Wing fanning by males during courtship.
Other		Undefined behaviors
		Copulation was recorded whenever it was observed, whether or not it was during a timed observation.
		Oviposition was recorded if the female could be directly observed to oviposit into an <i>O. nubilalis</i> larva.

method was chosen because it was more feasible than continuous recording, and it compared more favorably to continuous recording than did instantaneous sampling in preliminary observations. When wasps are active they shift rapidly among behaviors such as walking, flying, or preening. Because shifts among behaviors are rapid, wasps are difficult to follow with continuous recording methods, such as filming or voice recording, and because each behavioral event is brief, instantaneous sampling misses most of them. One-zero sampling is more appropriate for this sort of intermittent behavior (Martin and Bateson 1993), and has been shown to correlate well with frequency and duration (Leger 1977, Rhine and Linville 1980) of some types of behavior. Temperatures were also recorded each hour from thermometers in each cage, with bulbs placed at 10 and 70 cm above the floor of the cage.

During the study two males had to be replaced due to injuries, one in the second week, and one in the third week. In both cases they were replaced with a male from the same cohort in the evening after the first day's observations. One wasp died during the experiment, a male, in the afternoon on the last day of week three, which resulted in 5 missing values. Total missing values due to death, observer error, or an inability to locate wasps, were 7 for females (approximately 1% of the 702 observations), and 14 (approximately 2%) for males. Missing values were estimated using a formula from Zar (1984).

Behaviors chosen for analysis were inactive rest, combined walking and flying, and for females, combined searching and probing. Inactive rest was chosen because it was the single behavior in which wasps spent the most time (Figures 20 and 21). Walking and flying were chosen to indicate patterns of the highest level of activity, and searching and probing were selected because of their particular importance for *E. terebrans* as a biological control agent. These proportions were transformed for analysis using an arcsine transformation recommended by Zar (1984) for data with many very

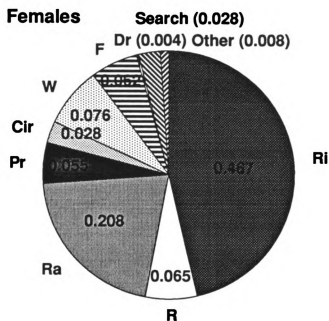


Figure 20. Proportions of total observed behaviors, for *E. terebrans* females. Numbers are proportions for the corresponding behavior. Abbreviations are defined in Table 11. Dr here includes both drinking and sugar-feeding. Other = copulation + oviposition + other undefined behaviors.

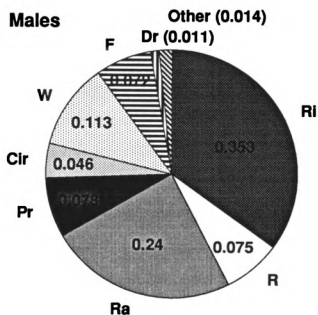


Figure 21. Proportions of total observed behaviors, for *E. terebrans* males. Numbers are proportions for the corresponding behavior. Abbreviations are defined in Table 11. Dr here includes both drinking and sugar-feeding. Other = courtship + copulation + other undefined behaviors.

small or very large proportions (proportion' = $1/2[\arcsin((X/(n+1))^{1/2} + \arcsin((X+1)/(n+1))^{1/2}]$, where X=no. observations on wick, and n=total no. observations). Females and males were analyzed separately. For ease of interpretation figures are presented as means of the proportions, rather than the transformed values.

Analyses were done with repeated measurements analysis of variance (SAS Institute 1988), with days and hours as repeated measurements, for a total of 39 measurements (3 d x 13 h) on each subject. The use of univariate analysis of variance to test the within-subject effects of day and hour requires the assumption of compound symmetry of the variance-covariance matrix (Gill 1986, Horton et al. 1991), which is tested by Mauchly's criterion (test for sphericity) (SAS Institute 1988). If this assumption is not met, the F critical values can be adjusted using the Huynh-Feldt Epsilon (H-F), or the more conservative Greenhouse-Geisser Epsilon (G-G), and the univariate tests may still be used. Results of the sphericity tests are presented for all analyses, and adjusted F critical values are indicated where they are employed. The more conservative G-G F value is used wherever it demonstrates significant differences. Where the G-G and H-F values yield different results they are both reported. If the assumption of sphericity is severely violated ($P \leq 0.0001$), the univariate tests should be interpreted cautiously, and multivariate tests for repeated measurements (Wilks' Lambda, Pillai's Trace, Hotelling-Lawley Trace, Roy's Greatest Root) may be used more appropriately (SAS Institute 1988).

Contrasts among days and among hours were made with transformation options in the SAS repeated measurement procedure. For days, the profile transformation, was used to contrast day 1 to day 2, and day 2 to day 3. For hours the means transformation was used to compare the value for each hour to the mean for hours. The SAS means option omits one comparison. For all the behaviors presented here the 1800 hour comparison was omitted, but in all cases the value for 1800 hours was nearly identical to that of 0600 hours, so its significance could be inferred from that of 0600 hours.

Specific contrasts of walking and flying at particular hours on particular days were done with Scheffe's multiple contrasts, to test the hypothesis that *E. terebrans* exhibits escape behavior in response to high temperatures. Though greenhouse temperatures were controlled, on sunny days direct radiation caused elevated temperatures in the cages. When temperatures in the cages were high wasps appeared to walk and fly more, often a sustained flight directly into the clear plastic side of the cage, in what could be interpreted as an attempt to escape from a stressful environment. With these measurements there was no way to distinguish walking and flying that might be escape behavior, from that which could be searching behavior by an unstressed wasp; however, walking and flying at different times of the day might indicate different types of behavior. Certain hours in the afternoon (1300-1500) were selected for contrasts because walking and flying at these hours, averaged over all days and weeks did not differ significantly from the mean, but on some days these hours were sunny and hot, and on other days they were more overcast and cool. Walking and flying on cool days versus hot days were contrasted at those selected hours. Scheffe's contrasts were used because the choice of contrasts was influenced by the data (Gill 1986); contrasts were selected after seeing the pattern of variation around the mean for afternoon hours. These contrasts were done using a standard error of the difference between means as an error term, derived from the mean squared errors for days and the day by hour interaction, and an associated estimated error degrees of freedom (Gill 1986, and Gill personal communication).

Other behaviors of interest occurred less frequently, making the data unsuitable for repeated measurements analysis of variance. Drinking or feeding, feeding at the sugar wick, courtship by males, and copulation were scored if they were observed during each hour, and the values of all 18 subjects, were summed for each hour of each day.

Results

Inactive rest accounted for a greater proportion of both female and male behavior than any other category (Figures 20 and 21). If all active behaviors were combined, including active rest and preening, in which wasps did not travel, but still appeared to be actively monitoring their environment, females were active for 46.9%, and males for 57.4% of the time. If the three categories of rest and preening were combined, wasps spent the great majority of their time stationary (females = 79.5%, male = 74.6%). Search for hosts accounted for only 2.8% of female activity.

The data for female inactive rest differed significantly from the assumption of compound symmetry of variance-covariance matrix (sphericity test) for both days ($P < 0.0089$) and hours ($P < 0.0077$). There was no difference in inactive rest among days ((G-G $P < 0.19$), though there was a numerical decline over the three days (Figure 22). There were significant differences among hours (G-G $P < 0.0001$). Looking at the means contrasts, values for inactive rest were significantly above the mean at 0600, significantly below the mean from 0800 through 1100, rising above the mean at 1300, falling again below the mean at 1500, and finally rising above the mean at 1700 and 1800 hours (Figure 23, all P values < 0.05).

For male inactive rest, the assumption of sphericity was not rejected for days ($P < 0.5578$), but was rejected for hours ($P < 0.0002$). Differences among days were only marginally significant ($P < 0.07$); contrasts showed no difference between days 1 and 2, but a marginally significant difference between days 2 and 3 ($P < 0.0969$), though there was a numerical decrease each day (Figure 24). As for females, differences among hours were significantly different (G-G $P < 0.0001$). Given the strong rejection of the sphericity test for hours it is also advisable to look at the multivariate tests for hours; all the tests provided by the SAS procedure were consistent with the G-G adjusted univariate results (P values < 0.0001). Hour contrasts were similar to those for females, with values significantly above the mean at 0600, below the mean during the morning hours of

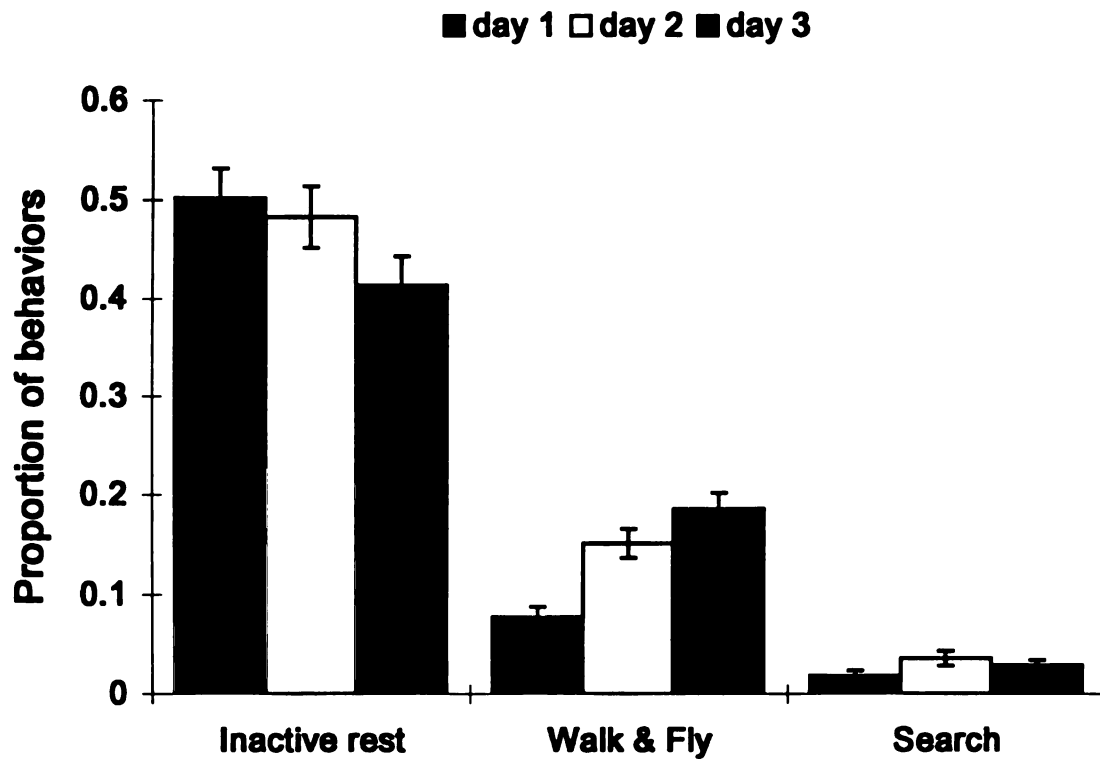


Figure 22. Day means for *E. terebrans* females, for inactive rest ($P<0.19$), combined walking and flying ($P<0.001$), and search for *O. nubilalis* larvae ($P<0.359$).

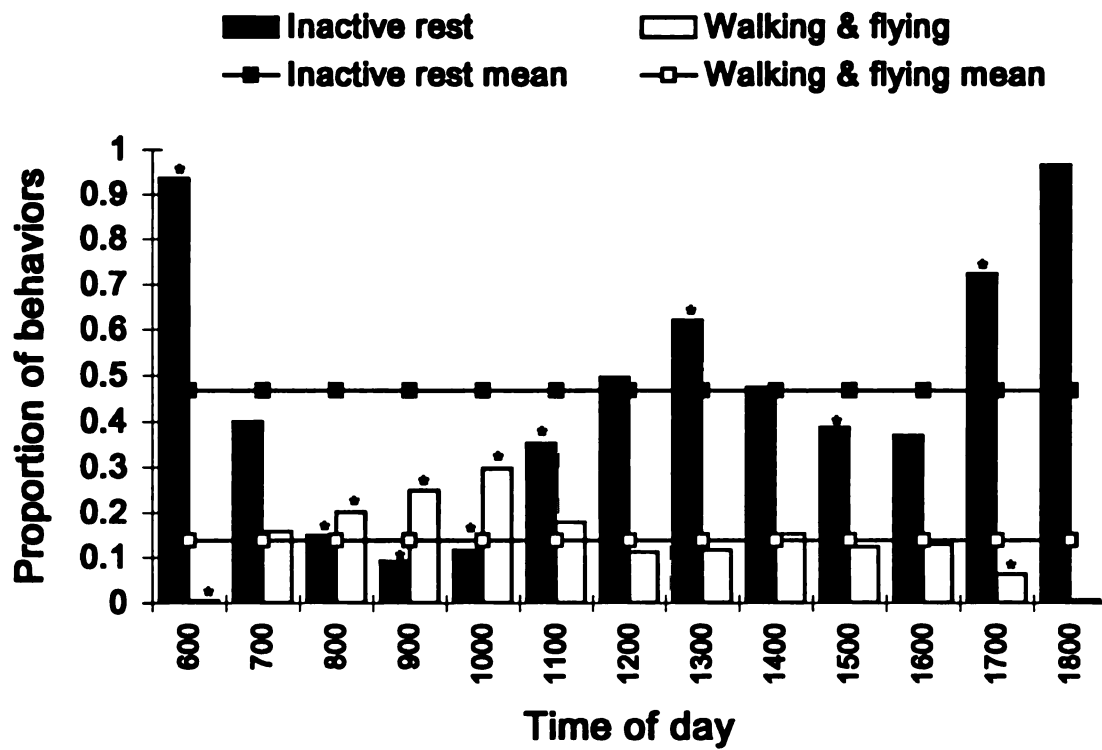


Figure 23. Hour means for *E. terebrans* females, for inactive rest ($P < 0.0001$), and combined walking and flying ($P < 0.0001$). Asterisks indicate an hour mean is significantly different from the overall mean ($P < 0.05$).

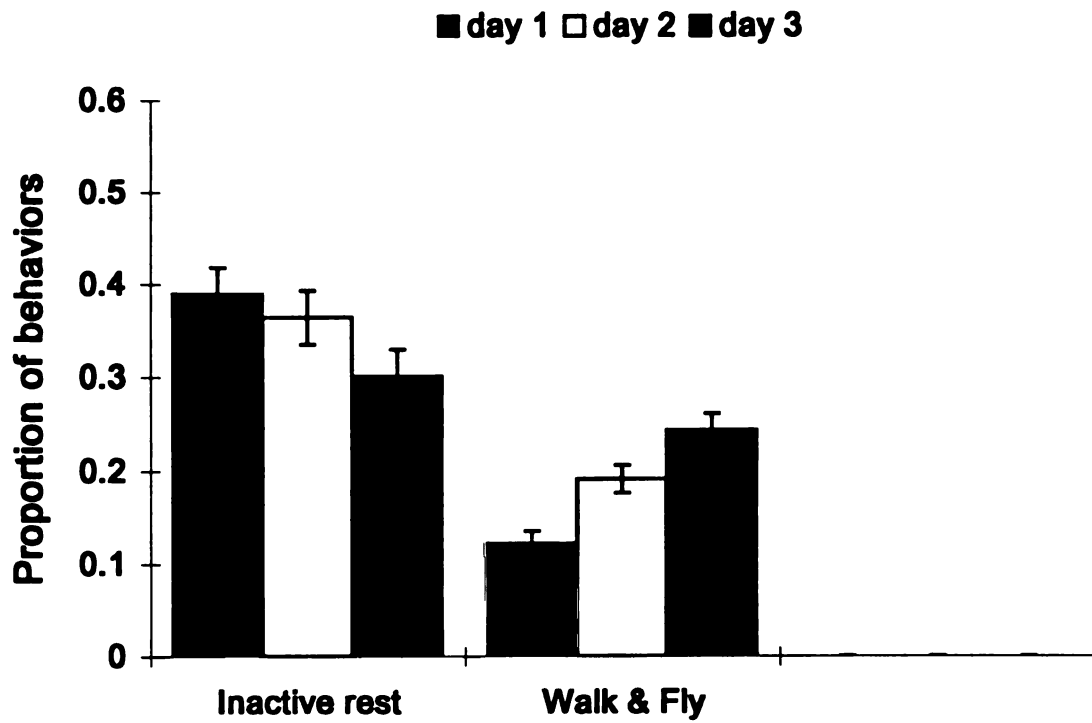


Figure 24. Day means for *E. terebrans* males, for inactive rest ($P<0.07$), and combined walking and flying ($P<0.0001$).

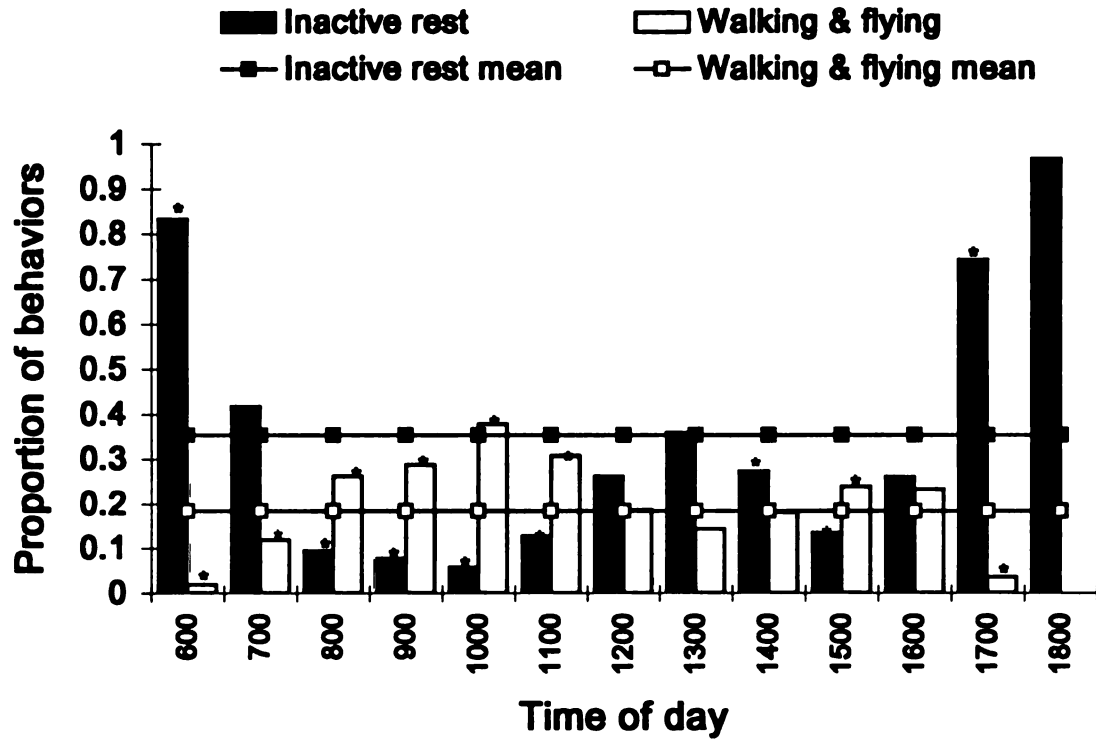


Figure 25. Hour means for *E. terebrans* males, for inactive rest ($P < 0.0001$), and combined walking and flying ($P < 0.0001$). Asterisks indicate an hour mean is significantly different from the overall mean ($P < 0.05$).

0800-1100, generally not different from the mean during the afternoon, but dipping below the mean during 1400 and 1500 then rising above the mean at 1700 and 1800 hours (Figure 25, P values <0.05).

Observations (15 females and 15 males) confirmed that wasps remained inactive during the night. In only one of those observations did a wasp move, when a female made a circling motion and preened briefly. She may have been disturbed by the red light used to observe at night. On 18 occasions the locations were recorded for both males and females, to determine if they changed their location between observations, from evening to morning, evening to nighttime, or nighttime to morning. In 15 of 18 observations for females, and 10 of 18 for males, they had not moved since the previous observation. When they had changed location, it was a distance of several to 20 cm, except for once each for males and females when the movement was 30–40 cm. Once wasps settle into inactive rest in the evening, it appears they remain inactive with very little movement until daybreak.

For female walking and flying, the test for sphericity was not rejected for days ($P<0.088$), but was rejected for hours ($P<0.0152$). There was a significant difference among days ($P<0.001$), and for hours (G-G $P<0.0001$). Walking and flying was greater on day 2 than day 1 ($P<0.0007$), but not significantly different between days 2 and 3 (Figure 22). Walking and flying was significantly below the mean during the first and last hours of the day (0600, 1700 and 1800), significantly above the mean during 0800, 0900, and 1000 hours (P values <0.05), and marginally so during 1100 hours ($P<0.0703$) (Figure 23).

The male pattern of walking and flying differed only slightly from that of females. The test for sphericity was not rejected for days ($P<0.2483$), but was rejected for hours ($P<0.0113$). Walking and flying differed among days ($P<0.0001$); day 2 was higher than day 1 ($P<0.0007$), but unlike females, day 3 was also higher than day 2 ($P<0.0047$) (Figure 24). Walking and flying also differed among hours (G--G

$P < 0.0001$). Values were below the mean for hours 0600 and 0700, above the mean for 0800 through 1100, above the mean as well at 1500, and below the mean at 1700 and 1800 (P values < 0.05) (Figure 25).

For females, the day by hour interaction was significant (G-G $P < 0.0234$), and the day by hour by week interaction was marginally significant (G-G $P < 0.1045$, H-F $P < 0.0237$). For males the day by hour interaction was marginally significant (G-G $P < 0.1481$, H-F $P < 0.0633$), and the hour by week interaction was significant (G-G $P < 0.0157$). These significant interaction terms warrant an investigation of particular day by hour contrasts.

In general walking and flying was greatest during the morning. During the afternoon, hourly means for walking and flying did not differ from the overall mean, however, the significant day by hour interactions suggested particular day by hour combinations might differ. Elevated temperatures tended to occur during the afternoon. In week one, temperatures were higher on day two than day three; in week two, temperatures were higher on day three than day two; and in week three, temperatures were very similar on days two and three. Day one was not considered because there was significantly less walking and flying than on days two and three. Combined values of 1300, 1400, and 1500 hours for days two and three of each week were contrasted, to test the hypothesis that wasps would walk and fly more in response to elevated temperatures. For males, there was no significant relationship between temperature and walking and flying. For females, the contrast was not significant in week three ($P > 0.75$) when temperatures were very similar; the contrast in week one was not significant ($P < 0.5$), but in week two there was significantly more walking and flying on day three, the hotter day ($P < 0.025$) (Figure 26). If the hot days of weeks one and two were combined (week one-day two + week two-day three) and contrasted with the cool days of those weeks (week one-day three + week two-day two), there was significantly more walking and flying on the hot days ($P < 0.05$).

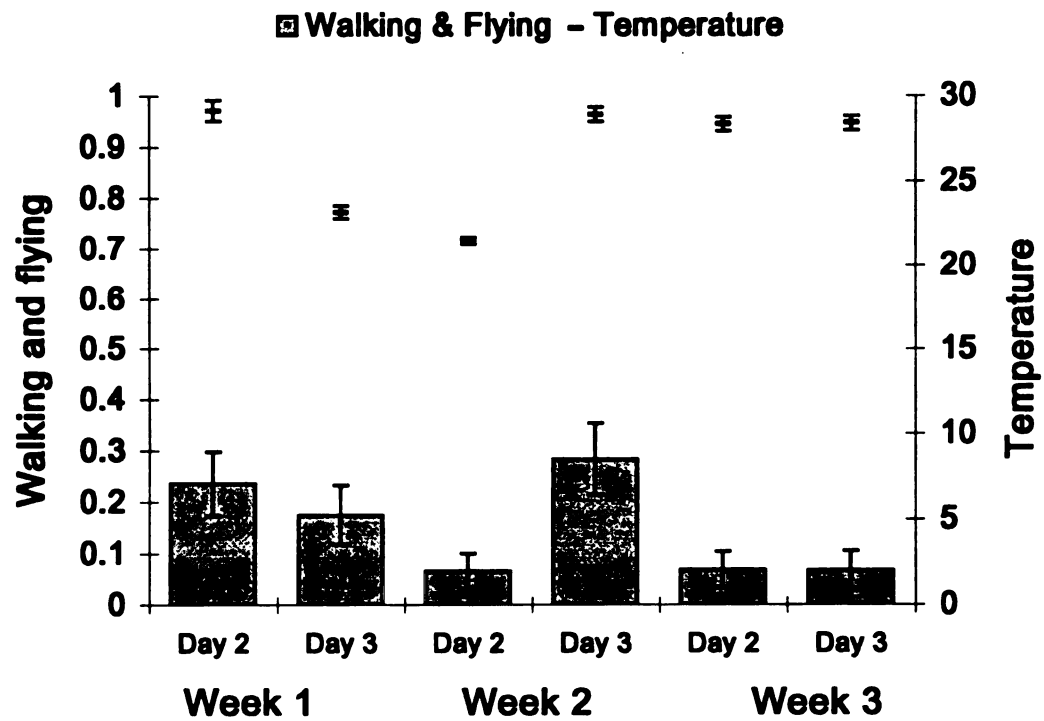


Figure 26. Contrasts between days 2 and 3 of each week (1300, 1400, and 1500 hours combined), for walking and flying by *E. terebrans* females: week one $P < 0.5$, week two $P < 0.025$, and week three $P > 0.75$.

Searching and probing by females did not differ among days (Figure 22). The univariate analyses for hours must be interpreted with caution, because the test for sphericity was rejected at a level of $P < 0.00001$. The univariate tests showed significant differences among hours (G-G $P < 0.0026$, H-F $P < 0.0002$), though the multivariate tests showed less striking results ($P < 0.1098$). The hour contrasts demonstrated a pattern similar to that for walking and flying (Figure 27). There was significantly less searching and probing in the morning (0600, $P < 0.0011$) and evening hours (1700, $p < 0.0009$, and 1800, presumed significant by inference from a value even lower than that of 0600 hours), higher levels at 0800 ($P < 0.0561$) and 0900 hours ($P < 0.0138$), then values throughout the day that did not differ from the mean, except for 1400 hours, when the value was below the mean ($P < 0.0003$). Females were clearly seen to oviposit into larvae only three times: day one at 1600 hours, day two at 1000 hours, and day three at 1000 hours.

Wasps were seen to drink or chew on a variety of surfaces, including the plant, soil, plywood floor of the cage, and even the cage surface, in addition to the water wicks and honey wicks provided. All of these values were combined, referred to as "drinking", and plotted (Figure 28). Females were not observed to drink during the first day of observations in any week, and most drinking and sugar feeding occurred on the third day. Males were observed to drink twice on the first day, three times on the second day, and as for females were mostly observed to drink on the third day.

Four of the seven copulations that were recorded occurred on the first day, two on the second, and one on the third. All copulation occurred before noon. Male wing-fanning and attempted copulation occurred throughout the day, on all three days.

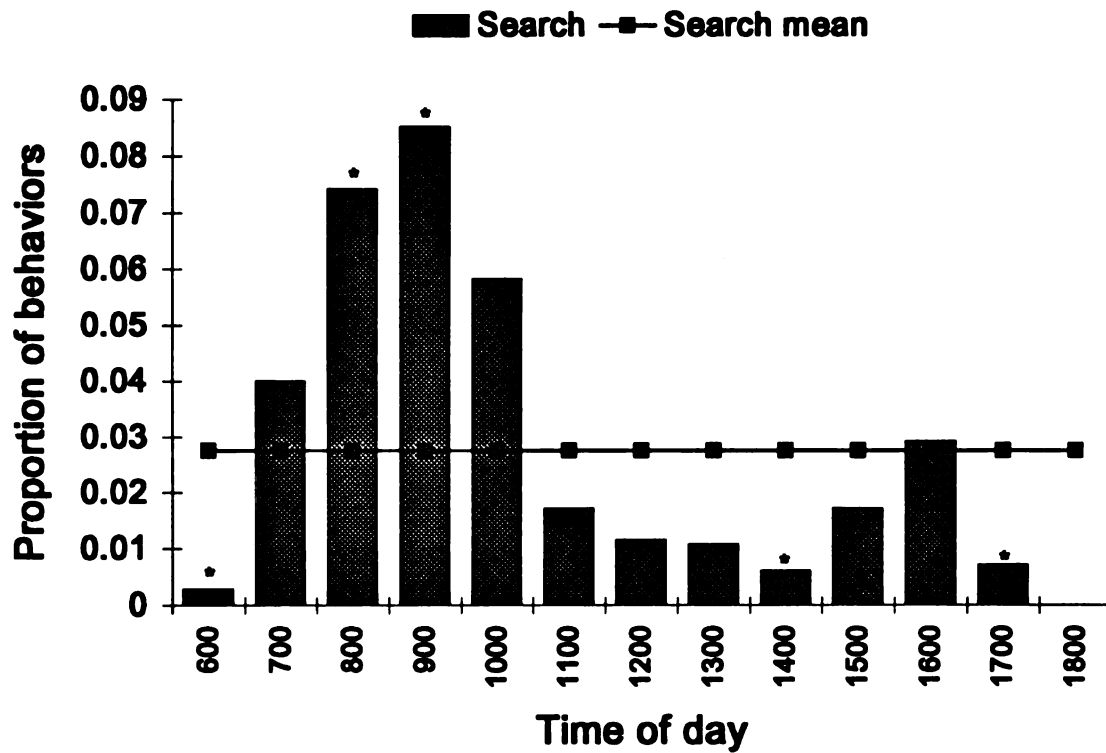


Figure 27. Hour means of search for *O. nubilalis* larvae by *E. terebrans* females ($P < 0.1098$). Asterisks indicate an hour mean is significantly different from the overall mean ($P < 0.05$).

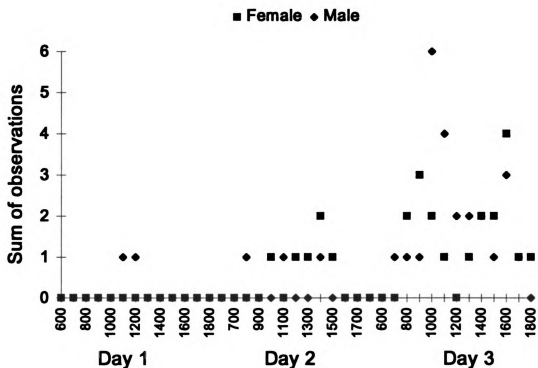


Figure 28. Drinking by *E. terebrans* females and males: drinking from water wick, sugar wick, plant and cage surfaces combined.

Discussion

Eriborus terebrans behavior followed clear and consistent daily patterns in this experiment. From late afternoon until early morning wasps remain in inactive rest, moving very little during the night. The highest levels of activity, for most behaviors measured were in the morning. During the afternoon, measurements of inactive rest, walking and flying, and searching and probing all hovered around the mean. Differences among days were not as pronounced, but several points are worth noting. Walking and flying activity increased after the first day for both females and males, and again after the second day for males; inactive rest showed a corresponding decrease over the three days, though not significantly. Searching and probing for larvae was expected to increase with time, as females gained experience, but this was not observed. Many parasitic Hymenoptera have the ability to learn and respond to cues associated with successful oviposition (Vet and Dicke 1992, Vinson 1976), and *E. terebrans* has been shown to respond to odors of *O. nubilalis* larvae, frass, and damaged plants (Galeota 1981, Ma et al. 1992). This ability to learn from experience did not result in increased activity with time in these observations. This arena, in which wasps presumably were continuously surrounded by the stimulus of these odors may not be as apt for demonstrating learning and experience as a more natural setting where wasps move among environments, some of which have stimuli and some of which do not.

The use of sugar and water resources increased in the second and third days. This may correspond to increased movement in the second and third days that enabled them to find the resources, or it may simply be that they were initially satiated, and it took a day or two for them to get hungry or thirsty. Because it was not feasible to begin with all newly emerged wasps on the same day, and it was important that the wasps all be in the same, unstressed condition at the start of observation, it was necessary to hold wasps for one or two days with provisions prior to observation. Newly emerged wasps in nature might behave differently. On the other hand, newly emerged *E. terebrans* have an

enlarged abdomen that shrinks during the first few days, so they may have adequate reserves to delay feeding (Dyer, personal observation).

Eriborus terebrans females are thought, in general to mate only once, though males will attempt to mate multiple times (Baker et al. 1949). Four of seven copulations observed in this study were on the first day, three of those during the 0800 hour observations. This suggests mating usually takes place early in life for females, though one copulation was observed on day three. Mating has been observed in older wasps in our lab colony (2-3 weeks old in one instance and at least 5 weeks old in another), so some mating and probably remating can occur among older wasps, though the crowded conditions of the lab colony are a poor model for what is likely to happen in nature. Copulation was seen in only seven of eighteen pairs, however mating may have occurred unobserved in others. None were observed to copulate more than once.

Temperature in the cages varied throughout the day, largely due to direct sunlight striking the cages, so wasps experienced diurnal patterns of temperature directly related to diurnal patterns of sunlight. The behavioral and physiological mechanisms underlying diurnal patterns of behavior may be in response to daily patterns in either temperature or sunlight, but the two phenomena are so closely linked in nature, that wasps probably respond to a combination of the two.

The range of temperatures experienced by wasps made it possible to address a hypothesis raised by previous studies, that *E. terebrans* move more in response to high temperatures, in an attempt to escape a stressful environment. The contrasts of hot and cool days should not be considered a definitive test of the hypothesis, but they do offer some insight into the question. The contrast between the combined cool days, and the combined hot days of weeks one and two was significant for females, confirming the relationship between temperature and walking and flying. But when days 2 and 3 of each week were contrasted separately the pattern was more variable. Scheffe's tests are more powerful for the more complex contrasts (Gill personal communication), so the more

variable results of the separate contrasts may be largely due to a lack of statistical power. However, the variation in results among different contrasts may also be instructive. *Eriborus terebrans* response to stressful temperatures may not be as simple as getting up and flying. An alternative behavior may be to seek refuge. Previous studies in growth chambers and greenhouse showed that in high temperatures wasps sought the refuge of a moist wick (Chapter 4). As temperatures rise they may first seek refuge locally, then later attempt to escape that environment as conditions worsen. Alternatively, seeking refuge may simply be an artifact of the cage environment. Wasps in cages may soon learn they can't escape the stressful environment, then seek shelter. Yet another consideration is the physiological state of the insect, which may influence its decision to abide stressful conditions or try to escape. When days in week one were contrasted separately from days in week two, the contrast was significant only in week two. Day two was the hot day in week one, whereas day three was the hot day in week two. Observations of drinking and sugar feeding indicate that by day three the wasps were actively seeking water and sugar. A physiological state of thirst or hunger may make the environment seem more inhospitable, and make them more inclined to attempt escape.

Based on the results of this and previous studies (Chapters 3 and 4) we can draw a picture of how *E. terebrans* is likely to behave in an agricultural landscape. When *E. terebrans* emerge in the spring, they find themselves in a field of corn stubble and very small plants of corn or some other crop. Even if they emerge in a second-year corn field they are likely to leave the field interior, because they would find no sugar sources in that field at that time of year, and on a hot day they would find little shelter. Females may begin to search for *O. nubilalis* larvae on the same day they emerge. By the time the corn field gets hot, or by early afternoon on a cool day, wasps probably fly to a woodlot canopy. In June when first-generation *E. terebrans* emerge, woodlots are in full leaf, so there is adequate shelter, and probably sugar sources, such as homopteran honeydew and dripping sap from torn leaves and broken branches, and flowering plants along the woods

edge. Flowering in the woodlot itself is mostly past by that time of year. They may also find mates in the woodlot. Males appear not to venture far from the woodlot, especially when it is hot, and males appear not to disperse as readily as females from the field in which they emerge. On a daily basis, females probably spend most of the afternoon and night resting in the canopy of the woodlot, in the morning they search for *O. nubilalis* larvae, then in the afternoon, or before the corn field gets too hot, they return to the shelter of the woodlot. On cool days they may remain in the corn field to rest if sugar is available. On the other hand, in addition to seeking a favorable microclimate, they may have a preference for taller vegetation as a resting site. The vertical structure of a late-season corn field may suffice in the second generation.

In the second generation *E. terebrans* are more inclined to remain in the corn field. By that time the corn canopy has closed, creating a more humid, and somewhat cooler microclimate. Probably more importantly, populations of the corn leaf aphid, *Rhopalosiphum maidis* (Fitch) (Homoptera: Aphidae), other aphid species on weeds, and some flowering weeds will have increased in the corn field, providing sources of sugar. Even if it is still hot in the corn field during the second generation, wasps with adequate access to sugar may be less inclined to leave. A female's daily pattern of activity probably remains very similar to the first generation, searching most actively during the morning, then resting during most of the afternoon and night; they are more likely to rest in the corn canopy than during the first generation. With females remaining in the corn field, males appear to fly along the top of the corn canopy searching for them (Chapter 3).

There were insufficient observations of drinking and sugar feeding to give a clear picture of when they engage in those activities. That is unfortunate, because it is of interest for purposes of habitat management for biological control to know if they drink and feed most when they are otherwise most active, or if those behaviors occur at different times of the day. In nature, behaviors such as searching for larvae and

searching for food and water could be partitioned, both by different habitats and different times of the day. The answer to that question could make the difference between management decisions to, for example, provide strips of nectar-producing flowers along the borders of a crop field where a parasitoid might go to rest and feed, or plant them in the same field where the parasitoid would search for hosts. Wildflowers that provide nectar and pollen have been shown to enhance the performance of parasitoids (Leius 1963, 1967, van Emden 1963, Foster and Ruesink 1984). Landis and Marino (in press) have demonstrated enhanced longevity of *E. terebrans* females given access to common lambsquarters, *Chenopodium album*, infested with aphids, and several flowers, especially wild carrot, *Daucus carota*. *Chenopodium album* is a common weed in corn fields, whereas *D. carota* is commonly found along field edges, though it is also common in no-till corn fields. Studies presented in chapter 4 demonstrate that sugar is essential for *E. terebrans*, so maintenance of habitat to provide sources of sugar must be a basic element of a conservation program for *E. terebrans*, and probably many other natural enemies.

An important lesson of this study for conservation of natural enemies is the amount of time *E. terebrans* spends in rest. With so much time spent resting, providing a habitat with adequate shelter is an important consideration in habitat management. Shelter has been demonstrated to enhance numbers of ground dwelling beetles (Dennis and Fry 1993, Speight and Lawton 1976). While much attention has been paid to host search, and to the importance of adult food resource availability, the importance of shelter, and favorable microclimate should be borne in mind as well.

Adequate shelter and adult food resources in most cases cannot be provided in the crop environment itself, early in the growing season. Perennial ecosystems adjacent to crop fields can make these resources available while the crop is developing. The temporal stability of perennial systems allows them to develop adequate structure to provide a cool moist microclimate, and allows for the maintenance of populations of

organisms that provide resources for beneficial insects. The proximity of such ecosystems to agricultural fields may well prove essential to the successful conservation of natural enemies.

CHAPTER 6

Summary and conclusions

Biological control is both a crop management process involving the decisions and actions of humans, and an ecological process involving the relationships between pests, their natural enemies, and other components of the agricultural ecosystem. The nature of the relationship between human management and ecological processes differs greatly in different approaches to biological control. In augmentative release of natural enemies, direct human management of the ecological process is fundamental to successful biological control; pest populations are monitored, and populations of natural enemies are augmented, either through inoculative or inundative releases, when pests are determined to be at an action threshold. In importation and conservation biological control, human intervention into the population dynamics of pests and their natural enemies is less direct. Rather, the strategy is to create an environment in which resident populations of natural enemies are able to maintain pest populations below economic injury levels. This preventive approach to pest control requires less knowledge of immediate conditions of pest populations on which to base management decisions, but it requires more knowledge of the needs of natural enemies, so favorable habitat can be provided. The research presented here was undertaken to provide a fuller understanding of the biology of *E. terebrans*. These results illustrate the importance of perennial habitat adjacent to crop fields to provide for the needs of *E. terebrans*, and offer insight into factors of importance for successful conservation of natural enemies.

Eriborus terebrans was introduced into Michigan as part of an effort to control the European corn borer, *Ostrinia nubilalis* (Baker et al. 1949). There has been no further management of *E. terebrans* since its release, but it is currently the primary parasitoid of *O. nubilalis* in Michigan (Landis and Haas 1992). Levels of parasitism of *O. nubilalis* by *E. terebrans* vary widely among fields. In 1989 and 1990, parasitism ranged from 1.4 to 37.4% in corn fields in Michigan (Landis and Haas 1992) and in 1991 and 1992 parasitism ranged from 2.5 to 44.7% (Chapter 3). Infestation of corn fields in Michigan by *O. nubilalis* is also highly variable. Between 1988 and 1992, *O. nubilalis* caused widespread economic damage only in 1991, was scarcely reported in 1992, and caused economic damage in relatively few fields in 1988 through 1990 (D. A. Landis, personal communication). The variable nature of *O. nubilalis* infestation suggests that natural controls work during most years, in most fields to control *O. nubilalis* populations. Weather is among the most important natural controls, but it is clearly beyond our ability to manage. Natural controls, however, also include predators, parasitoids and pathogens, and these can be managed. The range of percent parasitism by *E. terebrans* indicates conditions are variable for natural enemies. Creation of stable environmental conditions could result in more stable relationships between pests and their natural enemies, and increase the effectiveness of biological control.

Variable conditions for natural enemies may be a consequence of the nature of resource availability in highly disturbed, annual agricultural ecosystems. Resources sought by natural enemies include, food, shelter, favorable microclimates, overwintering sites, mates, and alternate hosts (van den Bosch and Telford 1964, Stehr 1975). In annual agricultural systems, the species composition and the ecosystem structure must develop anew each year. Many resources are not available in these ecosystems until the crop canopy has fully developed, and many resources are simply unavailable in such highly disturbed ecosystems.

Perennial agricultural systems have had more biological control successes than annual ones (Batra 1982, Stehr 1975), which may, in part be due to differences in the disturbance regimes. Perennial systems also tend to have greater species diversity and structural diversity than annual systems. The species diversity, and to some extent the structural diversity of annual agricultural systems can be increased by practices such as intercropping, and the use of covercrops. However, species diversity alone will not ensure the success of biological control, or the stability of relationships between pests and their natural enemies; of greater importance is the establishment of certain species interactions (van Emden and Williams 1974). The species diversity of agricultural systems can, to some extent be managed to facilitate particular species interactions. However, the temporal stability of the ecosystem must be a critical factor in allowing stable interactions to develop between species.

Temporal stability may be provided in annual agricultural systems by the inclusion of perennial ecosystems in association with crop fields. Many natural enemies are mobile enough to use different habitats during different times of the day, different times during the growing season, or different stages of their life cycle. Natural enemies may seek essential resources outside the crop fields, especially early in the season, prior to development of the crop canopy. Perennial non-crop ecosystems can provide those resources reliably and predictably.

The distribution of *E. terebrans* in corn fields is clearly influenced by adjacent non-crop habitats (Chapter 3). During the first generations of 1991 and 1992, in all seven fields where wasps were captured, more female *E. terebrans* were captured near edges of corn fields adjacent to woodlots, than in the field interiors. In two of four fields in 1992, more wasps were also captured near herbaceous edges than in field interiors. In the second generations of both years, there was no consistent pattern of distribution within fields, but wasps were found throughout corn fields. Apparently conditions in the corn field changed from the first generation to the second, such that female *E. terebrans*

were restricted to edges during the first generation, but were in the field interior during the second generation.

Conditions in the corn field change during the season as the corn canopy develops, such that a mature corn field can provide a favorable microclimate. Simultaneously, populations of aphids and flowering weeds increase, providing sources of sugar as well. Those resources are unavailable in the corn field early in the season, and wasps must depend on perennial habitats adjacent to corn fields, where resources are available as soon as foliage develops in the canopy. In the first generation of 1992, *E. terebrans* females apparently used resources in herbaceous vegetation adjacent to corn fields, as well as woodlots. Nineteen-ninety-two was a cooler year than 1991. Sugar sources were probably available in both herbaceous and woody habitats, but when temperatures were hot wasps may have been forced to seek the cooler microclimate of the woodlot.

The distribution of male *E. terebrans* was probably influenced by the same factors as that of females, and by the distribution of females itself. Males were not encountered in corn fields in the first generation of 1991. They were, however, captured in the first generation of 1992, mostly near wooded edges. In the second generation, males were captured mostly in traps placed at the top of the corn canopy, but not in the traps at ground level; presumably males were flying at the top of the corn canopy searching for females that remained in the corn field. The difference between the first-generation patterns of 1991 and 1992, as for females, is probably related to temperature differences. In 1991 females probably entered corn fields only to search for larvae during cooler morning hours, then returned to woodlots during the heat of the day. In 1992, when temperatures were cooler females may have remained in the corn fields, drawing males into the fields in search of mates.

Many resources and environmental conditions could influence the success of biological control agents, and their distribution in the landscape. Sources of sugar and

microclimate were proposed as the principal factors influencing the observed distribution of *E. terebrans*. The importance of sugar and temperature for *E. terebrans* were investigated in growth chamber and greenhouse studies (Chapter 4). Wasps were caged at 25 and 35°C, and provided with sugar and water, water, or neither. At 25°C in the growth chamber, both sugar and water enhanced longevity relative to dry treatments. Sugar further enhanced longevity of females 14 times, and of males 5 times relative to those given only water. Similarly, at 25°C in the greenhouse, longevity was enhanced 12 times for females and 6 times for males, provided with sugar. The availability of water enhanced the longevity of females at 35°C in the growth chamber, and sugar enhanced it further. Under greenhouse conditions, neither water nor sugar enhanced the longevity of females or males at 35°C.

Resource availability determines the suitability of a habitat for an organism. The suitability of habitats in the agricultural landscape for *E. terebrans* was tested by caging wasps in corn fields, woodlots, herbaceous vegetation, and wooded fencerows (Chapter 4). In all habitats wasps were provided water, or sugar and water. Experiments were run early in the season and late in the season to correspond to the first and second generations of *E. terebrans*. Sugar enhanced the longevity of both males and females in all habitats, both early and late in the season. Early in the season, longevity of females increased from herbaceous vegetation, to corn field, to wooded fencerow, to woodlot, though differences among the habitats were not significant. Longevity of males early in the season was significantly greater in the woodlot than in the herbaceous vegetation or corn field. In growth chamber and greenhouse studies, males were more sensitive to high temperatures than females, therefore males may be more sensitive indicators of significant habitat differences than females. It is likely the trend in female longevities among habitats is real, but the test was not powerful enough to detect significance.

In the late-season experiment, both female and male longevity was greater in the woodlot than in other habitats, though these data could not be analyzed due to missing

values. It is important to note that longevities of both females and males were greater in all habitats in the late-season experiment, than in the early-season experiment; longevity of females in the late-season corn field was nearly three times, and of males nearly two times greater than in the early-season corn field.

Habitats in the agricultural landscape differ in the resources they provide for natural enemies, and a highly mobile insect like *E. terebrans* uses different habitats for different purposes. In the first generation, *E. terebrans* females must search corn fields to find hosts, but they must use different habitats to find other resources, such as sugar, shelter, and a favorable microclimate. The behavior of individuals determines how resources are utilized. Knowledge of behavior patterns would offer insight into the ways resource availability could influence the performance of natural enemies.

The behavior of *E. terebrans* was observed in a greenhouse from before sunrise until after sunset, for three consecutive days (Chapter 5). Wasps were housed in cages provided with sugar, water, and a corn plant infested with *O. nubilalis* larvae. Each cage housed one pair of wasps. Greenhouse temperatures were controlled between 18 and 27°C, though temperatures in the cages ranged from 18 to 37°C, due to direct sunlight warming the cages. Each wasp was observed for three minutes during each hour.

The single behavior that accounted for the greatest proportion of observed behaviors was inactive rest (46.7% for females, 35.3% for males). All categories of rest combined accounted for 74.0% of female behavior and 66.8% of male behavior. Walking was 7.6% of female, and 11.3% of male behavior, and flying was 6.2% of female, and 7.2% of male behavior. Other behaviors of inherently great importance, such as drinking water and sugar water, searching for *O. nubilalis* larvae, courtship, and mating, constituted very small proportions of observed behaviors. Perhaps the most insightful lesson of these observations is the great proportion of time spent resting by *E. terebrans*. If rest occupies such a large part of a wasps day, it is crucial they have habitat with adequate shelter and suitable microclimate in which to rest.

Diurnal patterns of behavior were similar for females and males. From late evening until early morning wasps rested with little or no movement. In the first hours after sunrise, inactive rest decreased and walking and flying increased. Most search for *O. nubilalis* larvae also occurred during the morning. Throughout the afternoon activity levels were moderate; hourly values for inactive rest and walking and flying generally did not differ significantly from the hour mean. However, contrasts between specific days showed that females walked and flew more on afternoons when cages were hot. This flight was a sustained, rapid flight, often directly into the side of the cage, as opposed to a slower, hovering flight around the corn plant, which they were more likely to do in the morning.

This flight response to increased temperatures could be interpreted as an attempt to escape a stressful environment, and can be considered in light of observations from previous studies. Early-season corn fields are less suitable habitats for *E. terebrans* than woodlots because of a paucity of sugar sources, and to a lesser extent because of a less favorable microclimate. Nevertheless, *E. terebrans* females can survive for several days in early-season corn fields, even when provided only with water. Though the corn field is not a lethal habitat for *E. terebrans*, it is a stressful one. Presumably during cool morning hours female *E. terebrans* venture into corn fields in search of *O. nubilalis* larvae, but during the heat of the day they sense the stressful conditions of the corn field and return to the shelter of the woodlot. Thus, female *E. terebrans* infrequently penetrate deep into the field interior in the first generation, but are more commonly encountered near edges of corn fields adjacent to woodlots.

From the results of the studies presented here, supplemented with a bit of conjecture, we can draw a picture of how *E. terebrans* perform in the agricultural landscape of Michigan. *Eriborus terebrans* emerge from corn stubble in late May or early June, and find themselves in an environment of bare soil and very small crop plants. They must move to habitats adjacent to crop fields to find shelter, water, sugar,

and mates. It is possible *E. terebrans* use the tall, contrasting profile of the woodlot as a cue to locate these resources. Mating usually occurs early in life, probably before wasps disperse from the field in which they emerge. Males generally do not disperse from that field, but remain, waiting to mate with emerging females.

Females must find their host habitat. If they emerged in a field that was planted again to corn they may stay, otherwise they disperse to new fields. Corn plants at that time of year are small, and provide little of the resources needed by *E. terebrans*. So in addition to finding their host habitat, wasps must find a habitat that provides for their other needs. It is unknown if *E. terebrans* use adjacent woodlots as cues for selecting corn fields, but it would be worthwhile to test the prediction that corn fields with adjacent woodlots have higher populations of first-generation *E. terebrans* than those without.

Eriborus terebrans females are able to oviposit very shortly after emergence, so they begin to seek *O. nubilalis* larvae as soon as they are available. On a daily basis, females seek larvae during the cool morning hours. On a sunny June day, a corn field can be a hot, dry, windy environment. During the heat of the day females take refuge in the woodlot canopy, and rest, or look for sources of sugar and water during the afternoon. They spend the night resting in the foliage of the canopy. On a cool day they may remain in the corn field to rest.

Even on a cool day, wasps are unlikely to find sugar sources in the early-season corn field. Sometime during the day they must drink and find sugar. It has not been determined if *E. terebrans* drink or feed preferentially at a particular time of the day, but they probably consume sugar whenever they encounter it. A feeding bout of only a few minutes may be all that is necessary each day. They most likely drink water in the mornings; dew is a reliable source of water, even in relatively dry weather. But they are probably also opportunistic about water, and drink whenever they find it and are in need.

Eriborus terebrans females continue to oviposit throughout their life. The eggs hatch shortly after oviposition, and the wasp larva remains in the first instar until its host is in the fifth instar (Baker et al. 1949). The wasp larva then devours its host, and spins a cocoon of silk in which to pupate.

Emergence of second-generation *E. terebrans* begins in late July. The second generations of *E. terebrans* and *O. nubilalis* have been reported to be less synchronous than the first (Winnie and Chiang 1982). However, *E. terebrans* females live longer in the second generation (Chapter 4), which may compensate for less synchronous emergence.

Second-generation *E. terebrans* females may disperse from the field where they emerge, or not. It is not necessary to disperse to find their host habitat, however, fields that had high populations of first-generation *O. nubilalis* often have lower second-generation populations. This is because first-generation *O. nubilalis* females seek the largest plants, so fields planted early are often more heavily infested; second-generation *O. nubilalis* seek tasseling plants for oviposition, which are more likely to be in fields planted later (Showers et al. 1989). It is not clear that the density of *O. nubilalis* infestation exerts any influence on habitat selection, or population density of *E. terebrans* females.

The daily routine of second-generation *E. terebrans* females should be very similar to that of the first generation; females search for *O. nubilalis* larvae in the morning, and rest in the afternoon. An important difference is, it is not necessary for wasps to leave the corn field to find shelter, water, and sugar. Therefore, *E. terebrans* are not restricted to edges, and are found throughout the corn field. Females that remain in the corn field emit pheromone to call males to mate. Consequently, males fly at the top of the corn canopy searching for mates. At the end of the second generation, *E. terebrans* larvae enter diapause with their host larvae, and overwinter in tunnels in corn stalks.

This story of *E. terebrans* in Michigan offers insight into some important considerations for biological control by conservation of natural enemies. The most important lesson is that many resources required by natural enemies cannot be provided by the annual crop ecosystem, especially early in the growing season. More resources become available as the crop develops, but in the case of *E. terebrans* this is too late to benefit the first generation. Conditions are likely to be similar for other parasitoids and predators, and grassy edges and hedges have been shown to facilitate the colonization of crop fields by predaceous arthropods (Dennis and Fry 1992, Wratten and Thomas 1990). The needs of pest insects may be met largely by the crop plant, whereas predators are more likely to have additional needs that must be provided by other components of the crop ecosystem, or by neighboring habitats (Price 1974). The delay in availability of resources prevents predators from colonizing the crop ecosystem, and allows pest populations to increase. If additional necessary resources were available in adjacent habitats, natural enemies might be able to search crop fields for prey early in the season.

For habitats to provide the necessary resources early in the season, they must be perennial ecosystems. The vertical structure necessary to create a moderate microclimate and provide shelter must be established, and populations of animals and plants that provide other resources must be present early in the spring. The limitation of annual systems is that these features must develop, and species must colonize each year. Perennial ecosystems may be remnants of native ecosystems, such as forests or wetlands, they may be highly managed systems like hedges, orchards or plantations, or they could be systems designed and managed specifically for agronomic purposes, including soil conservation and biological control of pests.

Another lesson of these studies of *E. terebrans*, is that we should not depend on one control agent for control of a pest. Environmental conditions are variable, and no one predator or parasitoid should be expected to perform well under all conditions. A suite of natural enemies seems more likely to provide control under diverse weather

conditions. Diverse natural enemies, including generalists and specialists that attack different life history stages of a pest are more likely to give more complete control. Furthermore, agricultural systems have various pests that must be controlled simultaneously, that will require a diverse assemblage of natural enemies for their control.

The complexity of this pest and natural enemy assemblage may seem overwhelming to manage. If pest control depends upon carefully timed actions based on detailed monitoring of pest and natural enemy populations, and weather conditions, management may indeed be impractical under most circumstances. A more hopeful prospect is the design of agricultural ecosystems in which pest management is an ecosystem function, performed by members of the ecological community. Plants and animals that reside in the agricultural ecosystem respond phenologically to the same seasonal cues; the timing of pest and natural enemy emergence, and resource availability, that could only be accomplished with great difficulty by human managers, could reliably result from evolved qualities of organisms in the agricultural ecosystem. Control of some major pests may occasionally require more disruptive techniques, such as augmentation of natural enemy populations, or judicious use of pesticides; however, long-term pest control may be more effectively achieved by creating ecosystems where stable ecological relationships can be established and sustained.

Indigenous natural enemies in agricultural ecosystems may have provided a largely unrecognized service to agriculture through the years. It has been recognized that unmanaged natural enemies have provided the service of controlling minor and potential pests (DeBach and Rosen 1991). As field sizes increase and perennial ecosystems are removed from the landscape, those benefits are lost. If biological control has had few successes in annual agriculture, it may be largely due to the loss of ecosystem diversity in the agricultural landscape.

Our concept of the farming system should be expanded to include non-crop perennial ecosystems. Biological control by conservation of natural enemies is a preventive approach to pest management, and could be the primary pest management strategy in an ecologically based agriculture. Maintenance and management of perennial habitat adjacent to crop fields will be an essential component of conservation of natural enemies.

APPENDIX

APPENDIX 1

Record of Deposition of Voucher Specimens*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: 1995-2

Title of thesis or dissertation (or other research projects):

**Non-crop habitats and the conservation of *Eriborus terebrans* (Gravenhorst)
(Hymenoptera: Ichneumonidae), a parasitoid of the European corn borer, *Ostrinia
nubilalis* (Hübner) (Lepidoptera: Pyralidae)**

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums:

Investigator's Name (s) (typed)
Lawrence E. Dyer

Date April 21, 1995

*Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America. Bull. Entomol. Soc. Amer. 24:141-42.

Deposit as follows:

Original: Include as Appendix 1 in ribbon copy of thesis or dissertation.

Copies: Included as Appendix 1 in copies of thesis or dissertation.
Museum(s) files.
Research project files.

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

132
APPENDIX 1.1

Voucher Specimen Data
Page 1 of 2 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of:							Museum where deposited
		Eggs	Larvae	Nymphs	Pupae	Adults ♂	Adults ♀	Other	
<i>Eriborus terebrans</i> (Gravenhorst) (Hymenoptera: Ichneumonidae)	MI: Ingham Co. T.2N, R.1E, Section 3, SW 1/4 Malaise trap in corn, 20m from woodlot 13 June 1991 30 July 1991					1	6		MSU
	MI: Ingham Co., Michigan State University Lab Culture Source: MI, St. Joseph Co., field-collected larvae in corn, 30 Sep, 5 Oct, 14 Oct, 1995 28 January 1995 29 January 1995					7			MSU
							1		MSU
							3		MSU

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Lawrence E. Dyer

Date April 21, 1995

Voucher No. 1995-2

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

 Date 21 April 1995

Curator

133
APPENDIX 1.1

Voucher Specimen Data

Page 2 of 2 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of:							Museum where deposited
		Eggs	Larvae	Nymphs	Pupae	Adults ♂	Adults ♀	Other	
<i>Ostrinia nubilalis</i> (Hübner) (Lepidoptera: Pyralidae)	MI: Ingham Co. T.2N, R.1E, Section 3, SW 1/4 Malaise trap in corn, 20m from woodlot 8 June 1991						1		MSU
	MI: Ingham Co. T.2N, R.1E, Section 15, NE 1/4 Malaise trap in corn, 20m from woodlot 12 June 1991					1	2		MSU
	MI: Ingham Co., MSU Lab Culture Source: MN, French Agricultural Research Inc., 20 August, 1991 21 October, 1994 27 October, 1994					4	2		MSU
							2		MSU

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

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[Signature] 21 Apr 95

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