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## **Predation behavior of spiders (Arachnida: Araneae) in Massachusetts cranberry bog ecosystems.**

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PREDATION BEHAVIOR OF SPIDERS (ARACHNIDA: ARANEAE) IN  
MASSACHUSETTS CRANBERRY BOG ECOSYSTEMS

A Thesis Presented

by

CAROLYN J. BARDWELL

Submitted to the Graduate School of the  
University of Massachusetts Amherst in partial fulfillment  
of the requirements for the degree of

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Department of Entomology

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MASSACHUSETTS CRANBERRY BOG ECOSYSTEMS

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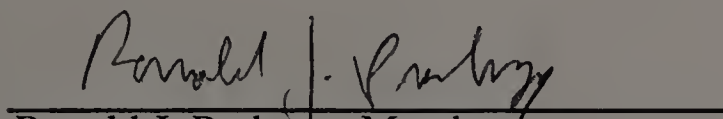
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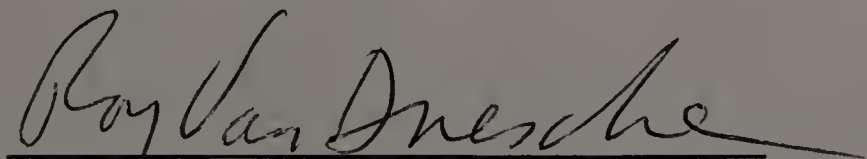
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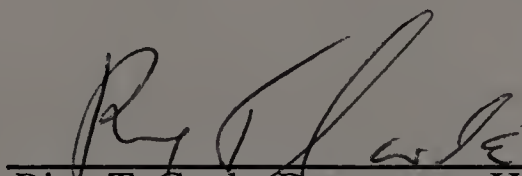
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## DEDICATION

This work is dedicated to my parents, Barbara & Frederick, who have been supportive throughout all of my “educational pursuits”, Vincent, who always encouraged and believed in me, and Jessica, whose energy and dedication are behind every page.



## ACKNOWLEDGMENTS

I am very grateful to the many people who have contributed their time, effort, and friendship during the years I have worked toward the completion of this thesis. My sincerest thanks to Anne, for providing me with the opportunity to pursue my research goals and her endless understanding, support and guidance as both advisor and confidant throughout my graduate career. She has always been, and will continue to be, an inspiration to me. Many thanks to Jessica for her eternally positive attitude that made all of our travels to and from the dunes of the Cape productive and full of laughter and also to Marty, the spice that made life in and out of the lab always entertaining, and who kept everything (and everyone) running efficiently during the summer field seasons. Special thanks go out to my family, whose continual support and love have been an essential part of the whole process.

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# CHAPTER I

## INTRODUCTION

### Spider Biology

Spiders (Arachnida: Araneae) are common constituents of virtually every terrestrial, and occasionally aquatic, ecosystem around the globe. Classified as generalist predators, most spiders feed on a wide variety of the arthropod fauna present in their environment (Nyffeler et al. 1994; Kaston 1981). Their invertebrate diet is not strictly limited to insects, however. Spiders at high population densities frequently engage in cannibalism (Hallander 1970; Edgar 1969) and a few large-bodied species have been documented with small vertebrate prey as well (Wise 1993).

Although the assortment of potential prey available to a foraging spider may be quite diverse in some habitats, prey size and defense combined with the degree of hunger, sex/reproductive status, and hunting behavior of a spider may influence what is ultimately consumed. Many spiders select prey that are 50-80% of their own length (Nentwig & Wissel 1986) and may discriminate against prey with physical or behavioral defenses (see Chapter III). Mate-finding behaviors in male spiders and the presence of an egg case attached to the abdomen of lycosid females has been shown to negatively influence predation as well (Moring & Stewart 1992; Workman 1979; Jackson 1977). In addition, laboratory studies have indicated that conspecific males and females have inherently different levels of satiation (Givens 1978; Horner 1972).

Spiders are separated into two fundamental types, hunters and web-builders, according to the foraging strategy they use to acquire prey. Web-builders use silk to fashion devices for ensnaring prey, the design of which varies with the species of the maker. Hunters do not build a web but instead rely on quickness to capture and overcome their quarry.

There are one-hundred and five families of spiders described worldwide (Platnick 1993), twenty-eight of which are found in the northeastern United States (Kaston 1981). A review article on the faunal surveys of spiders conducted in economically valuable crops commonly grown in the U.S., namely grain sorghum, guar, peanuts, rice, sugarcane, corn, alfalfa, cotton, and soybean, reported that representatives from 26 families were collected over the entire spectrum of habitats (Young & Edwards 1990). In addition, species of hunting spiders were often more common in the nine crop systems than web-builders, a difference attributed to the hunters' greater ability to adapt to physical disturbances in their immediate environment and rapidly recolonize from unaltered adjacent habitats.

#### Applicability of Spiders for Biological Control

Over twenty years have passed since Riechert (1974) proposed that the ecological significance of spiders as generalist predators is to **stabilize** rather than control invertebrate communities, particularly during the intervals between pest population increases and the delayed development of a more specific contingent of predators. Because of their long generation times and nonspecific feeding behavior, a contingent of spiders are often present during all stages of pest population development and consume most types of prey frequently encountered in the habitat. However, unlike specialist predators and parasitoids, whose fluctuating populations mirror changes in the density of a pest population, spider populations do not normally respond to variations in pest abundance (Riechert & Lockley 1984). This limitation in their effectiveness is a consequence of the annual life cycle and reproductive constraints of most spiders. Spider populations are also strongly self-limited by intraspecific competition (territoriality) for foraging/web-building sites, cannibalism, and migration, all of which occur when densities exceed a particular population threshold determined by the spider species/assemblage present in a given habitat (Riechert & Lockley 1984). Regardless, spiders have recently become a subject of interest to many researchers interested in



controlling pest insects using complexes of biological control agents because of their dominant presence as predators in most habitats, particularly agroecosystems.

Several investigators have assessed the impact individual species and/or assemblages of spiders may have on economically-important insect pest populations (see Nyffeler & Benz 1987 for review). Young & Lockley (1985) compiled a review article presenting, among other biological information, data on the importance and predatory significance of the striped lynx spider, Oxyopes salticus Hentz (Oxyopidae) in agroecosystems worldwide. Because of its abundance in many habitats and reported consumption of key pest species, this species of hunting spider is concluded to hold promise as a useful biological control agent, although long-term, quantitative field studies are reported lacking.

Spiders contained in cloth bags with pest insects on tree branches, were reported to be effective in reducing the amount of foliar/fruit damage done by the giant looper Boarmia selenaria Schiff in avocado orchards and also prevented scale insect pest populations from increasing to economically-damaging levels in citrus groves (Mansour et al. 1985; Mansour & Whitecomb 1986). In another confinement study conducted in rice fields, a species of hunting spider, Pardosa ramulosa McCook, significantly reduced both adult midge (Diptera: Chironomidae) and aster leafhopper (Homoptera: Cicadellidae) populations (Oraze & Grigarick 1989). While these three studies concluded that spider predation has a negative impact on insect pest populations, the authors acknowledge that the degree of control they report may have been overestimated as a result of the spiders' restricted movement.

Riechert & Bishop (1990) created a garden system that they used to assess the effect of vegetation complexity on spider assemblage density and insect damage to plants in the habitat. Vegetable plots that were augmented with a layer of mulch or mulch and flowers showed an increased number of spider predators and decreased numbers of pest insects (and their damage). These results were determined to be correlated, and



supported their argument that spider assemblages enhanced through the provision of additional refugia in agricultural systems may successfully limit pest insect population growth. Additional observations of predation events in the field and a significant reduction in the amount of insect damage to broccoli plants on which spiders were confined, further confirmed their findings.

My 1992 research (Chapter II), examined the various taxa of prey captured by spiders in noncommercial cranberry bogs located in Rochester, Sandwich, Truro, and Provincetown, Massachusetts. Spiders with prey in their chelicerae were collected using two methods, direct observation and sweep netting, and numerical estimates of the arthropods available to the spiders (potential prey) were obtained from Dvac® samples taken at the bogs. The data showed that the type of prey possessed by spiders was influenced by the frequencies of potential prey in their surroundings, and that most spiders in the bog system were feeding on adult Diptera. In addition to dipterans, hunting spiders commonly captured Collembola, Homoptera, and Araneae, while web-builders frequently trapped Hymenoptera and Homoptera flying above the cranberry vines. Overall, the predation trends we documented were similar to those reported for spiders in several other agricultural systems (Nyffeler et al. 1994 and references therein) and suggests that spider predators may also help to control population outbreaks of injurious insects in the cranberry bog system. Furthermore, comparison of the sampling methods used for collecting spiders indicated that higher numbers of spiders with prey can be collected using direct observation than sweep netting in cranberry bogs.

Regardless of their rather nondiscriminating palate and biological constraints, spiders are considered beneficial components of the indigenous natural enemy complexes that should be conserved and enhanced in agricultural ecosystems.

### Larval Defenses and Spider Predation

Many insect larvae possess physical and behavioral characteristics that negatively affect parasitization or predation by natural enemies, thus reducing the potential effectiveness of invertebrates responsible for the biological control of larval pests (Gross 1993; Montllor & Bernays 1993; Lederhouse 1990; Witz 1989). Larval defenses may include measures that reduce the probability of being located by an enemy (crypsis, mimicry, retreat building) as well as aggressive behaviors used to repel an attack (regurgitation, biting, vigorous movement). Experimenters have investigated both types of defense mechanisms in larva-predator (Witz 1989 and references therein; Evans 1986; Stamp 1986, 1992; Bernays 1988, 1989; Weseloh 1989) and larva-parasitoid relationships (Stamp 1982, 1992; Stamp & Bowers 1988; Gross 1993). However, with the exception of Eisner et al. (1974) and den Boer (1971), research addressing the influence larval defenses may have on spider predation is lacking.

In 1993, I conducted laboratory experiments to assess the effect various behavioral and physical defenses of Lepidoptera and Hymenoptera larvae may have on spider predation in cranberry bogs (Chapter III). Two genera of hunting spiders commonly found in bogs (Lycosidae: Pardosa; Salticidae: Habronattus) and four species of larvae that feed on cranberry foliage were used for 3-choice tests and observations. Each of the larval species offered to the spiders had different potential defensive characteristics. Results from 3-choice testing and observations of spider-larva interactions showed that the various larval defenses influenced prey selection, and in some instances significantly limited predation by lycosid and salticid spiders.

### Spiders and the Cranberry System

The American cranberry, Vaccinium macrocarpon Aiton, is a low-growing, woody perennial vine native to many bog habitats in the northern United States and the southernmost regions of the Canadian provinces. Cranberry vines produce vegetative "runners" (horizontal vines) that form a dense mat over the bog substrate. Vertical

branches called “uprights” arise from the runners and have terminal buds that generate 5-7.5 cm of new growth in the spring. Flowers are produced on the new growth in June/July and those that are pollinated set fruit. Cranberries have hollow, air-filled chambers that contain seeds and are covered with a waxy cuticle that helps the fruit retain moisture. This ability to resist immediate desiccation allows the fruit to be stored for long periods after harvest in the late summer/early fall.

Historically, cranberries gathered from wetland bogs were an essential component in the diet and culture of Native Americans. In addition to their daily use in baked goods and sauces, cranberries also became important to early colonists for the treatment of scurvy (due to their high vitamin C content). Despite its culinary significance, the cranberry was not cultivated in North America until 1810 in Massachusetts. Several other states also became, and have remained, prominent in commercial cranberry production, including New Jersey (1835), Wisconsin (1853), and Washington and Oregon (1883) (Eck 1990). Today there are more than ten thousand hectares of commercially-managed cranberry bogs in the United States. Nearly half of the bogs are located in Massachusetts, where cranberries are the number one agricultural cash crop in the state.

Although cranberry vines are long-lived and often remain productive for decades after establishment, disease and insect damage can substantially reduce the quality and quantity of fruit produced in a commercial bog. Control measures for the insect pests and fungal diseases of cranberry have been researched by entomologists and plant pathologists since the turn of the century. What began as a chemical crusade has been modified in recent decades to include investigations of the potential effectiveness of natural enemies such as predators, parasitoids and nematodes in the cranberry system.

Entomologist H. J. Franklin produced several bulletins between 1948 and 1952 that described the many pest insects found in the bogs of Massachusetts. In his 1950 publication, Franklin speculated that spiders and insect predators were of probable importance for suppressing insect populations, but that no studies or appraisals of their



influence had been performed (Franklin 1950). A recent text about the cranberry system (Eck 1990) reiterated Franklin's work, yet made no mention of any research conducted over the intervening years on the complement of beneficial arthropods present in natural and managed bogs. To my knowledge, there have been no organized studies of spiders in cranberry other than those performed during the past several years by myself and Rebecca Young (University of Tennessee, Knoxville TN) at the Cranberry Experiment Station in eastern Massachusetts. Supported in-part by the Cape Cod Cranberry Growers' Association, the Cranberry Station accommodates the research needs of the nation's cranberry industry.

Surveys conducted on cranberry bogs in Massachusetts indicate that ca 17 families of spiders may be found in commercially-managed and unmanaged systems (R. Young, unpublished data). Observations of the spider fauna present in these systems indicate that although hunting spiders are prevalent in unmanaged bogs, species of linyphiids (small, sheet-web spiders) predominate in managed bogs for the majority of the growing season (Bardwell & Averill, unpublished data). We suspect that pesticides repeatedly decimate lycosid and other hunting spider populations throughout the year, forcing the hunter guild to repeatedly re-colonize the cranberry bogs. As a result, hunting spiders are seen in very low numbers on commercial bogs until after the final spray has been applied, usually in late July. By the time the cranberry crop is harvested in late summer/early fall, huge numbers of penultimate lycosids are commonly seen exiting the bogs. Although the dynamics and implications of this trend in the cranberry ecosystem is currently undetermined, a similar transition documented in a 5-year successional study of predacious arthropods in a meadow system also showed the dominant spider family shifting from linyphiids to lycosids as time progressed (Nentwig 1988).

While I have focused on the prey spiders capture in undisturbed cranberry bogs and laboratory evaluation of the effects several larval defenses may have in deterring spider predation, there are many unanswered questions to address. Some of these

include the dynamics of spider re colonization in commercial bogs after insecticide and fungicide applications throughout the growing season and/or the removal of harvest floods in the spring. Studies of the prey captured by spiders on commercial bogs under standard and reduced chemical input management, combined with those I have conducted on unmanaged bogs, show potential for further clarifying our assessment of spider predation in the cranberry ecosystem. Additionally, field experiments to investigate the impact spiders have on insect pests prior to and during population outbreaks would be of certain importance to growers and ecologists alike (Wise 1993).

#### Research objectives

The purpose of this work was to begin documenting the role of spiders as predators in the cranberry ecosystem. My research has detailed the arthropod prey hunting and web-building spiders consume in unmanaged cranberry bogs as well as a range of physical and behavioral larval characteristics that may affect spider predation of pest insects in commercial bogs. Such research is imperative for ascertaining the potential effectiveness spiders may have as components of future biological control programs in cranberry.

As so little information about spiders in this unique habitat exists, every additional study contributes a valuable piece to the “big picture” of how the natural enemy complex in the cranberry system functions. It is my hope that future researchers involved in the assessment of biological agents that help to control pest insects in commercial cranberry bogs with limited chemical input objectives will find this information a useful contribution.



## CHAPTER II

### SPIDERS AND THEIR PREY IN MASSACHUSETTS CRANBERRY BOGS

#### Introduction

Surveys of spiders and their arthropod prey have been conducted in numerous non-agricultural and managed crop ecosystems and spiders have been shown to constitute a significant proportion of the predator guild (Young & Edwards 1990; Nyffeler et al. 1994). In field crops, spiders are believed to contribute to the biological control of arthropod pests (Riechert & Lockley 1984; Nyffeler & Benz 1987; Wise 1993). Our study is the first examination of spiders and their prey in unmanaged cranberry bogs.

#### Materials & Methods

##### Study Sites

In 1992, surveys of spiders with prey items in their chelicerae were carried out in seven noncommercial cranberry bogs in eastern Massachusetts ranging in size from 0.2 to 1.2 ha. Bogs were classified as either "wild" or "abandoned" and were dominated by cranberry vines (Vaccinium macrocarpon Aiton). Wild bog sites were located in Sandwich, Truro, and Provincetown, MA in depressions between sand dunes. In addition to cranberry vines, other vegetation at the wild sites included Sphagnum moss, bayberry (Myrica pensylvanica Mirbel), bog orchids (Habernaria spp.), round-leaved (Drosera rotundifolia L.) and thread-leaved (Drosera filiformis Raf.) sundews, poison ivy (Rhus radicans L.), various sedges, grasses, and rushes, and other herbaceous and woody plants commonly found in undisturbed bog habitats in the region. The abandoned bogs, located in Sandwich and Rochester, MA, were originally established for commercial cranberry production but were unmanaged for 5-10 years before this survey. Abandoned bogs had thick mats of cranberry vines and Sphagnum moss interspersed with grasses, brambles (Rubus spp.), poison ivy, small flowering shrubs, and saplings

of the early successional tree species found in adjacent wooded habitats (including, Acer rubrum L., Pinus strobus L., Populus spp., and Betula spp.).

Bogs were considered to be composed of 3 overlapping strata: ground surface, vines, and other (taller) vegetation (Figure 1, p.29). As hunting spiders generally forage on vegetation and web-builders trap prey from the air, we hypothesized that spiders within these strata would encounter and capture arthropod prey from the arthropod orders most commonly located there.

### Collection Methods

Surveys of spiders and their prey were conducted at all wild and abandoned bogs on alternate weeks between 1 June and 28 August, 1992. During this period, seven surveys were made at each site. Direct observation and sweep sampling to obtain spiders with prey were conducted at the sites between the hours of 0930 and 1530 h, weather permitting. The first sampling method employed after arrival at a study site was direct observation. We divided each site into three parts of similar size, using physical landmarks such as shrubs, trees, bog ditches, etc.; within each section, sampling was carried out by three observers who walked random paths for an hour. Bog vegetation was visually searched for spiders, which were aspirated into clear, 30 ml cups and inspected for the presence of prey in their mouth parts. If a spider possessed a prey item, alcohol was added to the cup to kill the spider and both spider and prey were brought back to the laboratory for identification. If a spider did not possess a prey item, the inspection event was recorded on a hand-held counter and the spider was released.

Next, 30 sets of five random sweeps were performed using a circular, 27.5 cm dia cloth net, with each person sampling one third of the bog. After five sweeps, the contents of the net were emptied into a light-colored dish pan; spiders were quickly aspirated into cups and their mouth parts checked for prey. Spiders with and without prey were treated in the same manner as those captured during direct observation. Before leaving a site, 25 randomly-selected 0.20 m<sup>2</sup> point samples of the arthropod fauna were

obtained using a Dvac® suction device (Dietrick 1961) and contents were placed in cyanide jars and transported back to the laboratory for identification. On several occasions, bogs were saturated with water, preventing use of the Dvac® and causing arthropod samples at some sites to be discontinuous.

In addition to the seven-week surveys, two extra direct observation examinations were conducted between normally-scheduled survey weeks at each of two abandoned bogs (Mello 1 and Mello 2) and two wild bogs (Herring Cove and Mt. Ararat). Direct observations were performed in exactly the same manner as previously described; however, no sweep net or Dvac® samples were taken.

### Identifications

I identified all spider specimens collected with prey in the laboratory to genus, and species when possible, using Kaston (1981). Voucher specimens preserved in 70% ethanol were sent to the American Museum of Natural History for confirmation and have been deposited in the University of Massachusetts entomology collection. Prey items removed from the mouth parts of spiders were identified to order. A few prey remains that were not identifiable were discarded and the capture event removed from the data record for the site where the spider with prey was collected. Arthropods from Dvac® samples were identified to order and preserved in 70% ethanol.

### Additional Field Trial

In 1993, we compared the effectiveness of the random, direct observation method we employed during 1992 with the “drunkard’s walk” (Southwood 1978) for capturing spiders with prey in the cranberry system. The latter method required the establishment of a centered transect line at a site and use of a random numbers table to select discrete areas where direct observation was performed. Two people with observation experience from the 1992 survey conducted the collection comparison. Once a point was selected, the spiders present within a 0.9 m radius were individually captured and inspected during a 15 min. period. A total of 4 individual points was selected by each observer during an



hour. Three wild bogs from the 1992 study, Mt. Ararat, Herring Cove, and Sandy Neck, were selected for the comparison of the two sampling methods. Each site was surveyed weekly using both methods between 21 July and 12 August, 1993. A Wilcoxon signed rank test was used to compare the number of spiders inspected and the number of spiders collected with prey (Ott 1984).

## Results

### Spiders Collected With Prey

During the survey, 188 spiders with prey were collected. Twenty-four of the specimens (13%) were obtained from the additional direct observations performed at the Herring Cove, Mt. Ararat, Mello 1, and Mello 2 bogs. On average, 3.3% (118/3590) of the spiders inspected at the four wild bogs and 2.1% (70/3419) of the spiders inspected at the three abandoned bogs had prey items (Table 1, p.20).

Sixty-one percent (115/188) of the spiders collected with prey were hunters and 39% (73/188) were web-builders (Table 2, p.21). Of the hunting spiders, 87% (100/115) were from the families Lycosidae (wolf spiders) and Oxyopidae (lynx spiders). Spiders from the families Araneidae and Tetragnathidae (both orb weavers) made up 89% (65/73) of the web-builders with prey. Although eight families were represented in the survey, 88% (165/188) of all the predation events we witnessed involved lycosid, oxyopid, araneid, or tetragnathid spiders.

The dominant families of hunters and web builders collected with prey differed between the wild and abandoned bogs. At the wild bogs, 81% (96/118) were lycosids and araneids while at abandoned bogs, 70% (49/70) were oxyopids and tetragnathids. Lycosids and araneids were captured with prey and observed in high numbers at all of the wild bogs. All of the oxyopids captured with prey were from the Mello 1 and 2 bogs, although the presence of oxyopids at Windmill was noted during collection outings. In addition, 13 of the 15 tetragnathids with prey from abandoned bogs were obtained at the Windmill bog.

In total, 24 genera of spiders with arthropod prey from 11 orders were collected and identified during the survey (Table 3, p.22). Three species (Pardosa saxatilis Hentz (Lycosidae), Oxyopes salticus Hentz (Oxyopidae), and Tetragnatha laboriosa Hentz (Tetragnathidae)) represented 58% (109/188) of all specimens collected with prey. Sixty-seven percent (34/51) of the prey recovered from P. saxatilis were Diptera (22/51) or Collembola (12/51); another 20% (10/51) were identified as Homoptera (5/51) and Araneae (5/51). Collembolans (35%, 12/34) and dipterans (24%, 8/34) were the dominant prey captured by O. salticus, and no predation on spiders by this species was observed during the survey. The majority of T. laboriosa with prey possessed chironomids (63%, 15/24) or homopterans (17%, 4/24). In addition to these three species, another 27% (51/188) of the spiders with prey were identified as various species of Pardosa, Mangora (Araneidae), Neoscona (Araneidae), and Argiope (Araneidae).

Thirty-nine percent (74/188) of the arthropods recovered from the chelicerae of all spiders captured with prey were dipterans. Small flies from the family Chironomidae represented 51% (37/73) of all prey captured by web building species and 32% (37/115) captured by hunting species. Other orders frequently possessed by the web building spiders included the Hymenoptera (16%, 12/73) and Homoptera (12%, 9/73). In addition to Diptera, the most common prey of spiders in the hunter guild were Collembola (27%, 31/115), Homoptera (11%, 13/115) and Araneae (10%, 12/115).

During the months that sampling was conducted, fluctuations in the proportions of arthropod orders possessed as prey by spiders at the wild and abandoned bogs were evident (Table 4, p.25). Between the months of June and August at the wild and abandoned bogs, the proportion of homopteran and hymenopteran prey captured by spiders increased, while the proportion of collembolan prey taken decreased. During the same interval, the proportion of the total prey from the orders Lepidoptera and Diptera was greatest in the month of July. Araneid prey items comprised a larger proportion of



the total prey taken by spiders at the wild bogs (from 6 to 25%) than at the abandoned bogs (from 0 to 5.3%) throughout the study.

### Potential Prey

Dvac® samples taken during the months of June, July, and August showed fluctuations in the abundance of potential prey (arthropods available to foraging spiders). The number of arthropods collected per sample was greatest during the month of July at both wild and abandoned bogs (Table 5, p.26). Collembola were the most abundant potential prey at the abandoned sites, comprising 40-50% of all arthropods collected each month. In addition, the emergence of chironomids in June, adult Lepidoptera in July, and oxyopid spiderlings in August was reflected in the composition of the samples from the abandoned bogs.

At the wild sites, the proportion of Collembola steadily declined from 59% (2143/3628) of the total potential prey in June, to just 21% (516/2464) in August. During July, increased numbers of arthropods from the orders Araneae, Diptera, Homoptera, and Hymenoptera were evident in the samples from the wild sites. Of the total potential prey present in Dvac® samples from all wild and abandoned sites throughout the survey, the most abundant orders were (in descending order) Collembola, Diptera, and Araneae/Hymenoptera.

### Comparison of Collection Methods

Of the two collection methods we employed in the cranberry system, direct observation was generally more effective for capturing spiders with prey than sweep netting. Although the mean number of spiders inspected using the two methods was similar over all 7 sites surveyed, the mean number of spiders collected with prey was greater using the direct observation method ( $P = 0.0001$ , Wilcoxon signed rank test) (Table 6, p.27).

During the field trial conducted in 1993, the protocol for direct observation used in the 1992 survey resulted in both a greater mean number of spiders inspected ( $P =$

0.001, Wilcoxon signed rank test) and collected with prey ( $P = 0.003$ , Wilcoxon signed rank test) than the “drunkard’s walk” method (Table 7, p.28).

## Discussion

### Spiders Collected With Prey

Over all sites, approximately 2.7% (188/7009) of the spiders that we inspected possessed prey. In the literature, the percentage of hunting spiders collected while feeding ranges from 1.4 to 8.3% (Nyffeler et al. 1987b, 1989; Young 1989), while <10% to 12% has been reported for web-builders (Nyffeler et al. 1989; LeSar & Unzicker 1978). Although collecting technique, vegetational architecture, spider species, potential prey and several other factors varied among the studies, the average percent of spiders with prey in unmanaged cranberry systems falls within the range of that found in other systems.

Of the total spider fauna found in field crops grown in the United States, 56% are estimated to be hunting species and 44% web-building species (Young & Edwards 1990). Surveys performed in alfalfa, peanuts, rice, and cotton cite percentages ranging from 42 to 93 for hunting spiders and 17 to 58 for web-builders (Wheeler 1973; Agnew & Smith 1989; Heiss & Meisch 1985; Whitcomb et al. 1963). We found the proportions of spider types collected with prey in cranberries to be similar to these other crops, i.e., 61% were hunting species and 39% web-building species. Though the diversity of species was not determined, it is likely that these values reflect the general composition of spider types present on cranberry bogs.

The feeding trends of spiders collected with prey at wild and abandoned cranberry bogs indicate that many of the web-building and hunting species present have a varied diet that is dominated by adult dipterans. Of the 188 spiders collected with prey, 51% of all web-builders and 32% of all hunters possessed dipteran prey. Relatively high proportions of Diptera (up to 77.8% of all prey captured) have also been reported in the diets of many web-building and hunting spiders in soybean, cotton, wheat field, alfalfa,

and grassland ecosystems (Nyffeler et al. 1994). In general, spiders collected with prey in cranberries possessed arthropods of types located in the microhabitat where the spider's foraging activity was concentrated; hunters possessed prey from the ground and vine strata, web-builders prey from the vine and tall vegetation strata (see Fig. 1, p.29 and Table 3, p.22).

Prey data for hunting spiders in many systems indicate that although a variety of arthropod taxa are accepted, the groups most commonly captured include Collembola, Diptera, Heteroptera, and Araneae (Edgar 1969; Hallander 1970; Yeargan 1975; Nyffeler et al. 1992, 1994). In addition to dipterans, most hunting spiders in cranberries possessed prey from orders located primarily on the ground or in the vines of bog, specifically, Collembola (27%), leafhoppers (11%), and immature spiders (10%).

The species of hunting spiders most frequently collected with prey in cranberry were Pardosa saxatilis Hentz and Oxyopes salticus Hentz. P. saxatilis was collected with a wide range of prey that was dominated by Diptera and Collembola, but occasionally included species of leafhoppers that vector cranberry false blossom disease and Lepidoptera whose larvae are foliar pests in the cranberry system. Yeargan (1975) observed that, despite an abundance of lepidopterans in alfalfa, the diet of the lycosid Pardosa ramulosa McCook consisted primarily of prey from the orders Homoptera, Diptera, and Araneae. Yeargan concluded that the predation exhibited by P. ramulosa may have been due to the rarity of encounters with Lepidoptera, which were located in the foliage above areas where the spiders most often foraged, and to attractiveness of the sudden movements often made by homopteran and dipteran prey. Although lepidoptera were scarce in the bogs we sampled, these factors may have affected the prey selection we observed for P. saxatilis.

Predation of spiders by oxyopids has been reported in several surveys conducted in cotton and wooley croton, Croton capitatus Michaux in Texas (Nyffeler et al. 1987a, 1987b, 1992). However, Lockley & Young (1987) noted a conspicuous lack of spiders



possessed as prey by O. salticus in cotton in Mississippi, U.S.A. Our data on the feeding behavior of O. salticus in abandoned cranberry bogs concurred with the latter findings for unknown reason(s), but which may have involved the availability of more easily captured prey items.

Studies of orb-weaving spiders (Araneidae and Tetragnathidae) in temperate regions have shown that most species capture Homoptera, Diptera, and small parasitic Hymenoptera in their webs (Nentwig 1987; Culin & Yeargan 1982; Provencher & Coderre 1987). In addition, large orb-weavers (Argiope spp.) may feed on aculeate Hymenoptera, grasshoppers, and various other 'difficult' prey (Nentwig 1985; Nyffeler et al. 1987c, 1989, 1991). Our data show that orb spiders capture winged prey, predominantly Diptera, Hymenoptera, and Homoptera, flying between cranberry vines and tall vegetation in bogs. Though uncommon in our study, several large-bodied Hymenoptera and Orthoptera were captured by females of the genus Argiope in late August as the spiders approached maturity. The majority of prey captured by species of sheet-web spiders (Linyphiidae) were from the same orders as those captured by orb-weavers.

The web-builder Tetragnatha laboriosa Hentz, one of the most frequently occurring spider species in field crops in the U.S.A. (Young & Edwards 1990), has been shown to commonly capture heteropteran and dipteran prey in cotton and soybean systems (LeSar & Unzicker 1978; Culin & Yeargan 1982; Nyffeler et al. 1989). In our survey of unmanaged cranberry bogs, T. laboriosa was the species of web-building spider most frequently observed with prey. The orders of prey possessed most often, Diptera and Homoptera, were consistent with the dominant arthropod groups reported for this species in the agricultural systems previously mentioned.

Spiders are considered by many to be generalist predators that capture the prey species that are most abundant, and thus most often encountered, in their environment (Turnbull 1960; Riechert & Lockley 1984; Wise 1993). Comparison between the

proportion of prey captured by spiders and frequencies of potential prey in cranberry bogs indicates that spider predation is influenced by prey abundance (Tables 4 and 5). Although the number of spiders collected with prey were low, the number and type of prey possessed by spiders fluctuated with the relative abundance of potential prey as captured in Dvac® samples, for most of the arthropod orders present in the system.

Foliage-feeding lepidopteran larvae and adult cranberry weevils (Anthonomus musculus Say) are the primary pest insects found in commercial cranberry bogs. Of the 13 spiders captured with lepidopteran prey in noncommercial bogs, 5 of the prey items were larvae. Two spiders were collected with coleopteran prey items during the study, however neither was a cranberry weevil. In sum, our data indicate that few spiders in noncommercial cranberry bogs capture pest insects such as lepidopteran larvae or weevils. This suggests that spiders with similar predation behavior in commercial bogs may not have a very high impact on insect pests, particularly low density populations such as were present in the noncommercial systems.

#### Comparison of Collection Methods

Over the seven-week period of this study, direct observation was more effective than sweep netting in collecting spiders with prey. Spiders collected using sweep nets were often damaged and rarely possessed prey. Both injury to the spiders and absence of prey was most likely the result of the sweeping motion and tumbling contents of the net. Under such conditions, it is likely that spiders entering a sweep net with prey in their mouth parts responded by releasing their prey. Prey may have also been released by spiders as the sweep samples were emptied into the dish pan and inspected.

Mean numbers of spiders inspected and collected with prey during 1993 show that the direct observation method used in 1992 was also more effective than the “drunkard’s walk” method in the cranberry system, despite the successful use of the latter method in other systems (S. E. Riechert, Univ. of Tennessee, Knoxville, TN, personal communication). Unlike many row crops, the cranberry bogs we surveyed were covered



in dense layers of vine with little exposed substrate. Hunting spiders were only visible when they were resting or actively moving on the uppermost layer of cranberry vine. Web-building spiders often positioned themselves in grasses and shrubs above the vines where they were visible to observers. Although they were easily spotted, there were not many present in any given area of bog. Given such circumstances, the probability of locating a hunting or web-building spider to inspect and/or capture with prey may have been improved by using the direct observation method because of the increased proportion of bog area searched by experimenters.

**Table 2.1.** Percentage of spiders collected with prey in wild or abandoned cranberry bogs in 1992.

Bog sites (ha)	No. spiders inspected	No. spiders with prey	% spiders with prey
Wild			
High Head (0.5)	947	37	3.9
Herring Cove (1.2)	962	23	2.4
Mt. Ararat (0.2)	968	36	3.7
Sandy Neck (0.8)	713	22	3.1
All wild bogs	3590	118	3.3
Abandoned			
Mello 1 (1.2)	982	23	2.3
Mello 2 (1.2)	1663	28	1.7
Windmill (1.2)	774	19	2.5
All abandoned bogs	3419	70	2.1
Total - all bog sites	7009	188	2.7

**Table 2.2.** Families of spiders collected with prey at wild and abandoned cranberry bogs in 1992.

Spider family	Abandoned bogs		Wild bogs		All bogs	
	n	%	n	%	N	%
Hunters - all	47	67.1%	68	57.6%	115	61.2%
Lycosidae	7	10.0%	59	50.0%	66	35.1%
Oxyopidae	34	48.5%	0	0	34	18.1%
Salticidae	2	2.9%	5	4.2%	7	3.7%
Thomisidae	2	2.9%	4	3.4%	6	3.2%
Clubionidae	2	2.9%	0	0	2	1.1%
Web-builders - all	23	32.9%	50	42.4%	73	38.8%
Araneidae	4	5.7%	37	31.4%	41	21.8%
Tetragnathidae	15	21.4%	9	7.6%	24	12.8%
Linyphiidae	4	5.7%	4	3.4%	8	4.2%
Total	70	100%	118	100%	188	100%



**Table 2.3.** Taxa of spiders and prey items collected in cranberry bogs in 1992.

Spider family	No. of predation events / order of prey <sup>a</sup>							
	ARN	COL	DIP	HOM	HYM	LEP	OTH	TOT
<u>Web-building spiders</u>								
Araneidae (orb-weaving spiders)								
<u>Argiope</u> spp.			2	2	3		2	9
<u>Acanthepeira</u> spp.	1							1
<u>Epeira</u> spp.			1					1
<u>Mangora gibberosa</u> (Hentz)			4	2	3	1	3	13
<u>Neoscona arabesca</u> (Walckenaer)			7	1	3			11
<u>Neoscona pratensis</u> (Hentz)			2		1			3
<u>Neoscona</u> spp.			1				1	2
<u>Singa</u> spp.			1					1
All species	1	0	18	5	10	1	6	41
<u>Linyphiidae (sheet-web spiders)</u>								
<u>Ceratinops</u> spp.		1						1
<u>Frontinella</u> spp.			1		2			3
<u>Helophora</u> spp.			1					1
<u>Neriene clathrata</u> (Sundevall)			1					1
<u>Neriene variabilis</u> (Banks)			1				1	2
All species	0	1	4	0	2	0	1	8

Continued, next page.

Table 2.3, continued.

Spider family	No. of predation events / order of prey <sup>a</sup>							
	ARN	COL	DIP	HOM	HYM	LEP	OTH	TOT
Tetragnathidae (orb-weaver spiders)								
<u>Tetragnatha laboriosa</u>	0	3	15	4	0	1	1	24
All web-building spiders	1	4	37	9	12	2	8	73
<u>Hunting spiders</u>								
Lycosidae (wolf spiders)								
<u>Arctosa</u> spp.							1	1
<u>Lycosa</u> spp.	1							1
<u>Pardosa floridana</u> (Banks)	1	2	2	1				6
<u>Pardosa milvina</u> (Hentz)			1					1
<u>Pardosa modica</u> (Blackwell)							1	1
<u>Pardosa moesta</u> (Banks)	1		3			1		5
<u>Pardosa saxatilis</u> (Hentz)	5	12	22	5	2	3	2	51
All species	8	14	28	6	2	4	4	66
Oxyopidae (lynx spiders)								
<u>Oxyopes salticus</u> (Hentz)	0	12	8	4	2	3	5	34
Salticidae (jumping spiders)								
<u>Evarcha flammata</u> (Clerck)		1						1
<u>Habronattus</u> spp.	1							1
<u>Metaphidippus</u> spp.	1							1
<u>Paraphidippus</u> spp.		3	1					4
All species	2	4	1	0	0	0	0	7

Table 2.3, continued.

Spider family	No. of predation events / order of prey <sup>a</sup>							
	ARN	COL	DIP	HOM	HYM	LEP	OTH	TOT
Clubionidae (wandering spiders)								
<u>Clubiona</u> spp.		1						1
<u>Castianeira</u> spp.				1				1
All species	0	1	0	1	0	0	0	2
Thomisidae (crab spiders)								
<u>Philodromus</u> spp.				1				1
<u>Thanatus</u> spp.	2			1			1	4
<u>Xysticus</u> spp.					1			1
All species	2	0	0	2	1	0	1	6
All hunting spiders	12	31	37	13	5	7	10	115
Totals	13	35	74	22	17	9	18	188

<sup>a</sup>ARN, Araneae; COL, Collembola; DIP, Diptera; HOM, Homoptera; HYM, Hymenoptera; LEP, Lepidoptera; OTH, Others, including: Orthoptera, Psocoptera, Coleoptera, Neuroptera and Acari; TOT, Totals.



**Table 2.4.** Seasonal variation in taxa of prey captured by spiders at four wild and three abandoned cranberry bogs in 1992.

Month sampled (No. sampling events)	Orders of prey captured by spiders <sup>a</sup>														Total No.
	Araneae No.	Araneae %	Collembola No.	Collembola %	Diptera No.	Diptera %	Homoptera No.	Homoptera %	Hymenoptera No.	Hymenoptera %	Lepidoptera No.	Lepidoptera %	Other No.	Other %	
Abandoned bogs															
June (11)	1	3.5	10	34.4	9	31.0	2	6.9	1	3.5	1	3.5	5	17.2	29
July (8)	0	0	5	22.7	9	40.9	3	13.6	1	4.6	2	9.1	2	9.1	22
August (6)	1	5.3	4	21.0	6	31.6	4	21.0	3	15.8	1	5.3	0	2.0	19
Wild bogs															
June (9)	5	25.0	7	35.0	5	25.0	2	10.0	0	0.0	0	0.0	1	5.0	20
July (13)	4	6.4	8	12.9	29	46.8	5	8.1	7	11.3	4	6.4	5	8.1	62
August (10)	2	5.5	1	2.8	16	44.4	6	16.7	5	13.9	1	2.8	5	13.9	36
All Bogs															
Season totals (57)	13	6.9	35	18.6	74	39.4	22	11.7	17	9.0	9	4.8	18	9.6	188

<sup>a</sup> Percentages = the number of insects from a specific order ÷ the total number of prey items captured by spiders during a month.

**Table 2.5.** Seasonal variation in potential prey at four wild and three abandoned cranberry bogs in 1992.

Month sampled (No. sampling events)	Potential prey orders <sup>a</sup>												Total No.		
	Araneae No.	Araneae %	Collembola No.	Collembola %	Diptera No.	Diptera %	Homoptera No.	Homoptera %	Hymenoptera No.	Hymenoptera %	Lepidoptera No.	Lepidoptera %		Other No.	Other %
Abandoned bogs															
June (8)	150	3.9	1534	40.3	1417	37.3	136	3.6	448	11.8	33	0.9	83	2.2	3801
July (5)	392	7.7	2558	50.4	558	11.0	204	4.0	565	11.1	633	12.5	170	3.3	5080
August (4)	942	30.0	1267	40.3	456	14.5	80	2.6	261	8.3	72	2.3	64	2.0	3142
Wild bogs															
June (7)	99	2.7	2143	59.1	664	18.3	228	6.3	357	9.8	21	0.6	116	3.2	3628
July (11)	798	11.4	1944	27.7	1801	25.7	786	11.2	932	13.3	190	2.7	557	8.0	7008
August (7)	550	22.3	516	20.9	600	24.4	166	6.7	295	12.0	221	9.0	116	4.7	2464
All Bogs															
Season totals (42)	2931	11.7	9962	39.6	5496	21.9	1600	6.4	2858	11.4	1170	4.6	1106	4.4	25123

<sup>a</sup> Percentages = the number of insects from a specific order ÷ the total number of potential prey collected during a month.

**Table 2.6.** Comparison of the mean number of spiders inspected and collected with prey using direct observation and sweep net methods in 1992.

Bog	Method used <sup>a</sup>	Mean number $\pm$ S.E.	
		Inspected	Collected with prey
High Head	Direct Observation	25.0 $\pm$ 2.7	1.6 $\pm$ 0.4
	Sweep netting	20.0 $\pm$ 2.1	0.1 $\pm$ 0.1
Herring Cove	Direct Observation	24.7 $\pm$ 1.9	0.8 $\pm$ 0.2
	Sweep netting	19.0 $\pm$ 2.4	0
Mt. Ararat	Direct Observation	24.2 $\pm$ 2.2	1.2 $\pm$ 0.3
	Sweep netting	14.7 $\pm$ 1.4	0
Sandy Neck	Direct Observation	26.2 $\pm$ 3.9	1.0 $\pm$ 0.2
	Sweep netting	7.7 $\pm$ 1.3	0
Mello 1	Direct Observation	21.7 $\pm$ 2.2	0.7 $\pm$ 0.2
	Sweep netting	19.0 $\pm$ 3.2	0.2 $\pm$ 0.2
Mello 2	Direct Observation	32.8 $\pm$ 4.0	0.6 $\pm$ 0.2
	Sweep netting	78.7 $\pm$ 37.9	0.4 $\pm$ 0.1
Windmill	Direct Observation	17.8 $\pm$ 2.3	0.7 $\pm$ 0.2
	Sweep netting	19.3 $\pm$ 3.2	0.2 $\pm$ 0.1
All Bogs	Direct Observation	24.6 $\pm$ 1.1	1.0 $\pm$ 0.1 <sup>b</sup>
	Sweep netting	25.5 $\pm$ 5.7	0.1 $\pm$ 0.0

<sup>a</sup>Spiders with prey collected during additional visits to sites were not used in comparison calculations. N = 21 h for direct observations and N = 210 sets of 5 sweeps for sweep net samples at each bog.

<sup>b</sup>Significantly more spiders with prey were collected using the direct observation method (P = 0.0001, Wilcoxon signed rank test).



**Table 2.7.** Comparison of the mean number of spiders inspected and collected with prey using the "drunkard's walk" and 1992 direct observation methods.

Bog	Method used <sup>a</sup>	Mean number $\pm$ S.E.	
		Inspected	Collected with prey
Herring Cove	Drunkard's walk	9.5 $\pm$ 3.0	0.3 $\pm$ 0.3
	Direct observation	54.8 $\pm$ 7.3	2.8 $\pm$ 0.5
Mt. Ararat	Drunkard's walk	22.8 $\pm$ 2.1	0.5 $\pm$ 0.3
	Direct observation	50.0 $\pm$ 5.6	3.5 $\pm$ 1.5
Sandy Neck	Drunkard's walk	8.5 $\pm$ 3.5	0.5 $\pm$ 0.5
	Direct observation	40.5 $\pm$ 7.2	3.3 $\pm$ 2.0
All bogs	Drunkard's walk	13.6 $\pm$ 2.5	0.4 $\pm$ 0.2
	Direct observation	48.4 $\pm$ 4.0 <sup>b</sup>	3.2 $\pm$ 0.8 <sup>c</sup>

<sup>a</sup>N = 8 h for each method at each site.

Significantly more spiders were inspected<sup>b</sup> ( $P = 0.001$ , Wilcoxon signed rank) and collected with prey<sup>c</sup> ( $P = 0.003$ , Wilcoxon signed rank) using the direct observation technique.



**Figure 2.1.** Wild and abandoned cranberry bogs consisted of three overlapping vegetational strata where spiders and potential prey were located: (A) ground (beneath the cranberry vines), (B) dense, layered cranberry vines, and (C) tall vegetation (composed of grasses, bayberry bushes, *Myrica pensylvanica* Mirbel, and/or tree saplings). Specific orders of arthropods were available to spiders foraging within the three overlapping strata of the wild and abandoned bogs surveyed. Collembola on the ground and on the vines (A), Araneae and larval foliage feeders within the vines (B), as well as Homoptera and Diptera moving between the topmost layer of vines and taller vegetation, and adult Lepidoptera and Hymemoptera alighting on the tall vegetation (C).

## CHAPTER III

# EFFECTIVENESS OF LARVAL DEFENSES AGAINST SPIDER PREDATION IN CRANBERRY ECOSYSTEMS

### Introduction

Spiders are generalist predators that often consume the most abundant and most easily captured prey in their habitat (Riechert & Luczak 1982; Nyffeler et al. 1994). When reduction of a specific insect pest is desired, such behavior often results in limited effectiveness when compared with specialist parasitoids or predators (Riechert 1974; Riechert & Lockley 1984; Riechert & Bishop 1990). Despite an inability to independently suppress insect populations in outbreak, spiders are believed to be valuable members of many biological control complexes, as indicated by numerous general surveys and several prey studies (Reichert 1974; Mansour et al. 1980, 1985; Reichert & Lockley 1984; Nyffeler & Benz 1987; Young & Edwards 1990). In the cranberry system, spiders are the most abundant generalist predator, averaging up to 40 individuals per m<sup>2</sup> in naturally-occurring bogs (R. Young, Univ. of Tennessee, Knoxville, TN, unpublished data). Preliminary data indicate that spiders prey upon the larvae of some cranberry pest insects and may thus be of some importance in commercial bog systems (unpublished data).

Larvae of many insect species possess a variety of morphological and behavioral characteristics that may deter attack by natural enemies (Stamp 1986; Cornell et al. 1987; Witz 1989). Such defenses are well documented for insect larvae subjected to wasp parasitism (Stamp 1982, 1992; Stamp & Bowers 1988; Gross 1993) and to predation by some families of generalist predators, including the Formicidae (Boeve & Pasteels 1985; Damman 1986; Bernays 1989; Weseloh 1989), Coccinellidae (Stamp 1986; Bernays 1989) and Pentatomidae (Stamp 1992). Although additional behavioral studies of the defenses used by larvae against generalist predators are warranted (Montllor & Bernays



1993), their use and effectiveness against spiders has received little attention (but see: Damman 1986; Gross 1993).

Here, we present a study of prey selection by two spider genera in choice tests. Spiders were provided several species of larvae that are common pests in the commercial cranberry bogs of Massachusetts and that varied substantially in their physical and behavioral defenses. We also conducted observations of individual spiders and larvae to help provide an understanding of the mechanistic factors underlying the differences in vulnerability of the various prey species.

### Materials & Methods

#### General 3-choice Experimental Design

Arenas were made from round, clear plastic containers (17.1cm x 13.2 cm, H x D) and covered with organdy secured with rubber bands. Sections of rooted cranberry vines were dug from an unsprayed commercial bog and placed in the arenas. At the time of placement, insects present on the cranberry substrate were removed by visual inspection and a hand-held Dvac® suction device. Vines were thinned to an approximate density of 10-15 uprights (cranberry shoots) per arena and trimmed to an appropriate height for the container. Two 2.5 cm holes were made 2.5 and 9.5 cm from the upper edge on opposite sides of the arenas (Figure 1, p.50). The upper hole in the wall of each arena was used for salticid tests and the lower hole was used for lycosid tests.

Depending on the spider species tested, one or the other hole was plugged with a rubber stopper. This was done to allow maximum mobility of the spiders tested: lycosids are ground wanderers and salticids forage predominantly in the uppermost regions of vegetative canopies (Cutler 1992). Five cm lengths of clear plastic tube were used to connect groups of three arenas to a central release chamber. Central release chambers were made from 150 ml paper cartons that were covered with organdy and had three 2.5 cm dia. holes, equidistant from each other, for the plastic connection tubes. All choice experiments were conducted at 22°C, 65% RH, and a photoperiod of 16:8 (L/D) h. A

Wilcoxon signed-rank test was used to analyze data for tests of both lycosid and salticid spiders (Ott 1984).

### 3-choice Tests for Salticid Spiders

Salticids were collected from a wild cranberry bog located in the Cape Cod National Seashore, Provincetown, MA on 26 May, 17 June, and 2 July. Spiders were mature individuals of different sexes, but could not be identified to species while living. Although most salticid females reach maturity and emerge several weeks after conspecific males (Gardner 1965; Kaston 1981), due to the inaccessibility of our collection site, we chose to obtain individuals of both sexes at the same time. Identification after testing revealed that males were Habronattus calcaratus Banks and that the females were Habronattus viridipes Hentz.

Spiders were held in 60 ml, organdy-covered cups with wet sponge cubes in the laboratory and were provided Collembola as food every second week. Individual spiders were starved between 5 and 8 days before the tests to ensure feeding would occur. Other studies of spider predation cite starvation periods ranging from 24 h to 7 d (Givens 1978; Provencher & Coderre 1987; Roach 1987; Guillebeau & All 1989; Mansour & Heimbach 1993). Preliminary 24 h observations showed that these species of salticids were only active diurnally for approximately 8-12 h during a 24 h period. Because acclimation to the choice-test arena design was required before location of the larvae and predation could occur, we allowed the tests to run for 48 hours.

We hypothesized that several species of larvae found in the cranberry system possessed physical and behavioral defenses that could potentially affect spider prey capture (Table 1, p.44). Brown cranberry spanworm larvae, Ematurga amitaria Guenée (6-15 mm), were field-collected in large numbers during June and held in a Percival® growth chamber at 16°C and a photoperiod of 16:8 (L/D) h. for later use in tests; gypsy moth larvae, Lymantria dispar L. (6-10 mm second instars), and Sparganothis fruitworm larvae, Sparganothis sulfureana Clemens (8-15 mm), were obtained from laboratory

colonies. Because prey size can potentially affect predation by spiders (Nentwig & Wissel 1986; Young & Lockley 1986), the length of the larvae used in choice tests and observations was standardized.

One set of 10 spiders was tested on 29 June - 1 July and another set on 6-8 July. Sets of 10 larvae were placed in randomly designated arenas. Arenas (one for larvae of each type) were then connected to a central release chamber and placed on shelving under florescent lights. A single spider was released into the central release chamber and observed until it entered an arena (< 5 min.). The larval type in that arena was recorded. After 48 hours, the arenas were dismantled and spider location at completion of the assay was also recorded. Larvae were removed and classified as either live, dead or missing (= consumed). No natural larval mortality was observed during the experiments or in groups held without a spider. Mortality resulting from spider attack was clearly distinguishable from natural mortality by the deflated, macerated appearance of the dead insect larva. In cases where maceration was not obvious, the dead larva was checked under a microscope for the presence of cheliceral punctures.

### 3-choice Tests for Lycosid Spiders

Mature female spiders representing two closely related species of lycosids were used in these tests. Pardosa saxatilis Hentz were collected from a wild cranberry bog in Provincetown, MA on 26 May. Pardosa milvina Hentz spiders were collected from abandoned cranberry bogs located in Wareham, MA on 3 June, and in Freetown, MA on 13 July. Both species are common inhabitants of cranberry bogs in Massachusetts and have also been observed together in a no-till corn agroecosystem (Clark et al. 1994). Pardosa saxatilis and P. milvina differ only slightly in their genital structure and are similar in size, coloration and life cycle (Kaston 1981). Preliminary observations of their predation behavior also showed little variation; thus, both species were collected and utilized for the choice tests.



Lycosids were held under the same conditions as salticids before testing. Unlike the salticid species, these spiders exhibited continual diurnal and nocturnal activity during our preliminary 24-h observations. Thus, we limited their time in the tests to 24 hours.

Larvae selected for the lycosid tests differed from those offered to the salticids only in the substitution of cranberry sawfly, Pristophora idiota Norton for S. sulfureana. This substitution was necessary because preliminary observations indicated that lycosid spiders did not climb higher than 2.5-5.0 cm on cranberry foliage. This vertical limitation in their distribution prevented them from contacting prey such as S. sulfureana that are concentrated at the uppermost portion of the vines. Pristophora idiota larvae, which appear cryptic when the light-colored dorsal midline is oriented horizontally along the margin of a leaf, were observed to feed in positions throughout the cranberry foliage where foraging lycosids could potentially encounter them as often as the other two species of test larvae. The P. idiota larvae (6-10 mm) were collected from an abandoned bog in Freetown, MA during June and July.

Three sets of 10 spiders were tested using an identical protocol as described above on 23-24 June, 24-25 June, and 19-20 July.

### Controls

Control arenas containing no spiders were assembled to evaluate the degree of error associated with retrieval of larvae released in test arenas. Sets of 10 arenas, one set for each larval type used in the 3-choice tests, were left for 24 hours after which time the numbers of live, dead and total larvae recovered out of 100 were recorded.

Levels of natural mortality of test larvae were not significant. At the end of 24-h holding periods, 99-100% of the E. amitaria, L. dispar, P. idiota, and S. sulfureana that were held without spiders were recovered alive.

### Direct Observations

Observations of interactions between individual spiders and prey larvae were made by two observers in the laboratory during the period from 25 June to 13 July.



Single arenas identical to those described for the choice tests were placed at eye-level and surrounded on three sides by off-white paper shields. Observers remained as motionless as possible. Successive sets of 10 larvae representing the species used for the choice tests with lycosid or salticid spiders were placed in arenas and allowed to "settle" for 5 minutes before introduction of a spider. Spiders were permitted to walk from holding cups into the arenas via the lower tube connection holes. Upon entry of a spider, observers recorded contacts with larvae, times of spider attacks, and outcomes. After three similar interactions were observed between an individual spider and a given larval type, the spider was removed, prey larvae replenished to 10, and a new spider was introduced. A total of 53 lycosids and 22 salticids were assayed.

## Results

### Choice Tests

Of the spiders assayed, 70% of all salticids and 86% of all lycosids moved between arenas during their respective 3-choice testing periods. Total number and type of larvae killed by salticid and lycosid spiders was not dependent on the first arena entered using the Kruskal-Wallis test for variable dependency (Table 2, p.45).

Two species of salticids were used in testing; therefore the statistical analyses for the salticid data are presented with the two species of spiders combined as well as separated (Table 3, p.46). If H. calcaratus and H. viridipes predation on the available larval types is separated (N=9 and 11, respectively), more E. amitaria larvae were killed than S. sulfureana larvae by H. viridipes ( $P = 0.05$ ), but there was not a significant difference in the mean number of these larvae killed by H. calcaratus ( $P = 0.10$ ). When the data are grouped (N=20), there is significance at the 0.02 level. Lymantria dispar larvae were killed by both species of salticid spiders significantly less often than either E. amitaria or S. sulfureana ( $P = 0.0001$  and  $P = 0.006$ , respectively).

In choice tests, lycosids killed more E. amitaria larvae than P. idiota larvae, both with the two Pardosa species separated ( $P = 0.02$ , P. saxatilis;  $P = 0.01$ , P. milvina) and

combined ( $P = 0.001$ ; Table 4, p.47). Ematurga amitaria and P. idiota larvae were killed more often than L. dispar larvae ( $P = 0.0001$  and  $P = 0.006$ , respectively), none of which were killed.

#### Direct Observation

We observed that 65% (130/200) of the test larvae (excluding L. dispar larvae) with which spiders made tarsal or cheliceral contact displayed a secondary defensive behavior. “Cheliceral attack” was considered to have occurred when a spider grasped a larva with its front pair of legs and touched its chelicerae to the larva’s cuticle. “Tarsal contact” was considered to have occurred if a spider touched a larva with its tarsi, often with a tapping motion. Tarsal contacts followed by cheliceral attack were counted in the latter category.

Lymantria dispar larvae. A secondary defensive response to tarsal contact or cheliceral attack was displayed by 14% (12/87) of all L. dispar larvae encountered by salticid and lycosid spiders. Responding larvae twitched their bodies or curled up and remained motionless. Larvae that did not respond to contact or attack continually moved around in the arenas, at times briefly contacting the spiders. Salticid spiders that contacted L. dispar larvae with their tarsi immediately backed away without attacking. After an average of 3 tarsal contacts with a L. dispar larva, salticids oriented toward a moving larva but did not approach or make contact with it.

Interactions observed between lycosids and L. dispar larvae were similar to the patterns observed for the salticids. Lycosids palpated larvae with their tarsus in 61% (33/54) of observed encounters and no further interactions were observed. In the remainder of encounters, the lycosids attacked L. dispar larvae with their chelicerae; 31% (17/54) of these larvae were unharmed by the cheliceral attack, while 8% (4/54) were killed.

Ematurga amitaria larvae. Of the 41 E. amitaria larvae contacted by lycosid spiders, 25 regurgitated a brown fluid and thrashed, hitting the spider with the head

capsule and smearing regurgitate on the spider's legs and cephalothorax. Eighty percent (20/25) of the contacted larvae were killed after such defensive behaviors were employed. Upon contact with a moving larva, lycosids attacked almost instantaneously and held onto their prey, allowing only 8% (2/25) of the larvae to escape. In contrast to the high percentage of larvae killed after displaying a secondary defense, only 21% (3/14) of the E. amitaria larvae that became or remained motionless when contacted by a lycosid were killed.

In contrast, salticids responded more slowly to movements made by E. amitaria larvae and followed a discrete series of behaviors that included orientation, pursuit and capture (Forster 1982). Furthermore, salticid spiders appeared to be deterred by a larva's thrashing and/or regurgitating more readily than lycosids. Release of a thrashing larva and delay in further pursuit by salticids allowed 55% (11/20) of E. amitaria larvae to escape following a cheliceral attack. Only 28% (5/18) of the observed E. amitaria-salticid encounters resulted in death of the larva after the larva thrashed and regurgitated.

Forty-four percent (17/39) of all E. amitaria larvae encountered by a salticid remained motionless and were not detected. On 8 occasions, salticids walked over a motionless larva, using the larva as if it were a "bridge" between cranberry uprights. Whether briefly contacted or walked over, none (0/17) of the E. amitaria larvae that remained in a cryptic posture were killed by salticids.

Pristophora idiota larvae. In total, 48 interactions between lycosid spiders and P. idiota larvae that were actively feeding or moving on the substrate or foliage in the arenas were observed. Forty-six percent (22/48) of the larvae contacted by a lycosid spider regurgitated while arching the head over the back and/or swinging the curled-posterior in the spider's direction. These behaviors were also used when larvae encountered feeding conspecifics. Regardless of whether a secondary defense was exhibited by a larva after contact or attack, all larvae were rejected as prey by lycosids, indicating that a defensive characteristic(s) other than regurgitation and aggressive responses was important.



Eisner et al. (1974) reported that only 1 of 8 Neodiprion sertifer Geoffroy larvae offered individually to caged lycosids was visibly injured by a spider's chelicerae. In our test, lycosids attacked P. idiota larvae with the chelicerae in 63% (30/48) of the encounters observed; however, the larval cuticle was never visibly punctured. Despite this, during spider-larva observations, 53% (9/17) of the lycosids that attacked P. idiota larvae with their chelicerae immersed their mouth parts in soil and cleaned their legs and palps immediately afterwards, allowing the larva to escape.

Sparganothis sulfureana larvae. Sparganothis sulfureana larvae are leaf tiers that create retreats at the tips of cranberry uprights where they feed and pupate. The retreats have two openings and the larvae often wriggle and drop down when their retreat is repeatedly disturbed or damaged (personal observation). In our tests, interactions between salticids and S. sulfureana larvae without retreats were more frequent, comprising 82% of all spider-larva observations. This occurred because we wanted to observe the effectiveness of both primary and secondary defenses and allowed introduced larvae only 5 minutes to settle in an arena before release of a spider. Completion of a larval retreat requires 30-45 minutes.

The majority of larvae (56/59) located outside of their retreats wriggled when contacted by a salticid's tarsi or chelicerae. The wriggling action appeared to elicit a startle response from the spider as well as move the larva rapidly away from the immediate area where an interaction occurred. Of the 59 larvae that wriggled in response to a salticid's cheliceral attack, 82% escaped, 8% were abandoned by the spider, and 10% were killed.

On 5 occasions, salticids walked over a motionless S. sulfureana located in a retreat and continued moving over the foliage without orienting toward the retreat. Eight of the 13 S. sulfureana larvae located by a salticid while in a retreat experienced tarsal contact and no subsequent attack. Of the 5 larvae that experienced an attack, 4 escaped by vigorous wriggling and 1 was killed by a salticid that positioned itself at one of the retreat



openings and grabbed the larva when its head capsule appeared. Wriggling was only used as a secondary defense when a spider entered a larva's retreat. In all other interactions, the S. sulfureana larva was motionless following tarsal contact.

## Discussion

### Choice Tests

Several authors have studied hunting spiders in laboratory settings (Lingren et al. 1968; Horner 1972; Holmberg & Turnbull 1982; Nentwig 1986; Young & Lockley 1986; Roach 1987; Guillebeau & All 1989; Mansour & Heimbach 1993). Of these, only three studies provided test spiders with a choice of prey. Spider species and prey used in all of the experiments differed from those used in our studies. No-choice experiments carried out by other authors were typically conducted in small containers with a water source but which lacked a complex substrate, thus allowing a test spider to encounter many prey without extensive searching. Overall, the number of prey killed/consumed by spiders in such no-choice tests was greater than that in our choice tests.

In a choice test that was conducted in Petri dishes, female oxyopid spiders were offered first-instar Heliothis spp., and either juvenile spiders or Geocoris spp. (nymphs/adults) as prey (Guillebeau & All 1989). The spiders consumed an average of 0.5-1 prey items in the 24 h test period. Despite differences in experimental design, results from our 3-choice tests are similar; individual salticid and lycosid spiders killed an average of 2 larvae per 48 h and 24 h test period, respectively.

### Direct Observation

Stamp (1986) and others (Witz 1989; Gross 1993 and references therein) review larval behaviors used for defense or escape when attacked, including regurgitation, biting, thrashing and falling to the ground. Such behaviors, called secondary defenses, are often used when crypsis or inconspicuous placement on a host plant/substrate, called primary defenses, fail to prevent a parasitoid or predator from locating a larva. Observations of spider-larva interactions and the effectiveness of larval defenses during

spider predation events are rare. However, examples include: lycosid response to P. idiota regurgitate (Eisner et al. 1974), effectiveness of chemical defenses and thick chitinization against web-building spiders (Nentwig 1983), the influence of larval movement on crab spider predation (den Boer 1971), and salticid response to coccinellid chemical secretions (Roach 1987).

Lymantria dispar larvae. Caterpillar hairs do not need to be urticating to provide a barrier against invertebrate predators or parasites (Bowers 1993). For example, the very dense hairs of unfed, neonate L. dispar larvae, while not considered urticating to arthropods, provide a high degree of protection against ant predation on the forest floor (Weseloh 1989). Rayor showed that Estigmene acrea Drury (Arctiidae) caterpillars whose setae were removed suffered increased predation by Polistes arizonensis Snelling (Vespidae) wasps (L. S. Rayor, Cornell Univ., Ithaca, N. Y., personal communication). We conducted a similar trial in which setae were singed off L. dispar larvae. On average, we also found that predation of treated larvae by lycosid spiders exceeded that observed for untreated larvae, suggesting that the setae of L. dispar larvae may negatively influence spider predation (unpublished data).

Lymantria dispar larvae were not killed by lycosids during 24 h choice tests, supporting our hypothesis that setae negatively affect spider predation. However, 8% (4/54) of the larvae contacted by lycosids during direct observation were killed, indicating that hairiness may be less of a deterrent to spiders in a no-choice situation.

The evasive behavior exhibited by salticids encountering L. dispar larvae during our direct observations suggests that the visual hunting spiders may have been learning to avoid unpalatable larvae. Aversion learning, characterized by the visual rejection and avoidance of noxious prey items previously encountered, has been documented in several other diurnal invertebrate predators including mantids, ants, and wasps (Montllor & Bernays 1993). Although no L. dispar larvae were killed after being located and

contacted up to 3 times in succession by individual salticids, additional research would be required to determine whether rejection of the larvae involved learning.

Ematurga amitaria larvae. Palatable geometrid larvae have been shown to experience higher levels of predation by invertebrates when they are mobile compared with when they are in an immobile, cryptic posture (Montllor & Bernays 1993). For example, den Boer (1971) found that the rare and conspicuous yellow-colored morphs of the pine looper, Bupalus piniarius L.(Geometridae), were significantly more likely to be taken as prey by crab spiders in the genera Xysticus and Philodromus (Thomisidae) than inconspicuous green conspecifics. He also showed that because the yellow larvae thrashed more when contacted by a spider, spiders pursued the yellow larvae more intensively than immobile green larvae.

During our behavioral observations of interactions between E. amitaria larvae and lycosid spiders, a similar elevated capture rate was noted as a result of larval thrashing (Table 5, p.48). In the former case, this may be a consequence of the physical characteristics and behavior of lycosid spiders, which possess poor vision and rely heavily on a tactile vibratory cue to locate their prey items (Uetz 1992). Movement by an E. amitaria larva contacted by a lycosid may have served to reinforce the spider's vibratory search image.

Despite their well-documented visual acuity, the salticid spiders we tested never responded to the motionless E. amitaria larvae that they contacted with their tarsi in a manner that indicated recognition of a potential prey item (Forster 1982). Because salticids rely entirely on visual prey movement for initiation of predation activity, E. amitaria larvae that did not move may have been, in effect, invisible to the foraging spiders.

In sum, our results suggest that assuming or remaining in a cryptic posture provides E. amitaria larvae with a better defense against predation than additionally thrashing/regurgitating when located by either lycosid or salticid spiders. However, the



active secondary defenses that we observed some E. amitaria larvae use when encountered by a spider may be a more effective deterrent against bird predation and/or parasitoids that locate larvae by cues other than those discussed here.

Pristophora idiota larvae. While it is not clear what caused P. idiota larvae to be killed by lycosids during the choice tests but not during direct observations, variation in the length of each type of test and/or larval chemical defenses may have been contributing factors. Boeve and Pasteels (1985) showed that ventral glands that produce defensive secretions were common in other Nematinae sawfly larvae. The compounds were determined to effectively deter ant predators and were repellent to birds, causing a delay in acceptance of the sawflies as prey. Although unconfirmed at this time, the presence of related compounds in the cuticle or regurgitant of P. idiota larvae may have elicited the cleaning responses observed in spiders after contact with a larva and the low level of predation that occurred in the choice tests and direct observations.

Sparganothis sulfureana larvae. Orientation behavior, which is key to salticid predation, normally indicates that a salticid has visually located a prey item (Forster 1982). The combined lack of such behavior by salticids moving over motionless S. sulfureana larvae, low frequency of cheliceral attack and small proportion of larvae killed while in a completed retreat during direct observation strongly suggest that retreats effectively limit spider predation. Similarly, Damman (1987) showed that shelters constructed by larvae of the leaf tier, Omphalocera munroei Martin, provided adequate physical protection from natural enemies, chiefly ants and spiders.

In addition, the high proportion (78%, 46/59) of unwebbed S. sulfureana larvae that escaped from or were abandoned by salticids after contact, suggests that in the absence of a foliar retreat, wriggling behavior provides S. sulfureana larvae with an effective secondary defense against salticid spiders.

Conclusions. Anti-parasitism defenses were discussed in a literature review compiled by Gross (1993), who stated that larvae employing two or more defensive



mechanisms increase their potential to reduce or repel wasp attacks. All of the larval species that we tested possessed morphological and/or behavioral primary and secondary defenses. We found that Gross' assertion held true for S. sulfureana larvae, whose use of a secondary defense, wriggling, strongly reduced successful spider attack. However, protection against foraging spiders was not always enhanced by the use of a secondary defense. As the E. amitaria data demonstrate, larvae that assumed or remained in a cryptic posture, a primary defense, were more effectively protected against spider attack than those that exhibited a secondary defensive response to spider contact. Lymantria dispar and P. idiota larvae, regardless of use of a secondary response to contact by a spider, were rarely killed, probably owing to protection afforded by effective primary defenses, hairs and chemicals, respectively.

In sum, our data from the 3-choice and observation experiments indicate that E. amitaria larvae are subject to a higher rate of predation by both lycosid and salticid spider predators than either L. dispar, P. idiota, or S. sulfureana larvae (Table 6, p.49). Whether or not an E. amitaria larva is killed by a spider appears to be influenced by the use of primary and/or secondary larval defense behaviors and the type of spider attacking. Finally, the low percentage of L. dispar, P. idiota, and S. sulfureana larvae killed during the 3-choice and observation tests provides evidence that the larval defenses of these three species may effectively limit predation by lycosid and salticid spiders in the cranberry ecosystem.

**Table 3.1.** Potential 1° and 2° defenses of E. amitaria, L. dispar, S. sulfureana, and P. idiota larvae found in cranberry ecosystems.

<u>Larval species</u>	<u>Larval Defenses<sup>a</sup></u>	
	1°	2°
brown cranberry spanworm	twig-like crypsis	thrashing
<u>Ematurga amitaria</u> (Guenée)		regurgitation
gypsy moth	long setae	twitch body
<u>Lymantria dispar</u> (L.)		curl up
<u>Sparganothis</u> fruitworm	webbed retreat in	wriggle body
<u>Sparganothis sulfureana</u> (Clemens)	terminal leaves	
cranberry sawfly	dorsal midline crypsis	“clubbing”
<u>Pristophora idiota</u> (Norton)	undescribed chemicals	regurgitation

<sup>a</sup>1° defenses are physical and/or behavioral characteristics of larvae that may reduce location or attack by predators. 2° defenses may be used by larvae when the primary defenses fail to deter natural enemies.

**Table 3.2.** Results of Kruskal-Wallis tests for variable dependency. The P values presented indicate that the number and type of larvae killed by spiders during choice tests are not dependent on the first arena entered or species of spider.

Independent variable	Larval species killed by spiders (Dependent variable)		
	<u>Ematurga</u>	<u>Sparganothis</u>	<u>Lymantria</u>
	<u>amitaria</u>	<u>sulfureana</u>	<u>dispar</u>
First arena entered by salticid	0.257	0.429	1.000
<u>Habronattus viridipes</u> versus <u>H. calcaratus</u>	0.484	0.502	1.000
First arena entered by lycosid	0.574	0.177	1.000
<u>Pardosa milvina</u> versus <u>P. saxatilis</u>	0.798	0.276	1.000

**Table 3.3.** Mean number of larvae killed by the spiders Habronattus calcaratus and H. viridipes during 48 h choice tests.

Mean number $\pm$ S.E. of larvae killed per spider					
Spider		<u>Lymantria</u>	<u>Ematurga</u>	<u>Sparganothis</u>	
Species	N	<u>dispar</u> <sup>a</sup>	<u>amitaria</u>	<u>sulfureana</u>	P value <sup>b</sup>
<u>H. calcaratus</u>	9	0	1.64 $\pm$ 0.5	0.55 $\pm$ 0.3	0.10
<u>H. viridipes</u>	11	0	2.89 $\pm$ 1.1	0.78 $\pm$ 0.4	0.05
<u>H. calcaratus</u> & <u>H. viridipes</u>	20	0	2.20 $\pm$ 0.6	0.65 $\pm$ 0.2	0.02

<sup>a</sup>L. dispar larvae were killed less often than E. amitaria (P = 0.0001) and S. sulfureana (P = 0.006).

<sup>b</sup>P-values calculated using the Wilcoxon signed-rank test for E. amitaria versus S. sulfureana larval prey.



**Table 3.4.** Mean number of larvae killed by the spiders Pardosa milvina and P. saxatilis during 24 h choice tests.

Mean number $\pm$ S.E. of larvae killed per spider					
Spider		<u>Lymantria</u>	<u>Ematurga</u>	<u>Pristophora</u>	
Species	N	<u>dispar</u> <sup>a</sup>	<u>amitaria</u>	<u>idiota</u>	P value <sup>b</sup>
<u>P. milvina</u>	19	0	1.80 $\pm$ 0.3	0.40 $\pm$ 0.2	0.01
<u>P. saxatilis</u>	10	0	1.70 $\pm$ 0.4	0.75 $\pm$ 0.2	0.02
<u>P. milvina</u> &	29 <sup>c</sup>	0	1.73 $\pm$ 0.3	0.63 $\pm$ 0.2	0.001
<u>P. saxatilis</u>					

<sup>a</sup>L. dispar larvae were killed less often than E. amitaria ( $P = 0.0001$ ) and S. idiota ( $P = 0.006$ ).

<sup>b</sup>P-values calculated using the Wilcoxon signed-rank test for E. amitaria versus P. idiota larval prey.

<sup>c</sup>one P. milvina died during 24h testing.

**Table 3.5.** Effectiveness of primary and secondary defenses of E. amitaria larvae against predation by spiders.

Larval Reaction	<u>Spider/larva; interaction outcomes</u>			
	Number of larvae			
	Killed	Escaped	Abandoned	Unharmed
<u>lycosids</u>				
Thrash/regurgitate <sup>a</sup>	20	2	3	0
Motionless <sup>b</sup>	3	0	0	11
No reaction	2	0	0	0
<u>salticids</u>				
Thrash/regurgitate <sup>a</sup>	5	11	2	2
Motionless <sup>b</sup>	0	0	0	17
No reaction	2	0	0	0

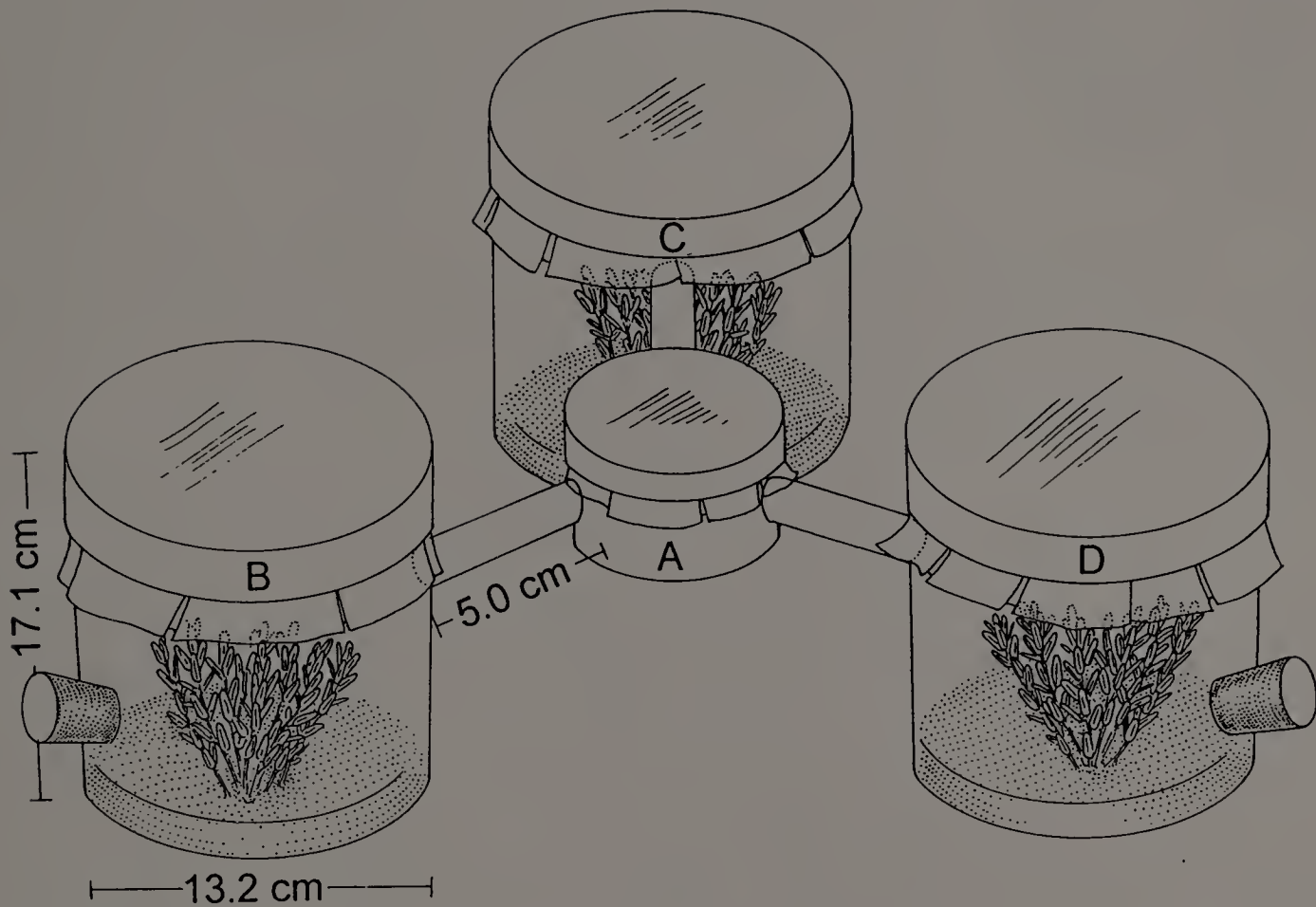
<sup>a</sup>Thrashing and regurgitating are the potential secondary defenses of E. amitaria larvae.

<sup>b</sup>“Motionless” represents the morphological and behavioral crypsis that is the potential primary defense of E. amitaria larvae.

**Table 3.6.** Percent of larval prey types killed in choice tests and direct observations by lycosid and salticid spiders.

	Larvae killed			
	<u>E. amitaria</u>	<u>L. dispar</u>	<u>S. sulfureana</u>	<u>P. idiota</u>
<u>Choice tests</u>				
salticids	22%	0%	7%	*
(N=20)	(44/200)	(0/200)	(13/200)	
lycosids	18%	0%	*	6%
(N=29)	(53/290)	(0/290)		(18/290)
<u>Direct observations</u>				
salticids	18%	0%	0%	*
(N=22)	(7/39)	(0/33)	(7/72)	
lycosids	61%	7%	*	0%
(N=53)	(25/41)	(4/54)		(0/48)

<sup>a</sup>percent = the number of larvae killed ÷ the total number of encounters observed (for the specified spider-larva combination).



**Figure 3.1.** 3-choice arena design. (A) Central release chamber where a spider was released at the beginning of a test. (B), (C) & (D) Arenas with cranberry vine where 10 larvae were placed. For salticid tests, each arena had either E. amitaria, S. sulfureana, or L. dispar larvae. For lycosid tests, each arena had either E. amitaria, P. idiota, or L. dispar larvae



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