8-1999

The effects of predator presence on insect behavior: consequences for individual fitness, population growth and pest suppression in agroecosystems

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Recommended Citation

Rivers, Rebecca Young, "The effects of predator presence on insect behavior: consequences for individual fitness, population growth and pest suppression in agroecosystems. " PhD diss., University of Tennessee, 1999.
https://trace.tennessee.edu/utk_graddiss/8915

To the Graduate Council:

I am submitting herewith a dissertation written by Rebecca Young Rivers entitled "The effects of predator presence on insect behavior: consequences for individual fitness, population growth and pest suppression in agroecosystems." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

Susan E. Riechert, Major Professor

We have read this dissertation and recommend its acceptance:

Dewey L. Bunting II, Paris L. Lambdin, M. L. Pan

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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M. L. Pan

Accepted for the Council:

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Associate Vice Chancellor and
Dean of The Graduate School

THE EFFECTS OF PREDATOR PRESENCE ON INSECT BEHAVIOR: CONSEQUENCES FOR INDIVIDUAL FITNESS , POPULATION GROWTH AND PEST SUPPRESSION IN AGROECOSYSTEMS

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Rebecca Young Rivers

August 1999

DEDICATION

For my grandfathers,

Kenneth Graham Morris (1908-1993)
and
Robert Edmund Stanley Young (1907-1993)

who first taught me to love the land
and to listen to its teachings

and for

Sarah Elizabeth Rivers (Born 1997)

who teaches me daily the meaning of joy.

ACKNOWLEDGMENTS

I am deeply grateful to the many people who have contributed their time, energy and resources to this work. First, I would like to thank Susan Riechert for serving as mentor and advisor to me during my years at the University of Tennessee. She has taught me many valuable lessons. Her red pen and forthright comments have made me both a better scientist and a better person. She and her husband, Mac Post, generously offered me the use of their farm in Powell for field work, along with tools and supplies necessary for its completion. Their family often allowed me to impose at odd hours, as I was gathering and returning equipment or rushing to meet deadlines. I am very thankful for their collective availability and openness.

My doctoral committee has been consistently supportive of me during my graduate career. Each member made suggestions that significantly improved the quality of this work. In particular, I thank Dewey Bunting for helping me get out of many a statistical quagmire. I thank Paris Lambdin for his insightful comments regarding experimental design, as well as his commitment to helping me improve my writing. I thank M.L. Pan for being an exceptional role model in the classroom, and for helping me to keep perspective at several critical junctures. I could not have been more pleased with the wise advice, constructive criticism and words of encouragement that these three individuals have given me over the years.

I am also especially grateful to Gary Huxel for collaborating with me on this project. Without him, I shudder to think how long it would have taken to get the computer simulation up and running. I particularly appreciated his prompt responses to my questions and his "can do" attitude. I am very fortunate to have had the opportunity to work with him.

Many other individuals have provided assistance without which this project could not have been completed. My research was funded in part by a Grant-in-Aid of Research from Sigma Xi and by the National Women's Farm and Garden Association. I am honored to have received their financial support. For helping me in the field, I extend my gratitude to Andrea Bixler, Kim Brown, Ivich Fraser, Rikki Hall, Heather Harris, Kendra Lawrence, William Rivers, Theresa Roberts, and Diana Wolfram and her children, Karen, Matt and Becky. I appreciate all their hard work on my behalf. Diana Wolfram and Sue Sewing, Rikki Hall and Danielle Mahanes and Suzi and Leo Blakeman made their property available to me for collecting specimens and making observations. I also thank the University of Tennessee for the use of the Cherokee woodlot.

Over the years, the members of the spider group at UT have made many helpful suggestions that improved this work. I am especially grateful to Kim Norris, Jennifer Maupin, and Monica Beals for their intelligent ideas and encouragement. Sam Marshall and Nicholas McCletchie also deserve special recognition for some early methodological suggestions and for telling me just what I needed to hear when I was struggling through my first two years. I am thankful to Rikki Hall for asking challenging questions that forced me to clarify my thinking about the indirect effects of predation.

During the writing of this dissertation, I received support in many forms, for which I will be eternally grateful. Diana Wolfram and Sue Sewing opened their home to me so that I had a quiet place to write without distractions. Amber Edmiston, Everett Lyde and Amelia Wallace, Lissa McLeod, and Linda McMillan lovingly cared for my daughter so that I could focus on my work. My mother, Barbara Young, held our home together during the "eleventh hour" crunch. Her alchemy is in these pages. Great meals, great love and great optimism

transformed into sentences and paragraphs. There are no words for how much these gifts meant to me and my family.

Lastly, I want to recognize the individuals who have given me the emotional support I needed to complete this degree. I thank my parents, Robert and Barbara Young, for setting me on an academic path and for never failing to believe in me. I am grateful to my sister, Kathleen Young Bellamy, for seeing the best in me even when I feel the worst is more obvious. She is a source of inspiration in my life. I am also fortunate to have many wonderful friends who have lent their support along the way. Sheila Frodermann, Vickie Henry, Jan Leone, Virginia Rassmussen and Hilary Sandler helped me find the strength to take this journey. Jonathan Bender, Julie Meltzer and Karen Hussion have encouraged me from afar. I am also grateful to Jane Howard and Joyce Wool Rosenfeld for all that they have taught me over the years. The many members of the Knoxville Relaxation and Crafting Kibbutz made my time at UT more enjoyable. Special thanks to Andrea Bixler, Jen Harris, Beth and Todd Vincent, Debby, Paul and Kassie Andreadis, Katie Ellis and Ti Crossman. Without them, these years would have been much more difficult and much less fun. I also want to thank Melora Doan and Lissa McLeod for the thousands of ways in which they enrich my life. They have taught me much about love, courage and friendship.

In the two short years since her birth, my daughter, Sarah, has helped me grow in countless ways that have made me a better person. I will always be grateful to her for her own unique contributions to this work. Finally, I thank my husband, Wil Rivers, for all that he is and all that he has done for me. Without him, this would have been a much lonelier journey.

ABSTRACT

Organisms respond to the presence of foraging predators with a variety of antipredator strategies including escape responses, microhabitat shifts, and the restriction of conspicuous activities such as movement, foraging, and reproduction. Although these effects have been well-documented in aquatic systems, relatively little information is available about their impacts in terrestrial systems. In addition, because conceptual models of predator-prey interactions form the basis of our understanding of pest suppression in agroecosystems, information regarding the impact of predator presence on economically important pest insects may help us to better understand the qualities embodied by successful biological control agents. In this two-part study, I examined the impacts of predator presence on the feeding activity of insects in garden test systems. In the first part, a series of experiments paired pest insects with single, spider species to measure the relative contributions of direct mortality and predator-induced reductions of feeding activity to reductions in crop damage. Direct mortality accounted for approximately 15% of the observed reduction in crop damage while predator-presence effects accounted for an additional 10-40% depending on the system. In the second part of this study, I present a detailed examination of a single system in which predator-presence effects proved to be important. An individual-based computer simulation of the fifth larval instar of the small, white cabbage butterfly, *Pieris rapae* L. was developed in conjunction with Dr. Gary Huxel of the University of California at Davis. This simulation incorporated experimentally-derived estimates of feeding activity and growth under predation pressure. The simulation was run at three different predator densities to evaluate the impact of predator-presence effects on population growth. At high densities, predators significantly lengthen the maturation time for fifth-instar *P. rapae* larvae resulting in probable losses of fitness and slowed population growth. These effects are discussed within the context of their ecological and evolutionary significance, as well as their implications for the biological control of insect pests in agroecosystems.

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PART I

THE EFFECTS OF PREDATOR PRESENCE ON PREY BEHAVIOR

A. Introduction

It is well known that as a predator forages in a given area, the rate at which it captures prey in its immediate vicinity decreases (Charnov et al. 1976). Much of this decrease is thought to be due to changes in prey behavior that reduce detection and capture. Because predation is so costly with respect to individual fitness, behavioral changes such as escape responses, microhabitat shifts, and the depression of conspicuous behaviors may have selective advantages for prey when predators are near. The purpose of this chapter is to review the literature on predator-induced changes in prey behavior and to discuss the implications of these changes at the level of the individual, population and community.

B. Escape Responses

Escape responses are directed movements of limited duration that are performed to evade an attacking predator. A considerable body of evidence suggests that they are commonly invoked as anti-predator strategies. Examples of taxa in which escape responses have been documented include rotifers (Gilbert 1985; Gilbert and Kirk 1988), asteroids (Mauzey et al. 1968; Van Veldhuizen and Oakes 1981), holothuroids (Legault and Himmelman 1993), bivalves (Mackie et al. 1968; Legault and Himmelman 1993), gastropods (Bullock 1953; Feder 1963), crustaceans (Stein 1977; Li and Li 1979; Main 1987;

Scarratt and Godin 1992), insects (Ruth et al. 1975; Soluk and Collins 1988; McConnell and Kring 1990), arachnids (Riechert and Hedrick 1990; Jackson et al. 1993), reptiles and amphibians (Bauwens and Thoen 1981; Taylor 1983), and birds (Buitron 1983; Curio et al. 1983; Cresswell 1993). In many cases, these responses appear to be successful, reactive defenses, employed when primary defense strategies such as cryptic coloration or microhabitat shifts fail (Sih 1987).

Some escape responses, however, can result in significant costs for the prey. For example, the presence of foraging spiders accelerates the breakup of larval aggregations of the lepidopterans *Spodoptera littoralis* Boisduval (Mansour et. al. 1981) and *S. litura* (Fabr.) (Nakasuji et. al. 1973). Larvae drop off their host plants and frequently fail to return. Thus, they survive their initial encounter with a predator only to be subjected to alternative agents of mortality. The authors hypothesize that the source of mortality for these larvae is primarily exposure to unfavorable microclimates. Ectothermic organisms are particularly vulnerable to even short periods in extreme environments. For these species, ending up in an inhospitable microenvironment is an unfortunate and potentially lethal consequence of escaping a predator. For example, the desert-dwelling grasshopper, *Trimerotropis pallidipennis* (Burmeister), is constrained in its antipredator behavior by high temperatures (Chappell 1983). During the day, these animals rest under shady shrubs to reduce their heat load. Attacks by lizard predators force them out of the shrubs and into open areas where they can quickly overheat.

Another example comes from the work of Roitberg et al. (1979) on the pea aphid, *Acyrthosiphon pisum* (Harris), which readily dislodges from its host plants in the presence of predatory coccinellids. Dislodged individuals are quickly threatened by overheating and dessication and must find new host plants rapidly to survive. Roitberg and Myers (1979) reported that in hot, dry areas, mortality due to unfavorable ground conditions is high enough to select for those aphids which exhibit some response other than dropping from the plant. Thus, it may be that exposure to the bare ground environment surrounding plants in agroecosystems is a significant source of mortality for some insects.

Predator avoidance may also lead to exposure to secondary predators, a phenomenon sometimes referred to as "prey flushing". Gerbils respond to the presence of owl predators by seeking cover in bushes (Kotler et al. 1991). Although this affords them safety from owl attacks, it increases the likelihood that they will be eaten by snakes (Kotler et al. 1993). Cryptic, bottom-dwelling larvae of the mayfly genus *Ephemerella* become more detectable to benthic fish when they engage in escape responses following encounters with predatory stoneflies (Soluk and Collins 1988). An indirect mutualism between crayfish and smallmouth bass has negative impacts on the johnny darter, *Etheostoma nigrum* Rafinesque. Crayfish drive the darters out of refuges where they become more vulnerable to attack by smallmouth bass, *Micropterus dolomieui* Lacepede (Rahel and Stein 1988). Conversely, smallmouth bass drive the darters into shelters occupied by the crayfish, enhancing the predatory success of the crayfish. Similarly, on coral reefs, octopi and moray eels drive small fish and crustaceans out of protective crevices where they are captured by groupers (Diamant and Shpigel 1985). Prey flushing of this type has also been reported between hogsuckers, *Hypentelium nigricans* (LeSueur), and smallmouth bass (Rankin 1986), and tropical birds and army ants (Willis 1969).

In agroecosystems, insects dislodged from host plants by predators are not only exposed to an unfavorable microhabitat, but also to other natural enemies. The absence of structural complexity in tilled ground between crop rows affords very little enemy-free space (*sensu* Jeffries and Lawton 1984). Vulnerability to ground-dwelling predators (i.e., spiders, carabid beetles and ants) is probably high.

C. Microhabitat Shifts

The presence of predators has important effects on the distribution of prey in space (Zaret and Suffern 1976; Stein 1977; Petranka 1983; Vuorinen et al. 1983; Cooper 1984; Wellborn and Robinson 1987; Jedrzejewski and Jedrzejewska 1989; Watts 1991) and time (Taylor 1983; Caldwell 1986; Helfman 1986; Holomuzki 1986; Peckarsky and McIntosh 1998). Many organisms increase their use of refuges when predators are near. For example, caridean shrimp migrate to the tops of seagrass blades where increased canopy density precludes maneuvering by pinfish predators (Main 1987). The libellulid dragonfly, *Pachydiplax longipennis* (Burmeister), seeks refuge from the bluegill sunfish, *Lepomis macrochirus* Rafinesque in leaf axils of aquatic macrophytes (Wellborn and Robinson 1987). Larvae of the smallmouthed salamander, *Ambystoma texanum* (Matthes), the two-lined salamander, *Eurycea bislineata* Green, and the Cope's grey treefrog, *Hyla chrysocelis* Cope, spend more time in refuges when the water in their aquaria is conditioned with the chemical cues of the sunfish, *Lepomis cyanellus* Rafinesque (Kats 1988; Petranka et al. 1987). Florida harvester ants, *Pogonomyrmex badius* (Latreille), respond to the removal of conspecifics (simulating predation) by decreasing their above-ground activity and shifting the entrances to their colonies to areas with grass overhangs and leaf cover (Gentry 1974).

If the increased use of refuges decreases foraging opportunities or restricts access to high quality forage, organisms will have to make trade-offs that balance the conflicting demands of resource acquisition and predation risk (Sih 1980, 1982; Cerri and Fraser 1983; Lima et al. 1985; Abrahams and Dill 1989). Several studies have shown that as energy demands increase, some organisms will leave refuges and assume greater predation risk (Dill and Fraser 1984; Wellborn and Robinson 1987). However, others remain in protected habitats, making compromises that reduce fitness components such as growth rate and fecundity. For example, small size classes of the bluegill sunfish, *L. macrochirus*, use safer but less profitable habitats in the presence of largemouth bass, *Micropterus salmoides* (Lacepede) (Werner et al. 1983; Belk

1998). Foraging return rates in these vegetated refuges are only one-third the rates of open habitats so that individuals that forage in them experience a 27% reduction in growth rate (Werner et al. 1983). Similarly, isopods who remain in algal mats in the presence of a sunfish predator have access to lower quality forage than those who venture out into open areas (Holomuzki and Short 1988). In the laboratory, isopods fed this lower quality forage had significantly lower growth rates than their counterparts in higher quality habitats. Harrassment by *Polistes* wasps drives buckmoth caterpillars, *Hemileuca lucina*, into the interior of host plants where cool temperatures and mature leaves (i.e., an inferior food source) double larval development time and lower weight gain by 30% (Stamp and Bowers 1990a, 1991). Populations of *Daphnia* that migrate between surface and deep water microhabitats in response to diurnal variability in predation risk have growth rates and birth rates that are significantly lower than those that do not migrate (Orcutt and Porter 1983; Stich and Lampert 1984; Dawidowicz and Loose 1992b; Loose and Dawidowicz 1994). The observed reduction in growth rate appears to be due to metabolic retardation brought on by exposure to the reduced temperatures of the hypolimnion (Orcutt and Porter 1983; Stich and Lampert 1984), while reductions in birth rates are a function of the combined influences of temperature and differences in food quality between the two microhabitats (Stich and Lampert 1984; Dawidowicz and Loose 1992b; Loose and Dawidowicz1994).

D. Reduction of Conspicuous Behaviors

Overall Activity

A strong correlation exists between activity level and predation risk (Dill and Fraser 1984; Gilliam and Fraser 1987; Bergelson and Lawton 1988; Lawler 1989; McPeek 1990; Azevedo-Ramos et al. 1992; Skelly 1994). Organisms that are more active appear to be more vulnerable to detection by predators than those that are less active. Empirical evidence demonstrates that reductions in activity are common responses to predator presence across a diverse group of taxa (Table 1.1). By decreasing activity levels, potential prey decrease their detectability and gain a selective advantage in predator-prey encounters.

There is no evidence that reduction in overall activity levels *per se* has any associated fitness costs. However, Werner (1991) argues that because all fitness related functions (i.e., food acquisition, courtship, mating, etc.) require activity for their discharge, these functions generate selection pressures for enhanced activity levels. Thus, selection for reduced activity should be counterbalanced to some degree by selection for activity when that activity enhances individual fitness.

Occasionally, prey species respond to the presence of a predator by increasing their overall activity levels (Li and Li 1979; Peckarsky 1980; Williams 1986). In stream communities, mayfly species that become more active in the presence of stonefly predators are those that are benthic and

Table 1.1- Selected studies that show that the presence of a predator causes a reduction in overall activity levels of prey.

PREY	PREDATOR	REFERENCE(S)
Fish		
Threespine Sticklebacks, *Gasterosteus aculeatus* L.	Great Blue Herons, *Ardea herodias* L. (a)	Giles 1981, 1983; Godin and Sproul 1988
Johnny Darters, *Etheostoma nigrum* Rafinesque	Smallmouth Bass, *Micropterus dolomieui*	Rahel & Stein 1988
Salamanders		
Two-Lined Salamader, *Eurycea bislineata* (l)	Brook Trout, *Salvelinus fontinalis* (Mitchill) (a)	Resetarits 1991
	Spring Salamander, *Gyrinophilus porphyriticus* (Green) (l)	Resetarits 1991
Anurans		
American Toad, *Bufo americanus* Holbrook (l)	Dragonfly, *Anax junius* (l)	Skelly & Werner 1990; Anholt et al. 1996
Fowler's Toad, *Bufo woodhousei* (Girard) (l)	Red-Spotted Newt, *Notophthalmus viridescens* (Rafinesque) (a)	Lawler 1989
	Black-banded Sunfish, *Enneacanthus obesus* (Girard) (a)	Lawler 1989
Gray Treefrog, *Hyla versicolor* LeConte (1)	Tiger Salamander, *Ambystoma tigrinum tigrinum* (Green) (1)	Skelly 1991
	Red-Spotted Newt, *Notophthalmus viridescens*	Lawler 1989

(a)-Adult, (l)-Larva, (j)-Juvenile, no distinction-unspecified or mixed age class

Table 1.1- (continued)

PREY	PREDATOR	REFERENCE(S)
Anurans (continued)		
Gray Treefrog, *Hyla versicolor* LeConte (1)	Black-banded Sunfish, *Enneacanthus obesus* (a)	Lawler 1989
	Dragonfly, *Pantala* sp. (l)	Lawler 1989
Pine Barren's Treefrog, *Hyla andersonii* Baird (l)	Red-Spotted Newt, *Notophthalmus viridescens* (1)	Lawler 1989
	Black-banded Sunfish, *Enneacanthus obesus* (a)	Lawler 1989
	Dragonfly, *Pantala* sp. (l)	Lawler 1989
Spring Peeper, *Hyla crucifer* (Wied-Neuwied) (l)	Red-Spotted Newt, *Notophthalmus viridescens* (1)	Lawler 1989
	Black-banded Sunfish, *Enneacanthus obesus* (a)	Lawler 1989
	Dragonfly, *Pantala* sp. (l)	Lawler 1989
Green Frog, *Rana clamitans* Latreille (l)	Dragonfly, *Anax junius* (l)	Werner 1991
Bullfrog, *Rana catesbiana* (Shaw) (l)	Dragonfly, Anax junius (l)	Werner 1991
Terrestrial Insects		
Locust, *Schistocerca gregaria* (Forskal) (n)	Water-dragon, *Physignathus cocinensis*	Gillett & Gonta 1978

(a)-Adult, (l)-Larva, (j)-Juvenile, no distinction-unspecified or mixed age class

Table 1.1- (continued)

PREY	PREDATOR	REFERENCE(S)
Aquatic Insects		
Backswimmer, *Notonecta hoffmanni* Hungerford (j)	Backswimmer, *Notonecta hoffmanni* (a)	Sih 1982
Mosquito, *Culex pipiens* L. (l)	Backswimmer, *Notonecta undulata* Say (a)	Sih 1986
Mosquito, *Aedes aegypti* (L.) (l)	Backswimmer, *Notonecta undulata* (a)	Sih 1986
Midge, *Chironomus tentans* Fabricius (l)	Fish	Macchiusi & Baker 1992
Damselfly, *Coenagrion puella* (l)	Threespine Sticklebacks, *Gasterosteus aculeatus*	Convey 1988
	Tenspine Sticklebacks, *Pungitius pungitius* (L.)	Convey 1988
Damselfly, *Ischnura elegans* (l)	Fish	Heads 1985, 1986
Damselfly,*Ischnura verticalis* (Say) (l)	Sunfish, *Lepomis gibbosus* (L.) (a)	Dixon & Baker 1988
Stonefly, *Phasganophora capitata* (Pictet) (l)	Trout	Williams 1986
Stonefly, *Megarcys signata* Ricker (l)	Brook Trout, *Salvelinus fontinalis* (Mitchill)	Peckarsky & McIntosh 1998
Mayfly, *Baetis bicaudatus* Dodds (l)	Brook Trout, *Salvelinus fontinalis*	Peckarsky & McIntosh 1998
	Stonefly, *Megarcys signata* (l)	Peckarsky & McIntosh 1998
Mayfly, *Ephemerella subvaria* Mcdunnough (l)	Stonefly, *Acroneuria lycorias* (Newman) (l)	Peckarsky 1980

(a)-Adult, (l)-Larva, (j)-Juvenile, no distinction-unspecified or mixed age class

Table 1.1- (continued)

PREY	PREDATOR	REFERENCE(S)
Aquatic Insects (continued)		
Mayfly *Ephemerella infrequens* Mcdunnough(l))	Stonefly, *Kogotus modestus* (Banks) (l)	Peckarsky 1980
Velid Bug, *Microvelia austrina* Torre-bueno (l)	Sunfish, *Lepomis cyanellus* (a)	Sih 1988
Other Aquatic Invertebrates		
Isopod, *Lirceus fontinalis* Rafinesque-Schmalz (a)	Sunfish, *Lepomis cyanellus* (a)	Holomuzki & Short 1988; Huang & Sih 1990
Crayfish, *Orconectes propinquus* (Girard) (a)	Smallmouth Bass, *Micropterus dolomieui* (a)	Stein & Magnuson 1976
Crayfish, *Cambarus bartonii* (Fabricius) (a)	Brook Trout, *Salvelinus fontinalis* (a)	Resetarits 1991
	Spring Salamander, *Gyrinophilus porphyriticus* (l)	Resetarits 1991
Crayfish, *Astacus astacus* (L.) (j)	Perch, *Perca fluviatilis* L. (u)	Hamrin 1987
Rotifer, *Asplanchna girodi* DeGeurre	Copepod, *Acanthocyclops vernalis* Fischer (a)	Li & Li 1979
Cladoceran, *Ceriodaphnia reticulata* (Jurine)	Copepod, *Acanthocyclops vernalis* (a)	Li & Li 1979
Copepod, *Cyclops vicinus* Uljanin	Beam	Winfield & Townsend 1983
Mammals		
Deermice, *Peromyscus maniculatus* (Wagner)	Short-Eared Owl, *Asio flammeus* (Pontoppidan) (a)	Clarke 1983
Fruit Bats, *Artibeus jamaicensis* Leach	Various Predators	Morrison 1978

(a)-Adult, (l)-Larva, (j)-Juvenile, no distinction-unspecified or mixed age class

have normally low activity levels (Peckarsky 1980). Thus, it may be that increases in activity observed among some prey are due to evasive behaviors or "moving target" strategies in which repetitive motions confuse predators or make capture difficult (Main 1987).

Foraging

Optimal foraging theory predicts that organisms should act to maximize their net rate of energy intake (Emlen 1966; MacArthur and Pianka 1966; Schoener 1971; Charnov 1976). However, it has become widely accepted that predation risk places constraints on foraging behavior which cause deviations from optimality predictions (Hassell and Southwood 1978; Sih 1980; Lima et al. 1985; Gilliam and Fraser 1987; Newman et al. 1988; Abrahams and Dill 1989; Gotceitas 1990; Nonacs and Dill 1990).

For many organisms, feeding creates a window of vulnerability to predation. Foraging behaviors that are conspicuous and, therefore, risky include travel to and from a feeding site, handling prey items and feeding in exposed environments (Roitberg et al. 1979; Dill and Fraser 1984; Montllor and Bernays 1993). As one might expect, reductions in feeding rates in the presence of predators have been reported for a large number of organisms including crayfish (*Orconectes propinquis*- Stein and Magnuson 1976; Stein 1977), juvenile notonectids (*Notonecta hoffmanni*- Sih 1982), coenagrionid damselflies (*Ischnura elegans* and *I. verticalis*- Heads 1985, 1986; Dixon and Baker 1988), sticklebacks (*Gasterosteus aculeatus*- Godin and Sproul 1988), caridean shrimp (*Tozeuma carolinense* Kingsley- Main 1987), marine snails

(*Thais lamellosa*-Appleton and Palmer 1988), grasshoppers (*Melanoplus femurrubrum* (De Geer)- Schmitz et al. 1997), bluegills (Werner et al. 1983) and mayflies (Peckarsky et al. 1993; Peckarsky and McIntosh 1998). Mechanisms underlying these reductions can include anti-predator behaviors (e.g., increased vigilance) which redirect time away from foraging efforts (Holmes 1984; Ydenberg and Dill 1986; Lima and Dill 1990), decreased movement (as described in Overall Activity, pp. 7-11), and use of inferior foraging sites (as described in C. Microhabitat Shifts, pp. 4-6).

Reductions in foraging activity have the potential to be particularly costly anti-predator strategies because of the degree to which energy intake is coupled to important fitness parameters such as growth rate and fecundity. It is generally assumed that rapid growth is advantageous because it allows an individual to more quickly begin to redirect energy from growth to reproductive output (Rowe and Ludwig 1991; Lafferty 1993). Larger organisms are typically less vulnerable to predation (Price et al. 1980; Sih 1982; Werner et al. 1983; Benrey and Denno 1997) and starvation (Lindsay 1966; Jones 1977; Millar and Hickling 1990; Stockhoff 1991). In addition, body size is an excellent predictor of lifetime fecundity for many organisms (Grison 1957; Jones et al. 1982; Haukioja and Neuvonen 1985). Thus, any behavioral decision which results in reduced energy intake or the redirection of energy away from growth should be viewed as a potential fitness cost.

In some cases, organisms may be able respond to the conflicting demands for energy aquisition and avoidance of predators by developing adaptive strategies that do not result in loss of fitness. Some species are clearly able to modify their behavior in response to variation in perceived risk (Dill and Fraser 1984; Scarrett and Godin 1992). Accurately assessing the relative threats of predation and lost foraging opportunities can enable an organism to change foraging strategies appropriately, thereby reducing costs. For example, juvenile notonectids balance their habitat use in direct response to predation risk (Sih 1980, 1982). Early instars, which are more susceptible to predation from adults, prefer safer habitats with low degrees of profitability, while older instars, which are less susceptible to predation from adults, spend more time in riskier, high profitability habitats. Deer mice (*Peromyscus maniculatus*) forage more efficiently (i.e., they get more food in less time) in the presence of fire ants (*Solenopsis invicta* Buren- Holtcamp et al. 1997). By confining their foraging to rich patches and increasing their in-patch harvest rate, the mice are able to compensate for the additional costs associated with predator presence (i.e., the energy expended to carry food items to cover for handling).

Reproductive Activity

Many behaviors associated with reproduction have conspicuous components that increase predation risk (Magnhagen 1991). Examples include searching for mates (Lloyd 1965; Eberhard 1977; Harris and Todd 1980; Gwynne 1987; Wing 1988; Godin and Briggs 1996), calling or displaying to mates (Cade 1975; Soper et al. 1976; Tuttle and Ryan 1981; Burk 1982; Sakaluk and Belwood 1984; Ryan 1985; Endler 1987), competing for mates (Gwynne and O'Neill 1980; Thornhill 1980; Gwynne and Dodson 1983), copulating (Ward 1986; Sih 1988; Sih et al. 1990) and egg carrying (Mellors 1975; Vuorinen et al. 1983; Winfield and Townsend 1983; Svensson 1988). Despite the considerable attention given to documenting these increased risks, relatively few studies have actually looked at the behavioral trade-offs that animals are undoubtedly making between reproductive activity and predation risk. Several studies have documented reductions in signaling (Tuttle et al. 1982; Ryan 1985; Belwood and Morris 1987; Wing 1988) or searching movements (Knowlton 1980) in response to predator presence, but these studies have not attempted to measure the costs associated with these trade-offs. Strong (1973) found that the length of amplexus in the amphipod *Hyalella azteca* Saussure was inversely correlated with predation intensity in a series of lakes. In this case, shortening the window of vulnerability associated with amplexus lowered predation risk but at the cost of parental certainty. Similarly, a study of mating behavior in the semiaquatic insect, *Microvelia austrina,* showed that tandem duration is reduced in the presence of predators and that these reductions are associated with decreased fertilization rates (Travers and Sih 1991). In addition, sex-ratios for this species are male-biased such that prematurely separating males face especially long search times before new mates are found.

E. Consequences of Predator-Induced Changes in Prey Behavior

The previous sections of this chapter focused on the implications of predator-induced changes in prey behavior on the components of individual fitness. However, the effects of these changes are not limited to the level of the individual. Reductions in fitness due to behaviorally-mediated changes in growth rate, fecundity or reproductive success can slow the growth of populations. They can also affect the dynamics of prey populations by altering their demographic characteristics. For example, age at maturity (or metamorphosis) is an important determinant of the intrinsic growth rate of populations (Roff 1992). Predator-induced changes in activity levels and foraging behavior can strongly influence age at maturity (Vanni 1987; Crowl and Covich 1990; Skelly and Werner 1990; Rowe and Ludwig 1991; Stibor 1992) resulting in important effects on population growth. Another impact on prey populations is additional mortality due to starvation resulting from severe limitations on foraging (e.g., Schmitz et al. 1997) or lethal escape responses (see A. Escape Responses, pp. 1-4).

In addition, predator-induced changes in prey behavior appear to play an important role in mediating interspecific interactions within communities. In a study of two coexisting species of anuran larvae, Werner (1991) found that larvae of the green frog, *Rana clamitans*, grow to just over half the size of their bullfrog competitors (*R. catesbeiana*) in the presence of the odonate predator, *Anax junius*. Both species reduce their activity levels and change their patterns of space use to avoid predation. However, the negative impacts of these behavioral changes are considerably greater for the green frog than for the bullfrog. Thus, the competitive dynamics between the two species are altered by the differential effects of behavioral depression.

Huang and Sih (1990) report that the dynamics between non-competing species can be influenced by predator-induced changes in prey behavior as well. In experimental pools, the presence of the isopod, *Lirceus fontinalis,* enhanced the survival of larval small-mouthed salamanders (*Ambystoma texanum*) in the presence of green sunfish. The mechanism was that the presence of isopods increased sunfish activity levels, eliciting stronger anti-predator behaviors from the salamander larvae.

Several empirical studies demonstrate that behavioral mechanisms alone are sufficient to initiate trophic cascades through food webs. Power et al. (1985) demonstrated that intimidation by piscivorous bass (*Micropterus* spp.) reduces the grazing activity of minnows (*Campostoma anomalum* (Rafinesque)) in stream pools resulting in changes in algal distribution and abundance. Similarly, the presence of brook trout and *Megarcys* stoneflies restricts the feeding activity of the mayfly, *Baetis bicaudatus,* leading to significant increases in algal biomass in streams (Peckarsky and McIntosh 1998). The addition of bass to experimental pools causes shifts in habitat use by bluegills, resulting in pronounced differences in zooplankton abundance and size structure (Turner and Mittlebach 1990). In an old-field ecosystem, the nursery web spider, *Pisaurina mira* (Walckanaer), reduces the feeding activity of grasshoppers (*Melanoplus femurrubrum*), decreasing the impact that the grasshoppers have on grass biomass (Schmitz et al. 1997).

F. Rationale for this Study

Peckarsky et al. (1993) argued that sublethal costs of predator avoidance are "nearly universal" consequences for organisms foraging under predation risk. However, the bulk of the empirical evidence supporting this conclusion comes from aquatic systems (see Dill 1987, Kerfoot and Sih 1987 and Peckarsky et al. 1993 for reviews). In terrestrial systems, there is considerably less information about the extent of these effects (which I refer to as "predator-presence" effects). A few studies in the behavioral and ecological literature document the existence of predator-presence effects on mammals (e.g., Clarke 1983; Holmes 1984; Lima et al. 1985; Kotler et al. 1993) and birds (e.g., Lendrem 1983; Lima 1988; Watts 1991). Stamp and Bowers (1988, 1991, 1993) conclude that caterpillars alter their foraging behavior in response to harassment by predatory wasps (*Polistes* sp.) and stinkbugs (*Podisus maculiventris* (Say)). These changes reduce survivorship and growth rate and increase larval development time. Schmitz et al. (1997) report that the spider, *Pisaurina mira*, influences the feeding behavior of grasshoppers, *Melanoplus femurrubrum*. However, if we are to conclude that the costs associated with predator-induced changes in foraging activity are universal and important, we need more information about their role in terrestrial systems.

In this two-part study, the impacts of predator presence on the feeding activity of insects in garden test systems were examined. In the first part, I performed a series of experiments which paired pest insects with single, spider species to measure the relative contributions of direct mortality and predator-induced reductions of feeding activity to reductions in crop damage. In the second part of the study, I completed a detailed examination of a single system in which predator-presence effects proved to be important. An individual-based computer simulation of the fifth larval instar of the small, white cabbage butterfly, *Pieris rapae* L. was developed in collaboration with Dr. Gary Huxel at the University of California at Davis. This simulation incorporated experimentally-derived estimates of feeding activity and growth under predation pressure. Three predator densities were used in assessing the impact of predator-presence effects on population growth. This study is unique in that it evaluates the effects of predator presence on individual fitness and population growth in a system where the findings have implications for pest suppression in agroecosystems.

PART II

PEST SUPPRESSION IN AGROECOSYSTEMS: THE RELATIVE CONTRIBUTIONS OF DIRECT MORTALITY AND PREDATOR-PRESENCE EFFECTS

A. Introduction

Predator-prey theory is of particular interest to those who seek to suppress pest populations in agroecosystems. Theoretical models are commonly used to generate predictions about the circumstances under which biological control agents will be successful (Murdoch et al. 1985; Riechert et al. 1999). These models (e.g., Lotka 1925; Volterra 1926; Nicholson 1933; Nicholson and Bailey 1935; Beddington et al. 1976; Free et al. 1977; Hassell 1978; Lawton and McNeill 1979) specify the conditions under which predators will regulate populations of their prey. These predictions and the empirical work they have generated (e.g., Caltagirone 1981; Erlinge et al. 1984; Messier and Crete 1985; Reynolds et al. 1988) have formed the foundation of our approach to biological control. However, there continues to be considerable interest in adding new levels of sophistication to conceptual models of predator-prey interactions so that we may better understand how predators act in agroecosystems (Taylor 1984; Hassell 1978). One area that has not received sufficient attention is the role that predator-induced impacts on prey behavior play in reducing herbivore damage to host plants.

Biological control agents can reduce plant damage in agroecosystems by developing stable population interactions with their prey. This can be accomplished through density-dependent tracking (Solomon 1949; Holling 1959; Readshaw 1973) or equilibrium point control (DeAngelis et al. 1975; Tanner 1975; Post and Travis 1979). In either case, several mechanisms can be involved. Both of these interactions limit prey populations by direct consumption of prey. However, predators can reduce prey numbers further by inducing mortality following encounters (i.e., through injury or dislodgment from the plant into unfavorable microenvironments (Roitberg et al. 1979; Roitberg and Myers 1979). They can also reduce prey fitness through impacts on prey behavior (see Part I: The Effects of Predator Presence on Prey Behavior, for a review). Of these actions, only the reduction of prey densities by predator consumption of prey has been well documented (see Sih et al. 1985 for a review). It remains the primary prey control paradigm, despite increasing evidence that the behavioral impacts of predators may be as important, or even more important than direct mortality in limiting prey population growth (Sih 1987; Peckarsky et al. 1993; Werner 1991; Schmitz et al. 1997).

Biological control agents may also be able to reduce pest damage in agroecosystems by depressing insect feeding activity to the point where plants are released from herbivory (as is the case in an old-field ecosystem- Schmitz et al. 1997). Predator-induced trophic cascades that are mediated entirely by effects on prey behaviors have recently begun to receive attention in the ecological literature (Schmitz et al. 1997; Peckarsky and McIntosh 1998). Although Strong (1992) initially predicted that trophic cascades would not occur in terrestrial ecosystems, empirical evidence to the contrary has come from studies involving generalist predators in both agroecosystems (Riechert and Bishop 1990; Carter and Rypstra 1995) and old-field ecosystems (Moran et al. 1996; Schmitz et al. 1997; Moran and Hurd 1998). These studies have shown reductions of insect densities and/or biomass associated with increased predator densities.

Schmitz et al. (1997) further found that grasshoppers forage less in the presence of the spider, *Pisaurina mira,* resulting in decreased consumption of plant biomass and enhanced mortality from starvation. Because of similarities between treatments in which spiders preyed freely on grasshoppers and those in which grasshoppers were exposed to spiders with glued chelicerae to prevent predation, they conclude that predator-induced depression of prey feeding behavior actually drives the trophic cascade in the old field ecosystem. In light of these results, it is possible that the reductions in plant damage and insect biomass reported in these other studies may be due in part to reduced feeding activity associated with predator presence. Riechert and Bishop (1990) found a 60-70% reduction in plant damage associated with elevated densities of spiders in a mixed-vegetable system. This estimate is a useful starting point for the partitioning of the effects of reduced insect numbers and reduced insect feeding on plant damage.

The purpose of the study reported here is to determine whether or not the presence of spiders influences the feeding activity of several important garden pests. In addition, I compare the impact of feeding losses with reductions in insect numbers as explanations for observed trophic cascades in agroecosystems. To measure the relative contributions of predator-induced mortality and behavioral depression to reduced herbivory, field experiments were performed using spiders and insects in eight test systems. In each test system, the three treatments included were: 1) a predation treatment in which a free-ranging spider consumed some of the insects feeding on a host plant; 2) a predator presence treatment in which a spider was present on the host plant but did not consume any insects (see B. Methods for a description of manipulations), and 3) a control treatment in which no spider was present on the host plant. In this way, I tested the null hypothesis that there is no effect of spider presence on the foraging activity of insects.

B. Methods

In an effort to integrate the results of eight separate experiments without undue repetition, I divided this section into two parts. The first part gives an overview of the experiments with a discussion of methods that were common to all. The second part gives specific information regarding the methods of each trial. In addition, pertinent aspects of the eight experiments are summarized in Table 2.1 for quick reference.

I. General Methods

Test Subjects

Insects- I tested the effects of predator presence on foraging by six insect species in field experiments using bagged host plants. I used a variety of insect species in my investigations to look for generalities across taxa (Table

Table 2.1- Summary of eight trials performed to assess the relative contributions of predator-induced mortality and predator-presence effects on insect consumption of plant material.

Trial #	Insect (#/Plant)	Spider	Host Plant	n
1	*Pieris rapae* L. (5)	*Phidippus audax* (Hentz)	*Brassica oleracea* var. *acephala* (DC.)	6
2	*Poecilocapsus lineatus* (Fabricius) (3)	*Pardosa saxitilis* (Hentz)	*Plantago major* L.	12
3	*Gastrophysa viridula* (De Geer) (3)	*Rabidosa rabida* (Walckenaer)	*Rumex crispus* L.	6
4	*Phyllotreta zimmermanni* (5) (Fabricius)	*Araneus cavaticus* (Keyserling)	*Brassica oleracea* var. *acephala* (DC.)	6
5	*Phyllotreta zimmermanni* (5) (Fabricius)	*Frontinella pyramitela* (Walckenaer)	*Brassica oleracea* var. *acephala* (DC.)	6
6	*Murgantia histrionica* (Hahn) (3)	*Pardosa saxitilis* (Hentz)	*Brassica oleracea* var. *acephala* (DC.)	6
7	*Anasa tristis* (De Geer) (3)	*Pisaurina mira* (Walckenaer)	*Cucurbita pepo* var. *zucchini* L.	6
8	*Anasa tristis* (De Geer) (3)	*Rabidosa punctulata* (Hentz)	*Cucurbita pepo* var. *zucchini* L.	6

2.2). The rationale for choosing these species was two-fold: (1) they are economically important pests or their close relatives, so that this work may contribute to biological control efforts, and (2) they were available at the time of the trials in sufficiently large numbers to permit replication of treatments. The imported cabbageworm (*Pieris rapae* L.), four-lined plant bug (*Poecilocapsus lineata* (Fabricius)), green dock beetle (*Gastrophysa viridula* (De Geer)), and harlequin bug (*Murgantia histrionica* (Hahn)), were each tested with a single spider species. Because of relatively large populations, the flea beetle (*Phyllotreta zimmermanni* (Crotch)) and squash bug (*Anasa tristis* (De Geer)), were each tested in two trials, using two different spider species. Insects were field collected from several locations prior to the trial (for descriptions of locations see Part II- Individual Trials). Identifications were made using Borror and White (1970), Wilcox (1972), Bland and Jacques (1978), Arnett et al. (1980) and Smith (1985). In the laboratory, all insects were maintained in either in circular plastic containers (15.5 cm. in diameter, 6.5 cm. in height) or rectangular plastic containers (20 cm X 9 cm X 8 cm) and held in the laboratory at approximately 26°C with a 16:8 [L:D] photoperiod. All insects were fed fresh, excised host plant leaves daily until the trial (<48 hours).

Spiders- Seven spider species representing four guilds were used as model predators (Table 2.3). Each species met the following criteria: (1) it co-occurred in space and time with the insect selected for the trial in which it was used, (2) it was present in sufficient numbers to permit replication and (3)

Table 2.2 - Insect species used in bag experiments, listed by scientific name with common names and classification into families and orders.

Scientific Name	**Common Name**	**Family**	**Order**
Gastrophysa viridula (De Geer)	Green Dock Beetle	Chrysomelidae	Coleoptera
Phyllotreta zimmermanni (Crotch)	Striped Flea Beetle	Chrysomelidae	Coleoptera
Anasa tristis (De Geer)	Squash Bug	Coreidae	Hemiptera
Poecilocapsus lineatus (Fabricius)	Four-lined Plant Bug	Miridae	Hemiptera
Murgantia histrionica (Hahn)	Harlequin Bug	Pentatomidae	Hemiptera
Pieris rapae L.	Imported Cabbageworm	Pieridae	Lepidoptera

it was observed taking the insect selected for the trial as a prey item in preliminary observations made under natural conditions. Spiders were field collected and maintained individually in rectangular plastic containers (20 cm X 9 cm X 8 cm) in the laboratory under the same temperature and photoperiod conditions as the insects (see above for specific values). Feeding regimes were different for spiders in the different trials, so I will discuss them further in the section on individual trials. However, all spiders were provided with fresh water in small petri dishes.

Host Plants- The host plants used in each of the different trials are listed in Table 2.4. They were chosen because they are known to be preferred food plants for the insect species being tested. I selected collards (*Brassica oleracea* var. *acephala*) as a representative host for insects that feed on members of the Brassicaceae family because the flat leaves of this variety are relatively easy to measure, compared with varieties that form heads.

Host plants were selected from either old-field locations or experimental garden plots (see descriptions under individual trials below). Individual plants were chosen at random from a pre-determined group that belonged to the same general size class. Once plants were selected, they were further standardized for size and leaf number to reduce variation associated with structural heterogeneity. Older leaves that were yellowed or toughened were removed because many insect species show both a preference for younger leaves (Barbosa and Greenblatt 1979; Lowman 1985; Thomas 1987;

Table 2.3- Spider species used in bag experiments, listed by scientific name with family and guild classifications. Guilds are taken from Post and Riechert (1977).

Scientific Name	**Family**	**Guild**
Rabidosa rabida (Walckenaer)	Lycosidae	Diurnal Hunters
Rabidosa punctulata (Hentz)	Lycosidae	Diurnal Hunters
Pardosa saxitilis (Hentz)	Lycosidae	Diurnal Hunters
Pisaurina mira (Walckenaer)	Pisauridae	Diurnal Hunters
Phidippus audax (Hentz)	Salticidae	Ambush Hunters
Frontinella pyramitela (Walckenaer)	Linyphiidae	Sheet-scattered Line Weavers
Araneus cavaticus (Keyserling)	Araneidae	Orb Weavers

Table 2.4- Host plant species used in bag experiments, listed by scientific name with common names and family classifications.

Scientific Name	**Common Name**	**Family**
Brassica oleracea var. *acephala* (DC.)	Collards	Brassicaceae
Cucurbita pepo var. *zucchini* L.	Zucchini	Cucurbitaceae
Plantago major L.	Broad-Leaved Plantain	Plantaginaceae
Rumex crispus L.	Curly Dock	Polygonaceae

Ernest 1989; Lynch and Simmons 1993) and increased survival, growth and development on younger foliage (Onstad et al. 1986; Larsson and Ohmart 1988; Nafus et al. 1991; Murugan and George 1992; Stamp and Bowers 1994). In preliminary experiments, I determined that all of the host plants tested would increase in size slightly during the four-day trial period. Most of this growth occurred in new leaves at the apical meristem. Thus, to avoid confounding measurements of plant consumption, I also removed the apical meristems and the newest leaves on each plant, in order to limit increases in total leaf area. When necessary, additional leaves were clipped at random so that host plants in a given trial all had the same number of leaves.

Study Sites

All trials except those involving plant bugs were conducted at P&R Farms in Knox County, Tennessee. P&R Farms is a 16 hectare site, containing old-fields and pastures, a maple-sweetgum woodlot, and a 700 m^2 experimental garden. The plant bug trial took place in an old-field adjacent to a private residence, in Anderson County, Tennessee.

Experimental Design and Methods

For each trial, the three treatments evaluated were: a predation by spider treatment in which insect numbers were reduced by a freely foraging spider, a spider presence treatment in which the test spider did not take prey during the trial (see Individual Trial Methods for descriptions of predator manipulations) and a control in which no spider was present. This design was selected in an effort to compare reduction of insect numbers (i.e., the direct effect of predation) with predator-induced depression of foraging activity (i.e., a predator presence effect). Both are hypothesized mechanisms by which plant damage is reduced in agroecosystems when spider densities are elevated. However, levels of spider predation on insects in all but one trial were very low and thus, I was frequently unable to compare plant damage estimates as a way to measure direct effect. For these trials, I calculated an alternative measure of direct effect by determining the mean number of insects killed per spider in each trial.

For the insects that produce visible foliar damage (i.e., the imported cabbageworm, the four-lined plant bug, the green dock beetle and the striped flea beetle), plant damage was assessed before and after the trial as a measure of insect feeding (see Part II- Individual Trials for descriptions of measurement techniques). For the phloem-feeding insects (i.e., the cabbage bug and the squash bug), weight gain during the trial was used as a measure of feeding activity.

Immediately prior to the trial, I slipped a bag made of fine-mesh netting, open at both ends, over each plant and tied it around the base of the plant. Then, I inserted an open-ended square wire frame (0.3 m^3) to prevent the collapse of the bag around the interior of the plant. Each bag was assigned to a treatment at random. Using blunt entomological forceps, I placed the insects directly onto the leaves of the host plants in predetermined locations selected at random. The insect density used for each trial were consistent with natural densities assessed during preliminary observations of unbagged host plants. When insects from more than one location were used in a single trial, assignment to bags and treatments was made at random.

A single spider was inserted into bags in the appropriate treatments (following Riechert and Bishop 1990). The bags were sealed and allowed to stand undisturbed for a 72-h period. On the fourth day, each bag was opened and the condition of each of the insects was recorded. Predation events were confirmed by the presence of empty carcasses or masticated insect remains. In the spider treatment bags, the test spider was collected to assure that it had, in fact, been present and in good condition throughout the duration of the trial.

II. Individual Trial Methods

Year 1

During year #1, an effort was made to separate the effects of predator consumption of prey from predator-induced reductions in prey feeding by manipulating predator mouthparts in the predator presence treatment so that predation could not occur (Peckarsky et al. 1993; Wissinger and McGrady 1994; Schmitz et al. 1997). Thus, the predator consumption treatment was actually a "free spider" treatment, while the predator presence treatment was a "waxed spider" treatment. Spiders in the "waxed spider" treatment were prevented from consuming prey by paraffin casts applied to their chelicerae. Spiders were held in a freezer at approximately 7°C for 1 minute to induce significant torpor. While the animal was immobilized by the cold, molten paraffin was applied to the chelicerae to seal them shut. Control animals (i.e., those used in the free spider treatments) were also subjected to a one minute period in the freezer, as well as handling that simulated the application of paraffin. All spiders were given an acclimation period of approximately 12 hours, following these manipulations before they were used in the trials.

A total of seven trials were performed using the methods described. However, five of those trials failed to yield meaningful results due to the occurrence of significant spider mortality during the trials. The two remaining trials are described later in this section.

Impact of Cheliceral Waxing on Spider Behavior:

To determine whether the waxing procedure or the casts themselves had any significant impact on spider behavior, behavioral observations were made on spiders before and after paraffin casts were applied. For this experiment, field collections of an additional 12 adult, female *Phidippus audax* were made from an old field in Anderson County. Spiders were individually maintained in the laboratory in circular plastic containers (see Test Subjects for specific rearing conditions). During the pre-waxing period, spiders were fed *ad libitum* an array of preferable prey items (e.g., crickets, moths, flies).

Each spider was removed from its container 15 minutes prior to the scheduled start time and placed in a clean observation arena (another circular plastic container). Following the 15-minute acclimation period, I began continuous observations of the animal during which I recorded time spent in the following five behaviors: resting, searching, palpal drumming, grooming, and retreat construction. The criteria used to classify behaviors are shown in

Table 2.5. Each individual was observed for a 15 minute period, three times a day between the hours of 0700-0800, 1300-1400, and 1900-2000. Between observations, the arena was wiped thoroughly with 95% ethanol and allowed to air dry for five minutes. Observations were performed for four days, generating a total of 12 pre-waxing observation periods. On the fourth day, I applied a paraffin cast to the chelicerae of each of the spiders and allowed them to acclimate overnight. I then performed another four days of behavioral observations, as described above.

Trial #1- Imported Cabbageworm (*Pieris rapae*): The imported cabbageworm trial was performed in experimental garden plots of 14-wk old collard plants, *Brassica oleracea* var. *acephala* at P&R Farms. To minimize the possible impacts of spatial heterogeneity on insect feeding patterns, plants to be used as hosts for the larvae were selected from a narrow range of heights (mean ± SE = 59.2 ± 0.44 cm), and standardized (by the procedure described under General Methods) to a leaf number of eight.

Prior to the trial, a map of each plant was drawn, depicting the location and orientation of each leaf. Each leaf was traced directly onto a paper grid divided into 25 squares per cm^2, with a label that identified its location on the map. This enabled me to calculate the pre-trial area of each leaf and compare it with the area of that same leaf after the trial. In addition to tracing the outside perimeter of the leaves, I traced any holes in the interior of the leaf, areas of previous feeding and damaged sections of the leaf, all of which were minimal in pre-trial plants. From these tracings, pre-trial areas of each plant

Table 2.5- Criteria used to classify five behaviors (resting, searching, palpal drumming, grooming and retreat construction) recorded during the evaluation of the impact of cheliceral waxing on the behavior of adult, *P. audax*.

Behavior	**Definition**
Resting	Animal is motionless throughout the observation.
Searching	Animal moves forward or backward, changing the orientation of its cephalothorax frequently and sometimes lifting its front legs or drumming its pedipalps.
Palpal Drumming	Animal is stationary and exercises repetitive, up-and-down movements of the pedipalps. Animal may or may not rear its cephalothorax in conjunction with this activity.
Grooming	Animal draws front legs forward and rubs them over or through the chelicerae.
Retreat Construction	Animal lays silk threads in a sterotyped pattern consistent with the construction of a retreat.

were obtained by counting the number of squares in each tracing. Calculations were made to the nearest 0.01 cm^2.

Early-instar imported cabbageworms were collected from plants in an adjacent plot and held in the laboratory in at densities of five per container. The larvae were checked several times a day and all molts were recorded so that it was possible to know the exact age of each larva used in the trial. Adult female *Phidippus audax* were field collected over a period of one week from P&R farms and the University of Tennessee Woodlot (hereafter described as the UT Woodlot). They were maintained in the laboratory until the start of the experiment during which time they were fed *ad libitum* European crickets, *Acheta domesticus* (Linneus).

On the first day of the trial, I selected 90 newly-molted (<12 hours) fifth-instar imported cabbageworms at random from the group being maintained in the laboratory. Five larvae were placed onto each of 36 host plants. This number was consistent with naturally-occurring densities of cabbageworms at the site. At the conclusion of the trial, leaves were traced onto a second set of paper grids (also divided into 25 squares per cm^2) using the same procedure I used for pre-trial plants described above. Post-trial area determinations were made to the nearest 0.01 cm^2.

Trial #2- Four-Lined Plant Bug (*Poecilocapsus lineata*):

The four-lined plant bug trial was performed in an old field on a naturally occurring population of *Plantago major*. Plants to be used as hosts for the plant bugs were selected from a narrow range of heights (mean ± SE = 8.75 ± 0.248 cm), and standardized (by the procedure described under General Methods) to a leaf number of three.

Prior to the trial, a map of each plant was drawn, depicting the location and orientation of each leaf. In a preliminary experiment, I had previously determined that four-lined plant bugs produce small, round stipple marks on the surface of plants where they have been feeding. The stipple marks are characteristically 1 mm. in diameter and thus, have an area of 0.00785 mm^2. I counted the number of pre-existing stipple marks and multiplied it by 0.00785 mm^2 to calculate the pre-trial amount of plant bug damage.

Adult male and female four-lined plant bugs were collected from four sites: the UT woodlot, an old-field in Anderson County, Tennesee and gardens at two private residences in Knox County, Tennessee. Plant bugs were held in the laboratory in at densities of ten per container. Adult female *Pardosa saxitilis* collected over the course of one week from P&R farms and an old-field in Anderson County. They were maintained in the laboratory until the start of the experiment and fed *ad libitum* assorted moth species.

A density of five plant bugs per host plant was used for this trial. Males and females were distributed at random across both bags and treatments. At the conclusion of the trial, I counted the number of stipple marks on each plant and subtracted the amount of pre-existing damage from the total. Thus, the amount of damage inflicted by the plant bugs during the trial could be calculated.

Years 2 and 3

Because of spider mortality that may be linked to experimental manipulations (see D. Discussion), I abandoned the waxing procedure during years 2 and 3. For the remaining four trials, I partitioned consumption and presence effects by using satiated and hungry spiders. I predicted that spiders in the satiated condition would forage less and, therefore, be less likely to take prey items than spiders who had previously been deprived of food. Thus, during the pre-trial period, spiders assigned to the "satiated" treatment were offered preferable prey items (such as crickets, moths, flies) *ad libitum* in an attempt to satiate them. In contrast, spiders assigned to the "hungry" treatment were fed nothing for the 72 hours immediately prior to the trial.

Trial #3- Green Dock Beetle (Gastrophysa viridula)

The impact of spider presence on the foraging of dock beetles (*Gastrophysa viridula*) was tested on curly dock, *Rumex crispus*, using penultimate female *Rabidosa rabida* as predators. The dock plants used as host plants were from a naturally occurring population located in an old-field at P&R farms. Plants to be used as hosts for the dock beetles were selected from a narrow range of heights (mean ± SE = 19.5 ± 0.76 cm), and standardized (by the procedure described under General Methods) to a leaf number of three.

Female dock beetles were collected from an old-field in Anderson County and held overnight on dock foliage at densities of five per container. *Rabidosa rabida* were collected at P&R farms prior to the trial.

A density of three dock beetles per host plant was used for this trial. The procedure for obtaining pre- and post-trial measurements of plant damage was identical to that used for the imported cabbageworm trial (see description above).

Trials #4 and #5- Striped Flea Beetle (Phyllotreta zimmermanni):

Two flea beetle trials were performed on a population of young (approx. 11 weeks old) collard plants, *Brassica oleracea* var. *acephala* in an experimental garden plot at P&R Farms. Plants to be used as hosts for the flea beetles were selected from a narrow range of heights (mean ± SE = 15.0 ± 0.39 cm), and standardized (by the procedure described under General Methods) to a leaf number of five.

Flea beetles for this trial were collected from plants in an adjacent plot at P&R Farms. They were held in the laboratory at densities of 10 per container. Adult female *Frontinella pyramitela* were collected from two old field locations in Anderson County. Adult female *Araneus cavaticus* (Keyserling) were collected from the eaves of three barns at private residences in Knox County.

A density of five flea beetles per host plant was used for this trial. To obtain measurements of pre-existing damage, I placed a clear, plastic grid divided into 25 squares per cm^2 over the surface of the leaf and marked the area covered by stippling inflicted by flea beetles. The number of squares that were greater than 50% filled by existing damage was recorded and multiplied by the area of the squares (0.02 sq. cm^2) to obtain a value for the total area damaged. Post-trial assessments were made using the same technique and compared with pre-trial areas.

Trials #6- Harlequin Bug (Murgantia histrionica):

The cabbage bug trial was performed on a population of young (approx. nine-week old) collard plants, *Brassica oleracea* var. *acephala* in an experimental garden plot at P&R Farms. Plants to be used as hosts for the harlequin bugs were selected from a narrow range of heights (mean ± SE = 10.97 ± 0.296 cm), and standardized (by the procedure described under General Methods) to a leaf number of five.

Harlequin bugs for this trial were collected from three private gardens: two in Knox County and one in Anderson County. They were held in the laboratory at densities of ten per container. Adult female, *Pardosa saxitilis* were collected at P&R Farms and at two old-fields in Anderson County.

A density of three harlequin bug nymphs per host plant for this trial. Because the damage that harlequin bugs inflict on their host plants is difficult to assess visually, weight gain during the trial was used as an indicator of feeding. Second-instar harlequin bug nymphs were paint marked with enamel paints to permit individual identification (Southwood 1978) and weighed to the nearest 0.0001 g immediately before and after the trial.

Trials #7 and #8- Squash Bug (Anasa tristis):

The squash bug trial was performed on a population of zucchini plants, in an experimental garden plot at P&R Farms. Plants to be used as hosts for the flea beetles were selected from a narrow range of heights (mean ± SE =

26.3 ± 0.69 cm). Standardization was not necessary in this case because all plants had a leaf number of four to begin with.

Squash bugs for this trial were collected from four private gardens: two in Knox County and two in Anderson County. A density of three squash bugs per plant was used. A fishing spider, *Pisaurina mira* and a wolf spider, *Rabidosa punctulata* were collected at the UT Woodlot and at P&R Farms. Adult female *P. mira* were used in the first trial and penultimate female *R. punctulata* were used in the second trial.

A density of three squash bugs per host plant was used in this trial. Squash bugs, like harlequin bugs, do little visual damage to host plants. Thus, weight gain was again used as an indicator of feeding in this trial. Female, adult squash bugs were individually paint-marked and weighed to the nearest 0.0001 g immediately before and after the trial.

Statistical Methods

A priori predictions consistent with the null hypothesis that predator presence alone has no effect on insect foraging included: 1) mean plant damage does not differ between the no spider and spider presence treatments, and 2) mean plant damage is significantly lower in replicates where insects were consumed than in those where spiders were present but did not reduce insect numbers. In trials #1-5, plant damage was subjected to one-way, model I ANOVA where predator condition (i.e., predation, predator presence or no predator) was treated as a fixed effect. Prior to the analysis, all data were tested for normality and homogeneity of variance in accordance with the assumptions of ANOVA (Sokal and Rohlf 1981). Corrections made to particular data sets are described in section C. Where appropriate, Student's t-tests were used as planned comparisons between pairs of treatments. T-tests were one-tailed because my *a priori* predictions were directional in nature (i.e., I predicted plant damage or weight gain would be higher in the control and presence treatments than in the no spiders treatments). For trials #6-8, individual bags were nested within treatments: insects within bags were not considered independent because they were all exposed to the same spider.

For the experiment in which the impact of cheliceral waxing on spider behavior was evaluated, a repeated measures design was used in which twelve individuals were observed prior to and following the application of paraffin casts to the chelicerae. Because of the repeated measures design, a mixed model, two-way ANOVA with replication was used to test for significance of fixed treatment effects. Individual spiders served as the second variable and were considered random. I pooled samples across date and time of day because any variation associated with these factors would be evenly distributed across treatments, and would, therefore, not confound treatment effects. Percentage data from this experiment were arcsine square root transformed prior to ANOVA (Sokal and Rohlf 1981). Because behavioral data sets were not independent, alpha levels were Bonferroni corrected prior to tests of significance.

C. Results

Impact of Cheliceral Waxing on Behavior:

Two of the 12 spiders receiving paraffin casts on their chelicerae died within four days of the procedure. After cheliceral waxing, spiders spent significantly more time resting than they did prior to waxing (Table 2.6; Fig. 2.1). They also spent less time searching than they did prior to waxing, and this difference was marginally significant ($0.09 < \alpha < 0.01$; Table 2.6; Fig. 2.1). Spiders with waxed chelicerae failed to exhibit an increase in grooming behavior, as originally predicted. In fact, spiders made very little attempt to remove the cheliceral casts. Time spent drumming pedipalps and constructing a retreat was reduced following waxing (Fig. 2.1), but these differences were not significant at $\alpha = 0.01$ (Table 2.6). Interactions between treatment effects and individual spiders were significant for resting, searching, and palpal drumming behaviors, indicating that waxing had different effects on different spiders (Table 2.6).

Trial #1- Imported Cabbageworm (*Pieris rapae*):

Only one of the six predation replicates contained evidence of predation. Thus, the remaining five replicates were actually additional predator presence replicates. The replicate in which predation occurred was removed from the plant damage analysis, but the remaining replicates were not pooled because insects in the two treatments were subjected to the presence of spiders of differing activity levels (see Impact of Cheliceral

Table 2.6- Probability values from two-way ANOVAs on percentage of time spent in five behaviors (resting, searching, palpal drumming, grooming and retreat construction) by adult, female *P. audax* prior to and following the application of wax casts to the chelicerae. Effects were considered to be significant at $\alpha = 0.01$ following a Bonferroni correction.

	df	F	P
Resting			
Treatment	1	10.62	<.005
Spider	9	7.15	<.0001
Treatment x Spider	9	2.01	<.05
Error	220		
Searching			
Treatment	1	3.05	<.10
Spider	9	5.23	<.0001
Treatment x Spider	9	2.49	<.01
Error	220		
Palpal Drumming			
Treatment	1	2.23	>.10
Spider	9	6.15	<.0001
Treatment x Spider	9	2.88	<.005
Error	220		
Grooming			
Treatment	1	1.97	>.15
Spider	9	3.42	<.001
Treatment x Spider	9	1.87	>.05
Error	220		
Retreat Construction			
Treatment	1	0.02	>.85
Spider	9	0.80	>.60
Treatment x Spider	9	1.56	>.10
Error	220		

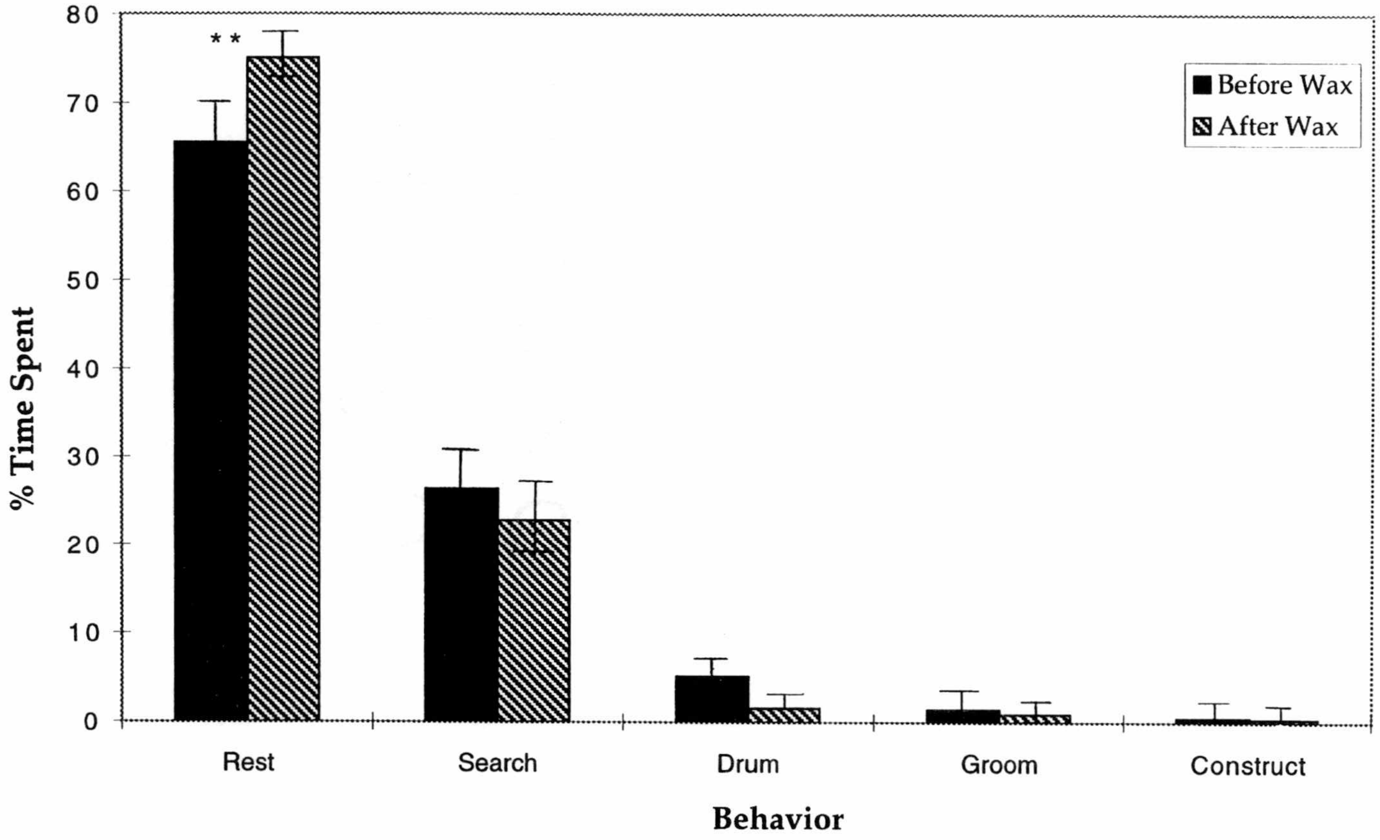


Figure 2.1- Mean percentage (± SE) of time adult, female *P. audax* spent engaged in five behaviors (resting, searching, palpal drumming, grooming and constructing a retreat) before and after cheliceral waxing. ** indicates pairs that are significantly different at $P < .01$.

Waxing on Behavior above). Because of heterogeneous sample variances (Bartlett's Test, F = 4.957, df = 2, P < .01), a Welch's ANOVA was used to test the significance of treatment effects (Welch 1938, 1951; Day and Quinn 1989). Mean plant damage was significantly different between treatments (Welch's ANOVA, F = 5.581, df = 2, P < .05).

Imported cabbageworms consume less plant material in the presence of a spider predator than they do when no spider is present. Plant damage in treatments where a spider was present was 30-35% lower than in control treatments without spiders. Replicates in the predation treatment (now referred to as the "free spider" treatment for this trial because no insects were actually consumed) had the lowest levels of plant damage, followed by those in the predator presence treatment (hereafter referred to as the "waxed spider" treatment). Damage was significantly lower in both the free spider and the waxed spider replicates than in the controls (Table 2.7, Fig. 2.2). The difference between damage levels in the free and waxed spider treatments was not significant at $\alpha = 0.05$ (Table 2.7).

Trial #2- Four-Lined Plant Bug (*Poecilocapsus lineata*):

In the plant bug trial, two of the 12 test spiders in presence replicates died. Because dead spiders cannot exhibit normal foraging patterns, these replicates were omitted from the analysis. Only two spiders in the predation replicates actually ate any plant bugs, and thus, these replicates were also removed from the analysis. As a result, the predation treatment in this trial becomes the free spider treatment and the predator presence treatment

Table 2.7- Mean comparisons for the experiment testing the effects of spider presence on consumption of plant material by imported cabbageworms, *P. rapae*. Treatments are presence of spider with waxed chelicerae (to prevent predation), presence of a spider without waxed chelicerae (i.e, a free spider) and a control with no spider present. The test spider was *P. audax*.

Treatment	**Test**	*df*	**t**	**P**
No Spider vs. Waxed Spider	Student's T-test (AUV)	5	2.128	<.05
Waxed Spider vs. Free Spider	Student's T-test (AEV)	9	-.0274	>.05
No Spider vs. Free Spider	Student's T-test (AUV)	5	2.866	<.05

(AUV)= assuming unequal variances, (AEV)= assuming equal variances, based on Bartlett's tests.

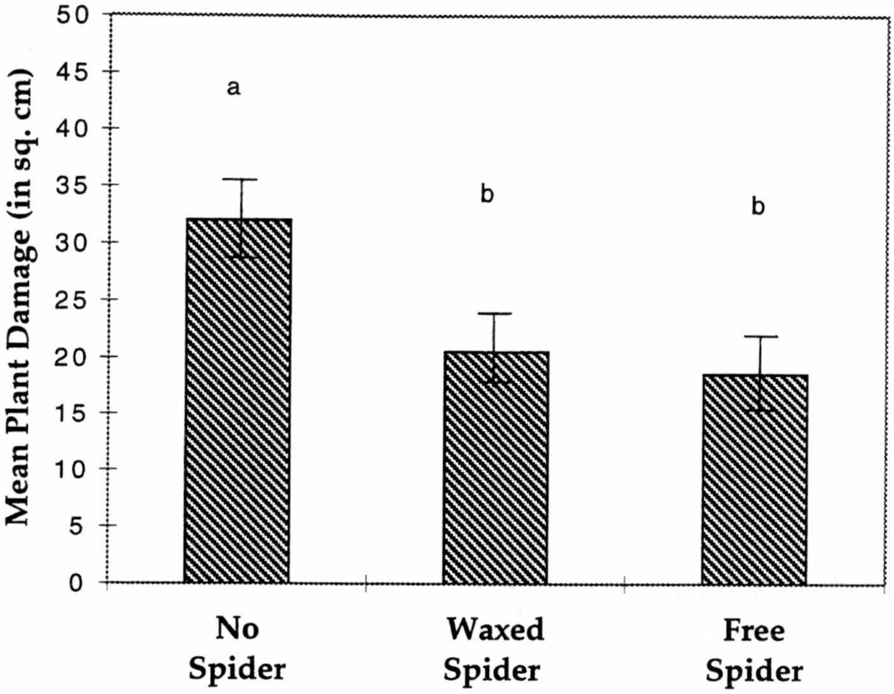


Fig. 2.2- Mean plant damage (± SE) inflicted by imported cabbageworm *P. rapae,* exposed to three predator conditions. Reductions in damage in the free spider treatment are due to presence effects alone, not due to reduction in insect numbers. Different letters indicate significant differences at P < .05.

becomes the waxed spider treatment.

Four-lined plant bugs feed significantly less in the presence of a spider predator than they do when no spider is present. Plant damage was significantly different between the three treatments (Table 2.8, Fig 2.3). Plant damage in the free (unwaxed) treatment was 43% lower than in control treatments without spiders. In this trial, however, it appears that spider activity level plays an important role in mediating the interaction. Waxed spiders (which have been determined to be less active) do not significantly lower the amount of feeding activity by the plant bugs (Table 2.9).

Trial #3- Green Dock Beetle (*Gastrophysa viridula*):

Five of the six replicates in the "hungry spider" treatment contained evidence of beetle consumption. The replicate in which no feeding took place was pooled with the six "satiated spider" replicates to make up the predator presence treatment. The leaf area of the dock plants increased significantly during the trial and so pre-trial areas were scaled using the long axis of the leaf. Mean plant damage differed significantly between the three treatments (Table 2.10) with the lowest levels of plant damage observed in the trials where dock beetles were consumed by spiders (Fig. 2.4). Consumption of plant material by beetles was significantly greater in the predator presence trial than in either the control or the predation treatments (Table 2.11). Differences between the no spider and predation treatments were not significant, but power analysis revealed an 85% chance of committing a Type II error by accepting the null hypothesis (i.e., concluding with statistical

Table 2.8- Results of the one-way ANOVA for the experiment testing the effects of predator presence on consumption of plant material by four-lined plant bugs, *P. lineata.* Treatments are presence of spider with waxed chelicerae (to prevent predation), presence of a spider without waxed chelicerae (i.e., a free spider) and a control with no spider present. The test spider was *P. saxitilis.*

Source of Variation	***df***	**SS**	**MS**	**F Ratio**	**P**
Treatment	2	.232	.116	4.8891	$P < .05$
Error	29	.688	2.37×10^{-2}		
Total	31	.920	3.00×10^{-2}		

Table 2.9- Mean comparisons for the experiment testing the effects of predator presence on consumption of plant material by four-lined plant bugs, *P. lineata.*

Treatment	**Test**	***df***	**t**	**P**
No Spider vs. Waxed Spider	Student's T-test (AEV)	20	-0.277	>.75
Waxed Spider vs. Free Spider	Student's T-test (AEV)	18	-3.212	<.005
No Spider vs. Free Spider	Student's T-test (AEV)	20	-2.562	<.05

(AEV)= assuming equal variances, based on Bartlett's tests.

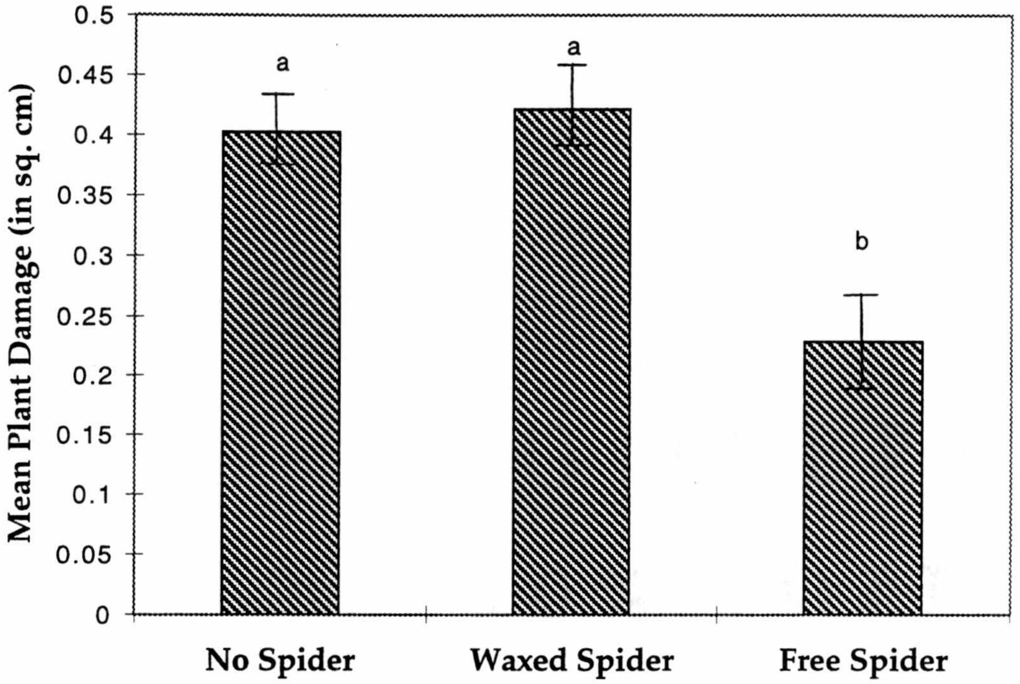


Fig. 2.3- Mean (± SE) plant damage inflicted by four-lined plant bugs *P. lineatus*, exposed to three predator conditions. Reductions in damage in the free spider treatment are due to presence effects alone, not due to reduction in insect numbers. Different letters indicate significant differences at P<.05.

Table 2.10- Results of the one-way ANOVA for the experiment testing the effects of predator presence on consumption of plant material by green dock beetles, *G. viridula*. Treatments are predation by spiders, presence of spider without predation and a control with no spider present. The test spider was *R. rabida*.

Source of Variation	***df***	**SS**	**MS**	**F Ratio**	**P**
Treatment	2	1950.4995	975.250	5.3509	P < .05
Error	15	2733.9018	182.260		
Total	17	4684.4013	275.553		

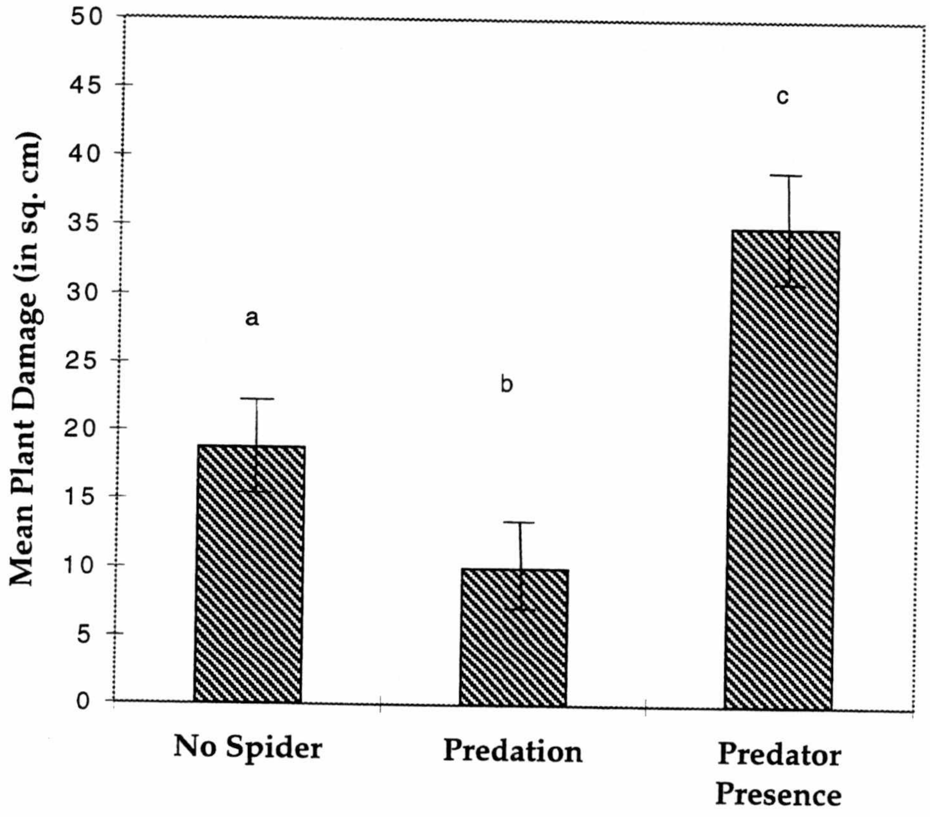


Figure 2.4- Mean (± SE) plant damage inflicted by green dock beetles, *G. viridula* (De Geer), exposed to three predator conditions. Different letters indicate significant differences at P < .05.

confidence that the hypothesized effect did not occur (Cohen 1988), given α = 0.05 and n = 5 and 6.

Trials #4 and #5- Striped Flea Beetle (*Phyllotreta zimmermanni*)

In the flea beetle trials, no flea beetles were consumed by either *F. pyramitela* or *A. cavaticus*. Because no cheliceral waxing was performed in these experiments and hunger was believed to have relatively unimportant impacts on spider behavior (Provencher and Riechert 1991), replicates that were assigned to the predation treatment were pooled with those in the predator presence treatment for the remaining analysis (new n = 12). Student's t-tests and Bartlett's tests were performed on the data prior to the pooling to assure that there were no significant differences in the means or variances of the pooled data sets (between no spider treatments: t = 0.032, df = 10, P > .95; between *F. pyramitela* treatments: t = 1.084, df = 10, P > .30; between *A. cavaticus* treatments: t = 0.397, df = 10, P > .70).

This study failed to show an effect of the presence of *F. pyramitela* on feeding by striped flea beetles. There were no significant differences between feeding levels in the predator presence and control treatments. Mean plant damage was 14% lower in the predator presence treatment using *F. pyramitela*, but this difference was not statistically significant at α=0.05 (Table 2.12; Fig. 2.5). Power analysis revealed a 77% chance of committing a Type II error by accepting the null hypothesis, suggesting that it would be inappropriate to conclude, given the level of replication in this study, that there are no effects of *F. pyramitela* presence on insect feeding.

Table 2.11- Mean comparisons for the experiment testing the effects of predator presence on consumption of plant material by green dock beetles, *G. viridula*.

Treatment	**Test**	***df***	**t**	**P**
No Spider vs. Spider Presence	Student's T-test (AEV)	11	-2.062	>.05
Spider Presence vs. Predation by Spider	Student's T-test (AEV)	10	-3.505	<.01
No Spider vs. Predation by Spider	Student's T-test (AEV)	9	-1.024	<.05

(AEV)= assuming equal variances, based on Bartlett's tests.

In contrast, the presence of *A. cavaticus* did seem to have an impact on feeding activity by striped flea beetles. Plant damage was 18% lower in treatments where *A. cavaticus* was present and this difference was marginally significant (Table 2.12; Fig. 2.5; $0.07 < \alpha < 0.05$). In this case, power analysis revealed an 85% chance of committing a Type II error by accepting the null hypothesis.

Trials #6- Harlequin Bug (*Murgantia histrionica*):

In the harlequin bug trials, four out of the six replicates in the "hungry spider" treatment contained evidence of bug consumption. The remaining two replicates were pooled with the six "satiated spider" replicates to make up the predator presence treatment (new $n = 8$). Weight gain did not differ significantly between individuals in the no spider and spider presence treatments (Table 2.13, Fig 2.6). The power of the test to detect a significant effect of treatment was very low ($1-\beta = 0.07$), given $\alpha = 0.05$ and $n = 8$. There were significant differences in weight gain between bags within treatments (Table 2.13). Thus, it would be inappropriate to conclude, given the level of replication in this study, that there are no effects of *P. saxitilis* presence on insect feeding.

Trials #7 and #8- Squash Bug (*Anasa tristis*):

In Trial #7 using *P. mira* as the test spider, none of the replicates in the "hungry spider" treatment contained evidence of bug consumption. The six "hungry spider" replicates were pooled with the six "satiated spider" replicates to make up the predator presence treatment (new $n=12$). In Trial #8

Table 2.12- Mean comparisons for the experiment testing the effects of predator presence on consumption of plant material by flea beetles, *P. zimmermanni*. Treatments are presence of spider without predation and a control with no spider present. The test spiders are *F. pyramitela* and *A. cavaticus*.

Spider Species/Treatment	**Test**	***df***	**t**	**P**
F. pyrimetela				
No Spider vs. Spider Presence	Student's T-test (AEV)	22	-1.285	> .20
A. cavaticus				
No Spider vs. Spider Presence	Student's T-test (AEV)	22	-1.961	< .07

(AEV)= assuming equal variances, based on Bartlett's tests.

Table 2.13- Results of the nested ANOVA for the experiment testing the effects of predator presence on weight gain in harlequin bugs, *M. histrionica*. Treatments are presence of spider without predation and a control with no spider present. The test spider was *P. saxitilis*.

Source of Variation	***df***	**SS**	**F Ratio**	**P**
Treatment	1	2.1 x 10	0.1904	> .65
Bag [Treatment]	12	3.66 x 10	2.7873	< .05

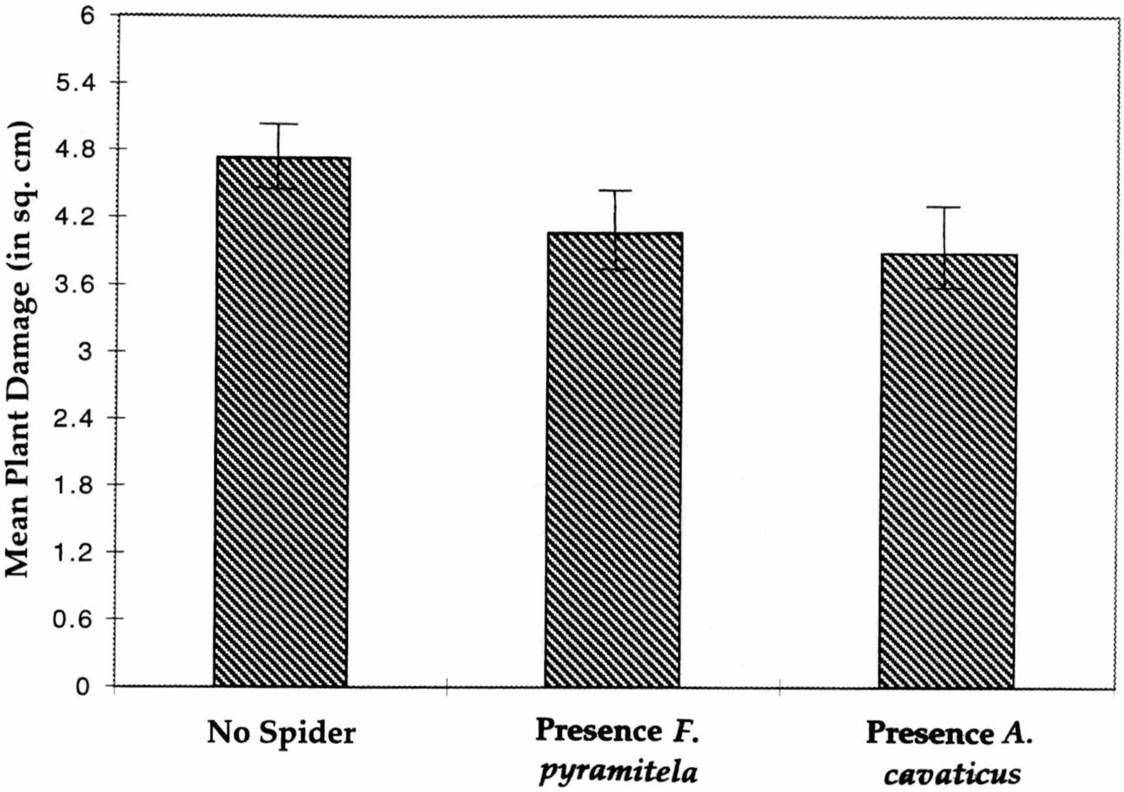


Figure 2.5- Mean (± SE) plant damage inflicted by striped flea beetles, *P. zimmermanni* , in no predator and predator presence treatments using the spiders, *F. pyrimetela* and *A. cavaticus*. Differences were not significant at P < .05.

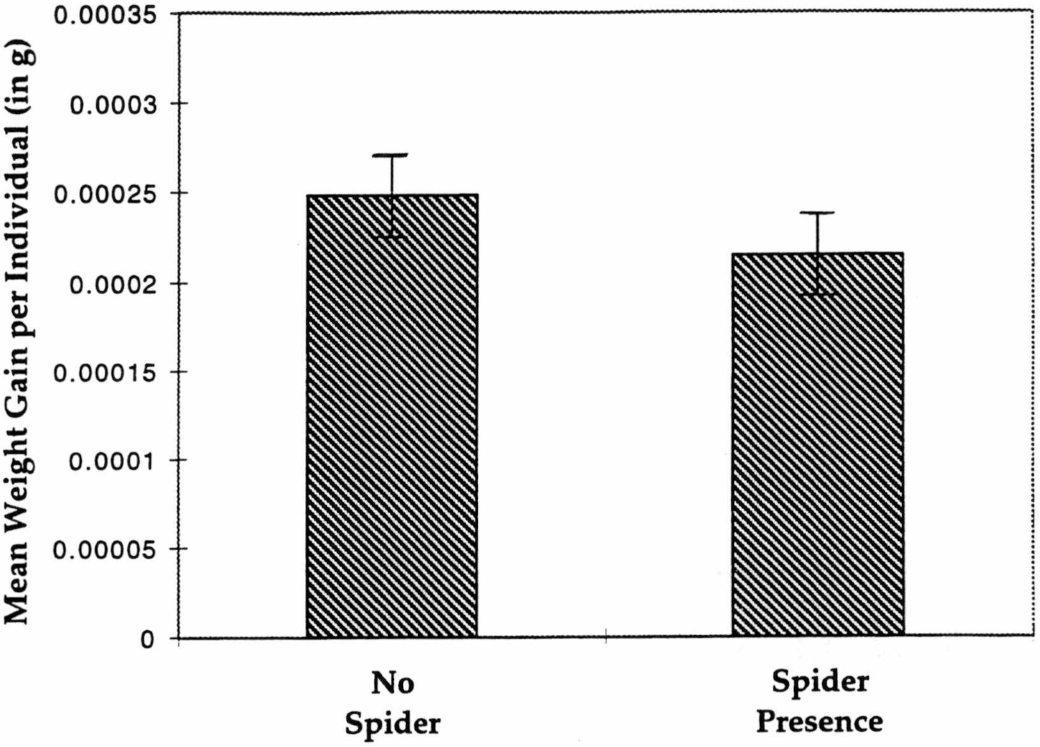


Figure 2.6- Mean weight gained (± SE) by harlequin bugs, *M. histrionica,* in no spider and spider presence treatments. Differences are not significant at P<.05.

using *R. punctulata* as the test spider, five of the replicates in the "hungry spider" treatment contained evidence of bug consumption. The one hungry spider replicate was pooled with the six "satiated spider" replicates to make up the predator presence treatment (new n = 12).

This study failed to show an effect of the presence of *P. mira* on feeding by squash bugs. Weight gain differed significantly between bags within treatments, but not between the no spider and spider presence treatments (Table 2.14, Fig 2.7). Power analysis revealed a 72% chance of making a Type II error by accepting the null hypothesis, given $\alpha = 0.05$ and n = 12.

The presence of *R. punctulata* did seem to have an impact on feeding activity by squash bugs. Squash bugs in the predator presence treatment lost an average of 0.009 g during the trials, compared with the controls which gained 0.002 g. This difference was statistically significant at $\alpha = 0.05$ (Table 2.14, Fig 2.7). Weight gain also differed significantly among bags within treatment.

Table 2.14- Results of the nested ANOVAs for the experiment testing the effects of predator presence on weight gain in squash bugs, *A. tristis*. Treatments are presence of spider without predation and a control with no spider present. The test spiders were *P. mira* and *R. punctulata*.

Spider Species/ Source of Variation	***df***	**SS**	**F Ratio**	**P**
P. mira				
Treatment	1	8.405×10^{-4}	1.9812	>.10
Bag [Treatment]	22	1.874×10^{-2}	2.0085	<.05
R. punctulata				
Treatment	1	1.655×10^{-3}	5.7691	<.05
Bag [Treatment]	12	1.467×10^{-2}	3.0076	<.005

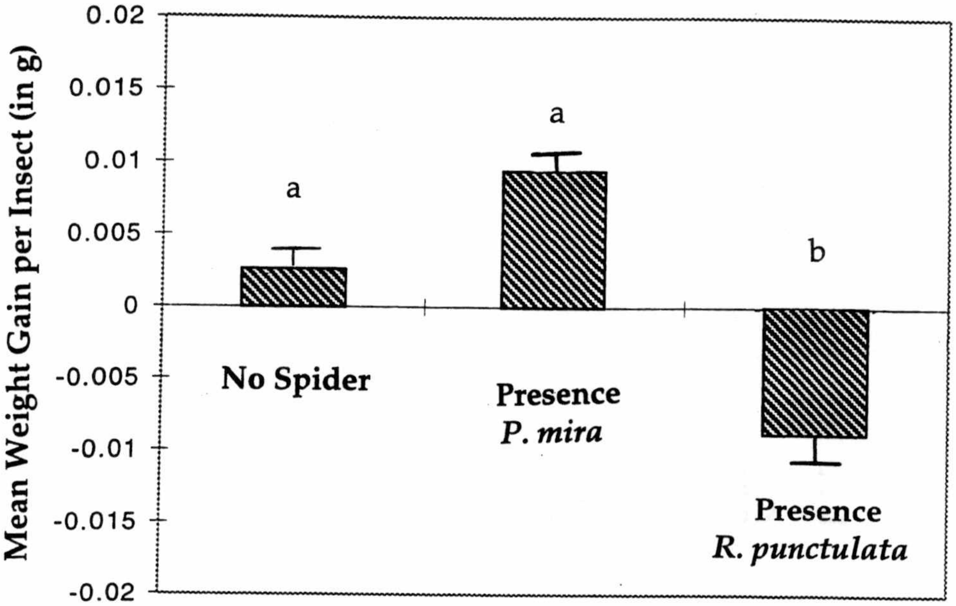


Figure 2.7- Mean weight gained (or lost) (± SE) by squash bugs, *A. tristis,* in no predator and predator presence treatments. Different letters indicate significant differences at $P < .05$.

Summary

Direct mortality inflicted by spiders across trials was relatively low (Table 2.15). For most insect-spiders combinations it was less than 15% (i.e., spiders in a given trials consumed less than 15% of the insects available to them. Predator presence effects varied by trial with some insect-spiders showing strong effects and others showing no effect at all (Table 2.16). Reductions in plant damage associated with significant presence effects were 30-35% for imported cabbageworms, 43% for four-lined plant bugs and 18% for striped flea beetles under the influence of *A. cavaticus*. Squash bugs lose approximately 10% of their body weight in the presence of *R. punctualata*. No significant predator presence effects were detected by this study for striped flea beetles under the influence of *F. pyramitela,* harlequin bugs or squash bugs under the influence of *P. mira*. A significant effect of predator presence in the direction opposite from my initial prediction (i.e., where plant damage was greater in the presence of a predator) was detected for green dock beetles.

Table 2.15- Measurements of direct mortality inflicted by spiders on insects in eight trials. Direct effect is calculated as the mean number of insects consumed by spiders in a given trial.

Trial #	**Test Insect**	**Test Spider**	**Direct Effect**	**n***
1	Imported Cabbageworm	*Phidippus audax*	13.3%	6
2	Four-lined Plant Bug	*Pardosa saxitilis*	13.8%	12
3	Green Dock Beetle	*Rabidosa rabida*	19.4%	12
4	Striped Flea Beetle	*Frontinella pyramitela*	0.0%	12
5	Striped Flea Beetle	*Araneus cavaticus*	0.0%	12
6	Cabbage Bug	*Pardosa saxitilis*	16.7%	12
7	Squash Bug	*Pisaurina mira*	0.0%	12
8	Squash Bug	*Rabidosa punctulata*	16.7%	12

*- **n** refers to the number of replicates in which an unconstrained spider could potentially prey on insects

Table 2.16- A summary of the conclusions drawn from eight trials comparing insect feeding activity in the presence of a predator with that in a no predator control. The null hypothesis (H_0) in this case is that predator presence has no effect on insect feeding activity. N/C= not calculated due to statistically significant differences between treatments at $\alpha = 0.05$.

Trial #*	**H_0**	**P**	**Power**	**Conclusion**
1	Reject H_0	<.05	N/C	Predator presence lowers insect feeding activity.
2	Reject H_0	<.05	N/C	Predator presence lowers insect feeding activity.
3	Reject H_0	<.05	N/C	Predator presence appears to increase insect feeding activity.
4	Fail to Reject H_0	>.05	0.233	This trial fails to show an effect of predator presence on feeding activity.
5	Reject H_0, with caution	$.07<\alpha<.05$	0.466	Predator presence probably lowers insect feeding activity.
6	Fail to Reject H_0	>.65	0.07	This trial fails to show an effect of predator presence on feeding activity.
7	Fail to Reject H_0	>.15	0.281	This trial fails to show an effect of predator presence on feeding activity.
8	Reject H_0	<.001	N/C	Predator presence lowers insect feeding activity.

*- Insect/spider combinations are as follows: Trial #1- Imported cabbageworm (*Pieris rapae* L.)/*Phidippus audax* (Hentz); Trial #2- Four-lined plant bug (*Poecilocapsus lineata* (Fabricius)/*Pardosa saxitilis* (Hentz); Trial #3- Green dock beetle (*Gastrophysa viridula* (De Geer)/*Rabidosa rabida* (Walckenaer); Trial #4- Striped flea beetle (*Phyllotreta zimmermanni* (Crotch)/*Frontinella pyramitela* (Walckenaer); Trial #5- Striped flea beetle (*Phyllotreta zimmermanni* (Crotch)/*Araneus cavaticus* (Keyserling); Trial #6- Harlequin bug (*Murgantia histrionica* (Hahn))/*Pardosa saxitilis* (Hentz); Trial #7- Squash bug (*Anasa tristis* (De Geer))/*Pisaurina mira* (Walckenaer); Trial #8- Squash bug (*Anasa tristis* (De Geer))/*Rabidosa punctulata* (Hentz).

D. Discussion

Impact of Cheliceral Waxing on Spider Behavior

This study demonstrates that the application of paraffin casts to the chelicerae of the spider, *P. audax*, has a significant impact on behavior. After the application of the casts, spiders become less active and engage in less searching activity than they do prior to waxing. Since active hunting is the preferred foraging mode for these animals (Roach 1987), it follows that *P. audax* do not engage in normal foraging activity following the application of cheliceral wax.

Because this effect was tested in a single spider species, it cannot be concluded that the outcome would be the same for other types of spiders. However, there are additional lines of evidence that point to the generality of this effect. In the four-lined plant bug trial (which was the only other trial to use the waxing procedure), there was a significant difference between plant damage in the waxed spider and free spider treatments, suggesting that test spiders in the two treatments may have had different behavior patterns as well. In this case, the test spider was *P. saxitilis*. Cheliceral waxing also impairs the ability of the black-and-yellow garden spider, *Argiope aurantia* (Forskal), to construct its highly stereotyped orb web (*personal observation*). In addition, cheliceral waxing is associated with higher levels of spider mortality relative to unwaxed controls, in field experiments using bagged host plants (R.Y. Rivers, *unpublished data*). Since the trials performed were only of 72 h duration, the cause of death was almost certainly not starvation (Anderson 1974). Probable causes include dehydration or injury incurred during the waxing procedure, either of which would also have potentially significant impacts on behavior. Because of these limitations (i.e., high mortality and significant impacts on behavior), I recommend that investigators avoid the use of paraffin cheliceral casts as a method of constraining spiders for the purpose of examining predator presence effects.

Significant interactions between the treatment (i.e., waxing) and the individual spiders suggests that some of the spiders were more affected by the wax than others or that the waxing affected different spiders in different ways. This could potentially introduce another source of variability into an experiment, further supporting my conclusion that cheliceral waxing is probably not the best way to constrain predators in this type of experiment.

Other studies that have looked at the impact of mouthpart manipulation have not found significant impacts on predator behavior (Peckarsky et al. 1993; Wissinger and McGrady 1994; Schmitz et al. 1997). Schmitz et al. (1997) recently used surgical glue applied to the chelicerae as a way to render spiders incapable of subduing prey, apparently with great success. Surgical glue may induce less mortality in test predators because no heat is used in the application process. It may also have less influence on behavior because it is lighter than the paraffin casts.

Relative Contributions of Direct Mortality and the Effects of Predator Presence

Spiders are known to reduce plant damage by 60-70% in mixed vegetable agroecosystems (Riechert and Bishop 1990). If one assumes that plant damage is roughly proportional to insect numbers, then this study suggests that as little as 15% of that reduction is actually due to predation. Direct mortality in these trials was relatively low (i.e., less than 20%) for all insects except the dock beetle. This was the case despite the fact that most of the test spiders were starved and the close proximity of the spiders and insects in the bags could have artificially elevated encounter rates. Many of the spiders ate nothing at all during the trials. While it is certainly possible that the bags themselves may have altered the behavior of the spiders (e.g., by raising ambient temperatures), corresponding reductions in plant damage in treatments where spiders were present suggest that reduction of feeding activity is an effective antipredator strategy.

This study also suggests that, for spiders who are having an effect on the behavior of their prey, 10-40% of observed reductions in plant damage may be attributable to reductions in insect feeding brought about by predator presence alone. These results lend support to the hypothesis that behavioral mechanisms are playing an important role in some terrestrial trophic cascades (Schmitz et al. 1997). They also suggest that, over longer time-frames, we might expect behavioral impacts to significantly impact the growth of prey populations. From a fitness perspective, feeding is arguably one of the most important components of an organism's behavioral repertoire. For most organisms, food intake is directly related to survivorship (Seale and Beckvar 1980; McNamara and Houston 1987; Nannini and Juliano 1998), growth rate (Robertson and Salt 1981; Werner et al. 1983; Dixon and Baker 1988; Peckarsky et al. 1993; Mackay and Elser 1998), speed of development (Chen et al. 1980; Ball and Baker 1996; Belk 1998) and lifetime fecundity (Hirschfield 1980; Jones et al. 1982; Clements and Boocock 1984; Haukioja and Neuvonen 1985; Gilliam and Fraser 1987; Schwarzkopf 1996; Wheeler 1996; Richardson and Baker 1997). Thus, even brief lapses in feeding can result in significant fitness losses (Richardson and Baker 1997). Adding fitness consequences associated with lost feeding time into classic models of predator-prey systems can make an important contribution where the application of predator-prey dynamic models to biological control problems is concerned. Current estimates based on traditional models may be underestimating the importance of some predators of insect pests.

Further investigation will undoubtedly reveal the importance of predator foraging mode on the magnitude of predator presence effects. Stamp and Bowers (1991) have shown that the importance of direct mortality and predator-presence effects are not necessarily proportional. For example, direct mortality inflicted by *Polistes* wasps accounts for a 36.9% reduction in the survivorship of buckmoth caterpillars, *Hemileuca lucina*. The effect of slowed growth due to predator presence accounts for a 20.3% reduction. In contrast, direct mortality inflicted by the stinkbug, *Podisus maculiventris*, reduces survivorship by 55.8%, but only an additional 2% reduction comes from predator presence effects. The differences in the relative impacts of the two predators come largely from differences in foraging strategy. Wasps spend a lot of time searching plants for caterpillars and thus, alert the caterpillars to their presence with airborne vibrations. In contrast, stinkbugs stealthily search for prey in a manner which does not alert the caterpillars to their presence.

In this study, trials involving a single insect species tested with more than one spider species showed similar differences in effects suggesting that different predators may be giving off cues of different types or intensities. For example, in the striped flea beetle trials, *Araneus cavaticus* seemed to impact prey foraging, but *Frontinella pyramitela* did not. While the low power of this test suggests that the absence of an effect is probably most parsimoniously explained as an artifact of small sample size, it is also potentially indicative of differences between the two predators. Both spiders used in this trial were web-builders which makes them different in their foraging mode than all the other spiders used in the trials. Because these spiders are not moving actively across foliage, any vibrational cues prey might use would come from web construction or spider anti-predator responses (Jackson et al. 1993) and would be expected to be minimal (although they might be enhanced artificially in the relatively close quarters of a bag experiment). Thus, prey responding to the presence of either of these predators would likely be relying on visual or olfactory cues. What is particularly interesting about the results of these two trials that the two spiders seem to differ so markedly in their effect. *Araneus* *cavaticus* is a very large-bodied spider (13 to 22 mm long) while *F. pyramitela* is considerably smaller (3 to 4 mm long) which might account for the difference, if visual cues are important. They also build different types of webs which may have different visual or chemical properties.

In pre-trial observations of the two spiders, I noticed that *F. pyramitela* webs contained many more striped flea beetles than did the webs of *A. cavaticus*. This was probably due both to proximity (*F. pyramitela* webs were in the garden plot itself, nestled among host plants, while *A. cavaticus* webs were high above the plots among tree branches or between fence posts and other high vegetation) and to the density of web threads within their snares (*F. pyramitela* build dense sheet webs while *A. cavaticus* build space (orb) webs). However, these results are also consistent with the hypothesis that the two spider species emit cues of differing type or intensity.

Similar results were obtained in the squash bug trial. *Pisaurina mira* does not seem to significantly impact squash bug feeding while *Rabidosa punctulata* does. Once again, the problem could be small numbers of replicates. However, observations of the two predators reveal very different foraging strategies that may account for the differences. *Pisaurina mira* tends to spend more time actively hunting or sitting-and-waiting for prey in the upper portion of plants among exposed leaves (*personal observation*). Squash bugs tend to congregate primarily at the interior of the plant and along the stems of zucchini plants. Thus, there may naturally be a lower encounter rate between the two. In contrast, *R. punctulata* spend most of their time foraging at the base of the plant where squash bugs are typically more numerous (*personal observation*). This leads to greater predation of squash bugs by *R. punctulata*, but it may also lead to the transmission of more cues by the predator.

This study suggests a third line of evidence supporting the hypothesis that the type and intensity of predator cues play an important role in mediating predator-presence effects, as well. This comes from the conflicting results of the trials involving imported cabbageworms and four-lined plant bugs. In the imported cabbageworm trial, the insects responded equally to the presence of waxed and unwaxed (and, therefore, more active) spiders. In the four-lined plant bug trial, insects responded only to the presence of the unwaxed (or more active) spiders. It is possible that these effects are artifacts of small sample size, particularly considering that the waxing procedure appears to affect some spiders more than others (possibly due to size or other variables). It may also be that *Pardosa saxitilis* is even more strongly affected by waxing than *P. audax*. However, this result is also consistent with the hypothesis that the two insect species detect their predators by using different cues (or conversely, that the two types of predators simply give off different types of cues).

We do not know much about the cues that cabbageworms use to detect the presence of predators, but an understanding of these cues may ultimately shed some light on this result. For example, if visual cues are important then one would expect that larger predator presence effects would be observed where spiders are more active. The only situation in which this wouldn't be true is if imported cabbageworms are able to visually identify spiders that aren't moving. Given that most lepidopteran larvae have limited visual acuity (Ichikawa and Tateda 1982), this seems highly improbable. Vibrational cues alone induce anti-predator responses in a number of lepidopteran larvae including the buckmoth, *Hemileuca lucina* (Stamp and Bowers 1988) and the noctuid *Heliothus puntiger* (Awan 1985). If imported cabbageworms are using primarily vibrational cues, then perception of a predator would depend on attack frequency and would almost certainly be affected by the waxing procedure. If, however, olfactory cues are an important part of the equation, then one might not expect to see differences between waxed spider and free spider treatments. Chemical cues from predators commonly elict anti-predator responses in aquatic insects (Peckarsky and Dodson 1980) and crustaceans (Dodson 1988). In addition, alarm pheromones released from conspecifics encountering a predator at a distance play an important role in the response of some terrestrial insects (Kault et al. 1973) to predator presence. These phenomena have not been investigated for either *P. rapae* or the spider predator used in this trial. However, dragline silk of salticid spiders does contain a pheromone which is recognizable to conspecifics (Willey and Jackson 1993; Jackson 1987). Thus, it is plausible that chemical cues present in silk drag-lines may be recognizable to prey as well.

In contrast, the results of the four-lined plant bug trial suggest that cues that are strongly influenced by spider behavior are playing a role the interactions between four-lined plant bugs and *P. saxitilis*. This suggests that visual or vibrational cues may be more important than chemical cues. Clearly, more research is warranted in this area so that we may better understand the mechanisms by which predators induce reductions in feeding behavior.

The significant increase in plant damage (46.4%) observed in the predator presence treatment of the green dock beetle trial is an unexpected result, especially considering that green dock beetles have a very pronounced dislodgement response when handled (i.e. greater than any other insect in this study, *personal observation*). This difference may be an artifact of high levels of within treatment variability and small sample sizes. However, two possible alternative explanations for these results exist. First, these animals exhibit a pronounced dislodgement response. Because of this, only about 60% of the individuals encountered were successfully collected (R.Y. Rivers, *unpublished data*). This may have resulted in the selection of a subpopulation skewed toward particularly low levels of "fearfulness" (*sensu* Riechert and Hedrick 1990). This explanation would be consistent with both the high levels of consumption in the hungry spider treatment, as well as, the lack of predator presence effects in the satiated spider treatment. It does not, however, explain why the amount of plant damage in the predator presence treatment is significantly greater than in the control. Alternatively, this result may arise from differences in plant nutritional quality that are not evenly distributed between treatments. In this study, a naturally occurring population of *Rumex crispus* was used. Only a minimal attempt was made to control for host quality variation, i.e., by selecting plants of the same general size class. No historical information about the age of these plants, or the distribution of soil nutrition at the study site was obtained. Thus, these plants may differ quite significantly with respect to nutritional quality and these effects would not be controlled for by my design. Given these small sample sizes, differences in host plant quality may have been more important than the effects of predator presence on the feeding activity of *Gastrophysa viridula*.

PART III

PREDATOR PRESENCE EFFECTS ON *PIERIS RAPAE*: AN INDIVIDUAL-BASED COMPUTER SIMULATION

A. Introduction

In Chapter 2, I demonstrated that the presence of the spider predator, *Phidippus audax,* significantly reduced the feeding activity of *Pieris rapae* larvae in a field experiment. Because *P. rapae* is an economically important pest and previous experiments showed that spider presence impacts its feeding activity, I completed further studies on this organism which are presented here.

The experiment described in Chapter 2 was of short duration, relative to the life cycle of the insect, and did not attempt to quantify the impact of reduced feeding on *P. rapae* fitness. In the literature, it is commonly assumed that reductions in feeding activity have negative fitness consequences. However, surprisingly few authors have attempted to quantify fitness losses associated with predator-presence effects on insect feeding. Peckarsky et al. (1993) found that the presence of stonefly predators reduces mayfly body mass by 20-30% and fecundity by 35-60%, depending on food availability. They did not, however, find any effect of predator presence on maturation times. Dixon and Baker (1988) found that instar duration was significantly longer in the coenagrionid damselfly (*Ischnura verticalis*) when exposed to fish predators. However, this was true only for the early instars. Cooper (1984) found that body weights and fecundities of water striders (*Gerris remigis*) in pools without trout were significantly higher than in those where trout were present. His results also suggest that this is true for only part of the year. In

October, trout had a significant impact but in July they did not. Thus, in all three studies, the presence of predators did have some effect on components of prey fitness. Their findings also suggest, however, that it is necessary to actually quantify fitness losses rather than simply assuming that they exist.

In addition, the experiment described in Chapter 2 isolates an interaction between *P. rapae* and a single species of predator. Under natural conditions, prey are exposed to complex, multispecies assemblages of predators with different life histories and foraging strategies. Little is known about the cumulative impacts of non-lethal exposure to multiple predators, though this is an area of current research interest (Peckarsky and McIntosh 1998).

One reason that these two important areas of predator-presence research (i.e., fitness consequences and the cumulative effects of multiple predators) have not received much attention is that they are difficult to pursue using the cage experiments that have become a staple of empirical agroecology. Testing for fitness effects requires long-term cage experiments which may present challenges in terms of predator or prey survivorship. In addition, all but the largest cages can potentially increase interactions between predators in ways that can complicate or obscure behavioral impacts on prey. They can also cause interference between prey, which may artificially elevate activity levels.

A potential alternative to the use of cage experiments is the development of computer simulations of biological phenomena that use a collection of experimentally-derived measurements to obtain estimates of variables of interest (e.g., Travers and Sih 1991; Ayers and Scriber 1994). Provided that the simplifying assumptions of the simulations are appropriate, this approach can generate realistic measures of variables that would be difficult to measure directly in the field. Riechert and Tracy (1975) were able to effectively assess the reproductive success of the desert spider, *Agelenopsis aperta*, at web sites that varied with respect to thermal balance and prey availability using this method. Hammerstein and Riechert (1988) also used this method to construct ESS models of territorial contests between ecotypes of *A. aperta*.

In this study, I estimated the consequences of the entire predator assemblage on the fitness of *P. rapae* by developing an individual-based computer simulation of the fifth larval instar. Individual-based modeling has received considerable attention recently because it departs from the simplifying assumption that all individuals in a population are the same with respect to genetics, behavior, physiology, environmental conditions, etc. (DeAngelis and Gross 1992; Huston et al. 1988). By allowing for individual variation in given parameters, individual-based models generate results and predictions that are more reflective of biological reality. Since part of the reason I performed this study was to determine the cumulative effects of individual antipredator responses on fitness (and, therefore, ultimately population growth), taking an individual-based approach was essential.

The simulation, designed in collaboration with Gary Huxel of the University of California at Davis, uses experimentally-derived measurements of parameters related to the feeding activity of fifth-instar *P. rapae* larvae under predation pressure. The outputs of the simulation are two parameters that are strongly coupled to organismal fitness: fecundity and time to maturation. In addition to fecundity, time to maturation is an important determinant of fitness for caterpillars (Weseloh 1984; Stamp and Bowers 1991; Johnson and Gould 1992; Montllor and Bernays 1993). For imported cabbageworms, which feed openly on host plants, a delay in time to pupation confers increased vulnerability to predators and parasitoids (Loader and Damman 1991; Benrey and Denno 1997). Early maturation may confer a competitive advantage for both ovipositioning females and their larvae. In addition, because many imported cabbageworms feed on crop plants, delayed maturation can increase the likelihood that their host plants will be harvested prior to the completion of the life cycle.

B. The Natural History of *Pieris rapae*

Pieris rapae, the small white cabbage butterfly, is a widely distributed member of the family Pieridae (Ehrlich and Ehrlich 1961). Introduced to Canada in the late 1800's, it spread rapidly throughout North America, becoming an established pest in agroecosystems (Slansky 1974). The larvae, often called imported cabbageworms, feed heavily on cole crops and cruciferous weeds. They are responsible for considerable annual losses to farmers and gardeners alike (Ehrlich and Ehrlich 1961). In the southeastern United States, there are typically five generations per year (Gaines and Kok 1995). The first flight occurs in early May with the eclosion of pupae that have overwintered from the previous fall. In most years, the last generation of larvae emerges in late September or early October.

Females lay eggs singly on both the upper and lower surfaces of host plants. The larvae hatch out and consume their eggshells before moving to the underside of the plant to begin feeding. They pass through five larval instars on their way to maturity. Each instar lasts approximately three days (Slansky 1974) making the total time from hatching to pupation about two weeks. After reaching the third instar, larvae begin to feed on both the upper and lower surfaces of the plant. Feeding by late instars is voracious; more than 20 mg of foliage is consumed per mg of dry weight body mass per day (Slansky and Feeny 1977). Despite the high feeding rate, larvae spend less than 15% of their day feeding (Slansky 1974; Mauricio and Bowers 1990). They feed continuously, i.e. both day and night, but feeding is concentrated into discreet bouts of 2-10 minutes in length, followed by long rest periods of up to 2 hours. Reynolds (1990) believes these "rest periods" to be obligatory because they reflect the time necessary to digest an optimal portion of ingested food. Thus, the total amount of time each larva has available for foraging is reduced by the need for non-feeding time during which digestion takes place.

Eighty-three percent of a cabbageworm's total weight gain occurs in the fifth instar. In this stage, individuals average between 60-85 mg of growth per day (calculations made from data presented in Slansky 1974). The factors leading to pupal initiation are unknown for *P. rapae*, but a study of tobacco hornworm larvae, *Manduca sexta* (L.) suggests that attainment of a threshold weight is a necessary condition (Nijhout 1975). Regardless of whether or not a threshold weight is present in *P. rapae*, weight at pupation is important in the imported cabbageworm because body size is tightly coupled to fecundity, with larger individuals laying up to 20% more eggs than their smaller counterparts (Gilbert 1984a; Jones et al. 1982). Thus, fifth instar imported cabbageworms should strive to minimize lost foraging time to avoid a corresponding loss of fecundity.

Defense strategies of imported cabbageworms are varied. The larvae are pale green in coloration like their host plants and, while resting, align themselves along leaf veins, presumably to further reduce the possibility of detection by a visually-oriented predator (Slansky 1974). They have also been observed retreating several cm from a feeding site following a feeding bout.

This behavior is generally thought to be a manuever to avoid detection by predators who may be using feeding damage as a visual cue (Mauricio and Bowers 1990; Heinrich 1979). Cabbageworms also sequester volatile mustard oil glycosides which probably confer a protective advantage on the larvae against vertebrate predators who would find them distasteful (Slansky 1974).

C. Simplifying Assumptions of the Simulation

In order to manage the size and complexity of the model, I limited the variables induded in the simulation. The justification for these simplifications follows.

Assumption #1- *The fifth instar is the most important, in terms of larval contribution to fitness.*

Because of the time-consuming nature of behavioral observations and logistical considerations associated with obtaining large sample sizes, a single instar was selected for use in the simulation. The fifth instar was chosen because it is the stage of maximum food consumption and maximum growth (Slansky 1974). Eighty-three percent of a cabbageworm's total weight gain occurs in the fifth instar. Because fecundity is a linear function of body size (Gilbert 1984a; Jones et al. 1982), this means that 83% of the biomass contribution to fecundity is obtained during the fifth instar. Thus, the fifth instar seemed a logical place to begin looking for consequences associated with lost feeding time. An added advantage of choosing this instar was that larger larvae were easier to observe in the field.

Some may argue that limiting the simulation to the fifth instar obscures important effects of predators during the earlier stages. It is generally accepted that for arthropods, mortality due to predation is greatest in the early instars. However, Dempster (1967) reports that for cabbageworms, mortality due to predation is relatively constant throughout the developmental period (i.e., ≈ 10% per instar). Early instars succumb to predation by parasitoids while later instars are more vulnerable to wasps and birds. Thus, while predator presence effects on early instars may be important, there is no evidence to suggest that they are necessarily <u>more</u> important than those that occur in the fifth instar.

<u>Assumption #2</u>- *Pupation is initiated following attainment of a threshold weight.*

The exact timing of metamorphosis is often a complex function of diet quality, photoperiod, temperature and circadian periodicity (Beck 1971; Watson et al. 1973; Nijhout 1975; Slansky and Scriber 1985; Beck 1988; Collier and Finch 1992). However, it is generally accepted that lepidopteran larvae must attain a threshold weight for pupation to occur (Nijhout 1975; Webb and Dahlmann 1985; Asano et al. 1987; Odero-Ochieng 1990; Ayers and Scriber 1994). Reaching some minimal size, i.e., the size necessary to produce a functional adult (Slansky and Scriber 1985), initiates the neurohormonal sequence that ultimately leads to pupation. Although there have been no published threshold weights for *P. rapae*, it was possible to obtain these data easily in a laboratory experiment (see *Threshold Weight* below). Thus, attainment of an experimentally-derived threshold weight was used as a way to signal the end of the fifth instar and the beginning of pupation for each individual in the simulation.

Assumption #3- Larval weight gain is a function of feeding time.

Many factors contribute to weight gain in caterpillars including ambient temperature (Scriber and Slansky 1981; Jones et al. 1982; Stamp and Bowers 1990a,b; Casey 1993), nutritional quality of host plants (Slansky and Feeny 1977; Rausher 1981; Stamp and Bowers 1990a; Loader and Damman 1991), and genotype (Gilbert 1984a, 1986). However, the purpose of this simulation is to determine the effects of reduced feeding in the presence of a predator on fitness parameters. Therefore, the assumption was made that potential weight gain is constrained by time available for feeding. This should be the case when both temperature and nutritional quality of host plants are not limiting. This simulation incorporates measurements that were derived between June and early August in east Tennessee. The temperatures during this period range from 18°to 35°C. These temperatures are well above the 10°C reported by Gilbert (1984 b) as the threshold for *P. rapae* development. In addition, measurements were obtained from larvae feeding on *Brassica oleracea* var. *acephala*, a high nutrition host plant for this species (Slansky and Feeny 1977; Benrey and Denno 1997). Thus, I conclude that neither temperature nor host plant quality limited the development of the larvae whose behavior was quantified for this simulation.

D. Methods

The development of an individual-based simulation of populations of fifth-instar *P. rapae* larvae under predation pressure, required the following data:

1) encounter rate between larvae and predators
2) weight upon entering the fifth instar
3) feeding bout and feeding interval lengths for larvae in the absence of predators
4) effect of larval age on feeding bout and feeding interval lengths
5) effect of temperature on feeding bout and feeding interval lengths
5) weight gain equivalents of feeding time
6) threshold weight for pupation
7) qualitative outcomes of predator-prey encounters (i.e., types of encounters and % of each type)
8) predation rate
9) % dislodgement
10) % of dislodging individuals that return to the plant
11) lost feeding time associated with dislodgement
12) lost feeding time associated with non-lethal, predator-prey encounters that do not result in dislodgement
13) the relationship between pupal weight and fecundity

The relationship between pupal weight and fecundity was established for *P. rapae* by Gilbert (1984a). All other parameter estimates were derived in field or laboratory studies described below.

Encounter Rate, Qualitative Outcomes of Encounters and Predation Rate

An experimental plot containing 36 collard plants (*Brassica oleracea* var. *acephala* "Georgia") was established at a private residence in Anderson County in East Tennessee. Seeds were germinated indoors under a growlight and transplanted when the seedlings reached five cm in height. Plants in the plot were arranged in six rows with one meter between rows and one-half meter between plants. All the experiments described in this section were performed in this plot on a naturally occurring infestation of *Pieris rapae* L. The temperature during the experimental period ranged from 18-33°C (mode for observation periods = 24°C).

To determine the rate of encounter between *P. rapae* larvae and potential predators, I performed spot observations of larvae during three time periods: a morning period between 0600-0900 h, an afternoon period between 1100-1400 h and an evening period between 1800-2100 h. These times were selected because they corresponded with the diurnal activity patterns of the predominant predators in this system. Most species of spiders are crepuscular (Riechert and Tracy 1975), while predatory wasps are most active during midday (Gould and Jeanne 1984). Making observations during periods of peak predator activity made it possible to get maximum estimates of predator encounter rates. I performed a total of 285 observations which were evenly distributed between the three time periods.

All observations were made from vantage points within the experimental plot or within a border around the plot's perimeter that had a width of 3 m (Fig. 3.1). The decision to include vantage points outside the experimental plot was made after I began making observations. I determined that some of the more visually oriented predators (i.e., wasps and birds) would not forage at plants immediately adjacent to where I was sitting. Thus, when observations were made from greater than one-half meter, binoculars (10 x 40, 5.2° field) were used for assistance.

The vantage point for each observation was determined by use of the random walk method (Southwood 1978). After the site was selected, I seated myself and identified the nearest host plant. From this host plant, four focal larvae were sequentially selected, one in each of four quadrants delineated using compass points. Occasionally, a host plant had less than four visible larvae, in which case the nearest visible larva from any host plant in the remaining quadrant(s) was selected. If a quadrant had more than one larvae in it, each larva was assigned a number and used a random numbers table to select the focal larva.

After each settling, no data were collected for five minutes to give the larva time to recover from any disturbance I may have caused. This was followed by a fifteen minute observation period, during which I recorded the number of encounters with predators, the outcome of each encounter, and the type of encounter. The two possible types of encounters are hereafter referred to as the air disturbance and capture-release types. The air disturbance encounter entails disruption of the air space surrounding the larva by airborne vibrations of a potential predator. Such disturbances may

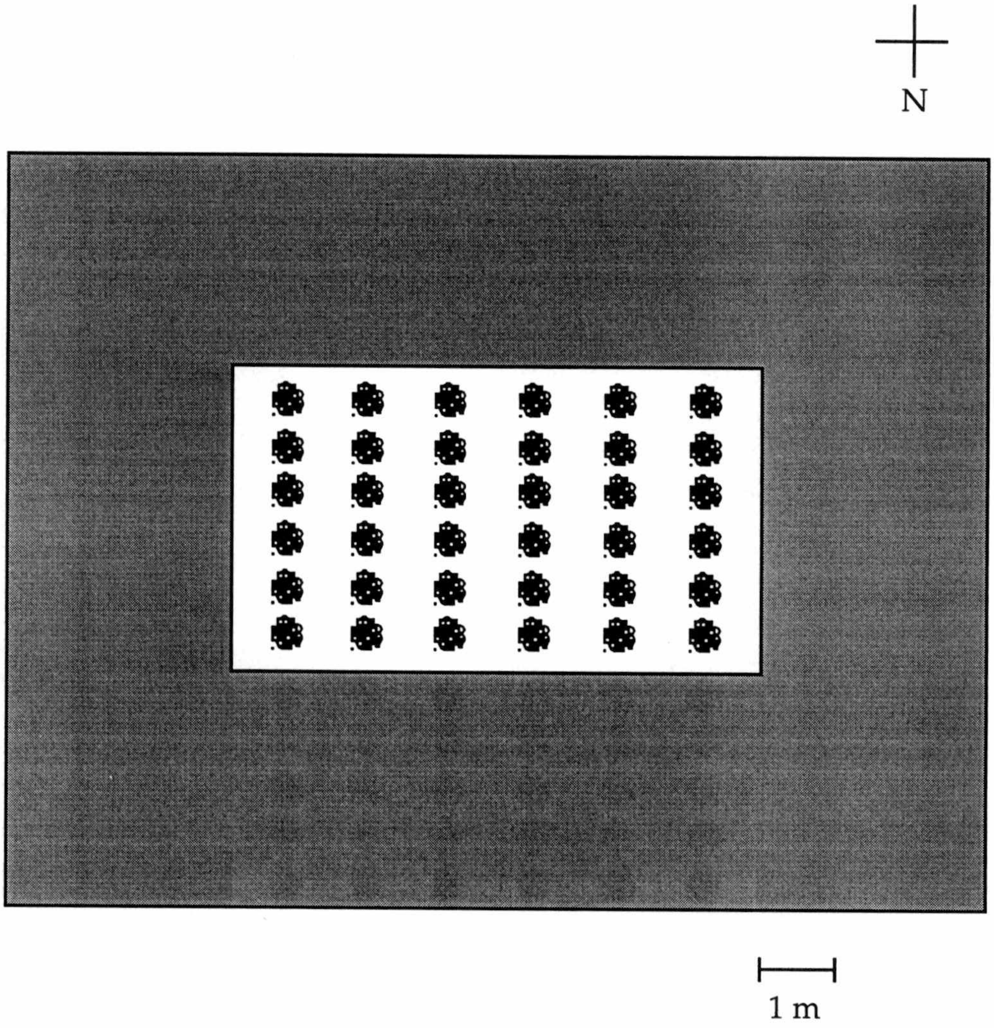


Fig. 3.1- Diagram showing the layout of the experimental plot of *Brassica oleracea* var. *acephala* used for obtaining field-derived parameter estimates. All observations were made either within the plot itself or within a 3 m border around the plot (shown here as the shaded area).

occur when a predator attempts a capture but misses entirely. Lepidopteran larvae are known to possess sensory hairs that enable them to detect disturbances in the air surrounding them (Myers and Smith 1978; Tautz and Markl 1978). Vibrations produced by foraging wasps (Stamp and Bowers 1993) or birds (Riechert and Hedrick 1990) commonly produce such disturbances.

The second possible type of encounter is the capture-release encounter in which a predator makes direct contact with the integument of the larva, but does not kill the larva. In many cases, this type of encounter involves an attack by a predator in which the larva is pinched in the predator's mouthparts but released due to a thrashing or wriggling response. Thrashing and/or wriggling responses are common larval defenses against invertebrate predators (Bardwell and Averill 1997; Gross 1993; Cornell et al. 1987) and have been observed in *P. rapae* larvae as well (Benrey and Denno 1997; *personal observation*). Most of the capture-release encounters were of this type. However, also included in this category are those encounters in which contact was made with the integument without pinching (e.g., a spider trying to subdue the larva by wrapping it with silk). This was a small percentage of the encounters classified as capture-release (<15 %), but I placed them in this category because they elicited responses that were more similar to the encounters that involved pinching than those that involved air disturbances.

Predators were identified to the lowest possible taxonomic level in the field or collected following the observation period for later identification. An encounter was defined as any of the following: 1) consumption of the larva by a predator; 2) touching of the larva by a predator; 3) disturbance of the host plant or air surrounding the larva by a predator; or 4) presence of a predator within a 2.5 cm radius of the larva. The last criterion may or may not constitute an encounter from the larval point of view, since we do not know what cues these animals use to detect the presence of a predator. However, larvae were frequently observed engaging in antipredator behaviors (e.g., cessation of feeding, cessation of movement, withdrawing the head capsule, etc.) when predators were present at this distance, and thus, it was selected as a minimal estimate for the presumed transmission of predator cues.

A total of 55 predator encounters were observed. The predator encounter rate was calculated as the number of observations in which predator encounters were observed divided by the number of total observations. The number of encounters in which larvae were killed following an air disturbance encounter was divided by the total number of encounters classified as air disturbance to get the predation rate for air disturbance encounters. Similarly, the number of encounters in which larvae were killed following a capture-release encounter was divided by the total number of encounters classified as capture-release to get the predation rate for capture-release encounters.

Starting Weights

Fifty first and second instar *P. rapae* larvae were collected from collard plants (*Brassica oleracea* var. *acephala* "Georgia") in an experimental garden located at P & R farms in Knox County in east Tennesseee (see description in

PART II under Study Sites). Larvae were maintained individually in medicine cups in the laboratory at 25° C with a 16:8 [L:D] photoperiod and a relative humidity of 68-74 %. A disk of moistened filter paper was placed on the underside of each lid to add additional humidity. The larvae were fed squares of young (i.e. new leaves from <10 week old plants), excised collard foliage, selected at random from an experimental plot containing host plants (see description under *Study Site* below). The cups were cleaned and the foliage was changed daily. Individual larvae were weighed daily to the nearest 0.0001 g. The width of the head capsule was measured at the level of the most anterior ocelli using a dissecting microscope fitted with an ocular micrometer. The timing of all molts was recorded, as well as the presence of the "muzzle" that forms over the developing head capsule of the new instar as an immediate precursor to the beginning of a molt (Nijhout 1975). Using these methods, I was able to obtain measurements of starting weights for the fifth instar.

Feeding Bout and Feeding Interval Lengths

Feeding bout and feeding interval lengths were measured in undisturbed fifth-instar larvae as part of a larger experiment which included simulated predator attacks (described under *Lost Feeding Time* below). Observations took place in the experimental plot of collard plants previously described. Fifth-instar larvae were selected for testing using the random walk method (Southwood 1978). If a focal caterpillar was already feeding, it was abandoned and a second larva was selected for testing. An appropriate vantage point was selected within 0.5 m of the plant. I waited five minutes after settling before beginning a trial in order to avoid any potential effects of disturbance. The length of the next feeding bout and feeding interval was recorded. Temperature was measured using a protocol described below under *Effects of Temperature.* The length of the feeding bout was recorded as the time during which the larva actually consumed plant material. Movement to a feeding site was not include in the measurements of feeding bout length. The length of the feeding interval was recorded as the time between feeding episodes. Thus, all movement to and from the feeding site is included in this measurement. Forty-three feeding bout-feeding interval combinations were obtained for use in calculating average feeding times in the absence of predators.

Effect of Larval Age

Caterpillars undergo significant changes in somatic size, energy requirements and feeding rates during the course of a single instar (Slansky 1974; Williams 1980; Thomas and Wardlaw 1992; Reavey 1993). Thus, one might expect to see changes in larval feeding patterns that correspond to changes in larval age within an instar. To better understand the mechanisms that control feeding bout and feeding interval length in *P. rapae,* I tested the null hypothesis that larval age has no effect on the duration of feeding bouts or feeding intervals using first generation, laboratory-reared *P. rapae* larvae.

The laboratory colony was established using 75 fifth-instar larvae collected from an experimental plot of collard plants (*Brassica oleracea* var.

acephala), located at P &R farms in Knox County in east Tennessee. The larvae were brought into the laboratory (25° C, 16:8 [L:D] photoperiod, 68-74% RH) and held in circular plastic containers (15.5 cm. in diameter, 6.5 cm. in height) at densities of five per container. Each day, the foliage in the holding containers was replaced with fresh, excised collard leaves, until all the larvae pupated. Pupae were removed from the containers and placed inside a flight cage (90 cm X 45 cm X 30 cm). When adults emerged, artificial flowers (modified from Troetschler et al. 1985) containing a 30% honey solution were placed in the flight cage along with potted collard plants for oviposition. The honey solution in the flowers was refilled daily and exchanged twice weekly for the duration of the adult lifespan.

Following eclosion, the larvae were allowed to feed on the potted collard plants until they reached the third instar. At that time, they were transferred to individual medicine cups where they received squares of young, excised collard foliage, selected at random from the experimental plot at P & R Farms. A disk of moistened filter paper was placed on the underside of each lid to add additional humidity. Cups were cleaned and foliage was changed daily.

Thirty-three newly-emerged (< 6 hours old), fifth-instar larvae were randomly selected from the colony. Larvae were removed from their cups with a paint brush, paint marked with fast-drying, enamel paints for identification, and placed singly on freshly excised leaves whose stems were inserted into small glass vases filled with water. Assignment to a particular leaf, as well as to a location on the leaf, was made at random. Once larvae were placed on host leaves, they were stored during non-observation periods in a large common cage (90 cm X 45 cm X 30 cm) under the same environmental conditions described above but with mesh sides and roof to ensure protection from any spiders or flying insects that might be inhabiting the laboratory. Two of the original 33 individuals left their assigned host leaves during the experimental period for unknown reasons and were, therefore, eliminated from the data set (new n=31). Their host leaves were discarded.

Observations were made at three larval ages: within the first 12 h following molting, at approximately 36 h after molting, and again at approximately 60 h following molting. Slansky (1974) reports that the average duration of the fifth instar in the laboratory is 66 h, so these three time frames should provide reasonable estimates of feeding patterns in the early, middle, and late part of the instar. During an observation, a host leaf containing a *P. rapae* larva was removed from the common holding cage and placed on a laboratory bench. The duration of the next feeding bout initiated by the larva was recorded, as was the duration of the following feeding interval. At the end of each observation, I weighed the larva to the nearest 0.0001 g.

Effect of Temperature

It is well known that temperature can affect both activity levels and foraging patterns in other caterpillar species (Casey 1976; Fields and McNeil 1988; Kirsten and Topp 1991; Joos 1992; Stamp and Bowers 1994; Kingsolver and Woods 1997). Therefore, I tested the null hypothesis that there is no relationship between temperature and feeding bout or feeding interval length in fifth-instar *P. rapae* larvae. To test this hypothesis, I obtained data as described under *Feeding Bout and Feeding Interval Length.* Larvae were selected for observation at random using the random walk method (Southwood 1978). Following selection of a focal caterpillar, an appropriate vantage point was established within 0.5 m of the plant. After a five minute waiting period, I measured the temperature of the air surrounding the larvae using a thermocouple held at a distance of 3 cm directly above the larval head capsule. In preliminary observations, disturbances of the air at such a distance did not produce any visible response from a resting larvae (i.e., not moving or feeding). Temperature was measured every five minutes until the larvae began a feeding bout. The length of feeding bout and the subsequent feeding interval were measured as previously described.

When the animal returned to a resting position after a feeding bout, the temperature was recorded. It was then recorded at five minute intervals, until the animal fed again. The temperature associated with each feeding bout was obtained by calculating the mean of the measurements closest to the beginning and end of the feeding bout. The temperature associated with each feeding interval was obtained by calculating the mean of the measurements closest to the beginning and end of the feeding interval. Each larvae was only tested once for an n= 43.

Weight Gain Equivalents of Feeding Time

The data generated by the experiment testing for an effect of larval age was used to quantify the relationship between feeding time and insect weight gain. The methods for establishing the laboratory colony of *Pieris rapae* have been previously described and will not be repeated here. However, I will repeat the description of the methods used to obtain feeding times and weight gains so that the reader may more easily follow my calculations.

Thirty-three fifth instar larvae (< 6 years old) were selected from the colony at random. Larvae were removed from their cups with a paint brush, paint marked with fast-drying enamel paints for identification and placed singly on freshly excised leaves whose stems were inserted into small glass vases filled with water. Assignment to a particular leaf, as well as to a location on the leaf, was made at random. Once larvae were placed on host leaves, they were stored during non-observation periods in a large common cage (90 cm X 45 cm X 30 cm), under the same environmental conditions described above but with mesh sides and roof to ensure protection from any spiders or flying insects that might be inhabiting the laboratory.

During an observation, a host leaf containing a *P. rapae* larva was removed from the common holding cage, placed on a laboratory bench, and the duration of the next feeding bout initiated by the larva was recorded. The duration of the following feeding interval was also measured. At the end of each observation, the larva were weighed to the nearest 0.0001 g.

Conversion factors for feeding time to weight gain were calculated as using the procedure described below:

Step #1- The weight of the newly-molted larva was subtracted from the weight of the larva at the end of the instar. This value will be hereafter referred to as Δ Weight Gain.

Step #2- The mean lengths of the three feeding bouts and feeding intervals were obtained for each larvae.

Step #3- Mean feeding bout and feeding interval length were summed for each larvae (hereafter referred to as Σ Bout-Interval).

Step #4- The time between the two measurements of larval weight was calculated (hereafter known as Δ Time).

Step #5- I divided Δ Time by Σ Bout-Interval to get an estimate of the total number of feeding periods (i.e. bout + interval) that were possible during the instar given Δ Time. This number will be hereafter referred to as the # of feeding periods.

Step #6- The mean feeding bout length was multiplied by the number of feeding periods to get an estimate of total feeding time.

Step #7- Δ Weight Gain was divided by total feeding time to get a measure of weight gain per unit of feeding time (where the unit is minutes).

In addition to the two individuals that failed to remain on their host leaf, a larva that died prior to pupation was eliminated from the analysis. Thus, the above calculations were made for 30 test subjects.

Threshold Weight for Pupation

Larvae were collected, measured and reared as described under *Starting Weights*. Fifth-instar larvae were weighed to the nearest 0.0001 g at the initiation of the "wandering phase" (signaling the onset of pupation), and then again, following the tanning of the cuticle. The latter were recorded as pupal weights. Threshold size for pupation was determined following Nijhout (1975).

Dislodgement Experiment

Thirty-four, newly-emerged (< 12 hours old) fifth instar larvae were paint-marked (Southwood 1978) and randomly assigned to collard plants in the experimental plot. To eliminate any potential effects of intraspecific competition, only one animal was assigned to each plant and all other *P. rapae* larvae were removed from the plant prior to its introduction. The larvae were allowed to become established during a 14 hour overnite period. The next morning, each non-feeding animal was squeezed gently with forceps (mode= 6 times) until it dislodged from the plant. Plants were searched at 3 h, 6 hours, 12 h, 24 h and 48 h for the presence of larvae. The location of recaptured individuals was recorded. Individuals that did not return to the plants within 48 h were presumed dead. From this experiment, dislodgement mortality, the percentage of individuals returning to the plant following dislodgement, and the amount of feeding time lost following dislodgement were obtained.

Lost Feeding Time

To assess the impacts of predator encounters on larval foraging, I simulated two types of predator attacks in the field and made control observations of undisturbed larvae for comparison. Air-disturbance simulations were produced by generating puffs of air with a lens duster, directed at the head capsule of the larva at a distance of approximately 2.5 cm (modified from Riechert and Hedrick 1990). Capture-release simulations were produced by pinching the larvae behind the head capsule with broad-tipped entomological forceps (modified from Stamp and Bowers 1988).

Fifth-instar larvae were selected for testing using the random walk method (Southwood 1978). Once a larva was chosen, it was randomly assigned to one of the three treatments: air disturbance simulation, capture-release simulation or control. An appropriate vantage point was selected within 0.5 m of the plant. A five minute waiting period preceded the simulated attack. I administered simulated attacks 30 s after the initiation of feeding by each larvae. All behaviors as well as the latency to forage, the length of the interrupted feeding bout, and the length of the subsequent feeding interval were recorded. Only one larva was tested on each plant per day, and this larva was removed from the plot following the test to avoid duplication. A total of 92 trials were performed resulting in 43 control trials, 29 air-disturbance trials and 20 capture-release trials.

From the predator simulations, I obtained feeding bout and feeding interval lengths for larvae experiencing air-disturbance and a capture-release encounters. I also calculated values for feeding time lost following each encounter type. For capture-release simulations, the percentage of individuals that died as a result of predator-induced injury and the percentage of individuals that dislodge from the plant was calculated.

Relationship between Pupal Weight and Fecundity

The equation for converting pupal weight to fecundity was derived from data presented in Gilbert (1984a, Fig. 1, pp. 582). From the figure, I deduced data points to calculate the equation of the regression line linking pupal weight with fecundity (Fig. 3.2).

E. Results

Encounter Rate, Qualitative Outcomes of Encounters and Predation Rate

Fifty-five predator encounters were observed (Table 3.1). The rate of encounter between fifth-instar *P. rapae* larvae and predators was 0.19 (55/285). Because this value was obtained in an experimental plot that was managed according to conventional farming practices (i.e., alternating crop rows with rows of bare ground), it was assumed to reflect a relatively low density of predators (Riechert and Bishop 1990). A high predator density value to be used for a simulation run was calculated by multiplying this number by 30, based on the densities of spiders found in plots that were mulched for ground cover (Riechert and Bishop 1990). Thirteen out of the 55 observed predator encounters resulted in mortality of the larva. Thus, the predation rate (or percentage of individuals killed during encounters) was 23.6%. Of the 42 non-lethal encounters, 83.3% were of the air-disturbance type, while 16.6% were of the capture-release type.

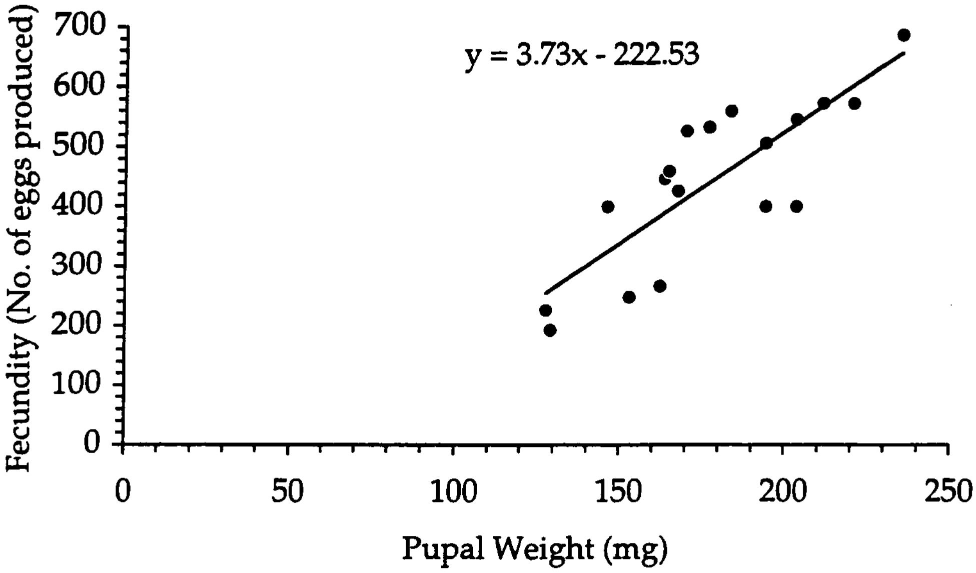


Figure 3.2. Linear relationship between pupal weight and fecundity. Data are taken from Gilbert (1984a).

Table 3.1- Outcomes of 55 encounters between fifth instar *Pieris rapae* larvae and potential predators* observed in an experimental plot of collards (*Brassica oleracea* var. *acephala* "Georgia"). Squeeze type and buzz type refer to the two possible types of non-lethal encounters. Encounters classified as squeeze type involve direct contact made between the predator and the integument of the larva. Encounters classified as buzz type are those in which a predator disturbs the air space around the larva but does not make contact with the larval integument.

Predator	**# of Encounters**	**# of Larvae Killed**	**# Squeeze Type**	**# Buzz Type**
Birds				
Robin (*Turdus migratorius*)	1	1	-	-
Song Sparrow (*Melospiza melodia*)	1	1	-	-
Spiders				
Comb-Footed Spider (*Achaearanea rupicola*)	1	-	1	-
Jumping Spider (*Phidippus audax*)	3	2	-	1
Jumping Spider (*Thiodina iniquies*)	1	-	1	-
Crab Spider (Philodromidae sp.)	3	-	-	3
Predatory Wasps		-	-	-
Black and Red Paper Wasp (*Polistes* sp.)	7	3	1	3
Red Paper Wasp (*Polistes* sp.)	10	5	3	2
Whitefaced Hornet (*Vespula maculata*)	2	1	-	1
Yellow Jacket (*Vespula* sp.)	2	-	-	2
Unidentified (Vespidae sp.)	1	-	-	1
Parasitoids				
Braconid Wasp (Braconidae sp.)	1	-	1	-
Flying Insects				
Damselfly (Coenagrionidae sp.)	1	-	-	1
Halictid Bee (Halictidae sp.)	1	-	-	1
Syrphid Fly (Syrphidae sp.)	14	-	-	14
Soldier Beetle (*Chauliognathus* sp.)	1	-	-	1
Scorpion Fly (Panorpidae sp.)	2	-	-	2
Robber Fly (Asilidae sp.)	2	-	-	2
Unidentified (Diptera sp.)	1	-	-	1
Total	55	13	7	35

* Some of the flying insects on this list are not actually predators of *P. rapae*.. However, they were observed to elicit antipredator behaviors (e.g. cessation of foraging, cessation of movement or withdrawing of the head capsule) from the larvae upon encounter.

Starting Weights

To reduce the impact of outliers, I used the middle 80% of the starting weight data set as the range of values for the simulation. Thus, starting weights used in this simulation ranged from 0.04 to 0.06 g.

Feeding Bout and Feeding Interval Lengths

Regression analysis revealed that a significant portion of the variation associated with feeding interval length can be explained by variation in feeding bout length (Table 3.2; Fig. 3.3). Thus, for the simulation, feeding interval values (Y) were derived from feeding bout lengths using the following equation: $Y = 4.35X + 26.42$ where X equals feeding bout length in minutes. Mean feeding bout and feeding interval lengths for control observations are shown in Table 3.3. The range of values used in the simulation for feeding bout lengths of undisturbed larvae was 1.77 to 7.90 min. This reflects the middle 80% of the total data set.

Effect of Larval Age

Separate analyses were performed for feeding bout and feeding interval data sets. Because of the repeated measures design of this experiment, I used two-way, mixed model ANOVAs (Sokal and Rohlf 1981), with age class as fixed treatment effects and individual larvae as random effects. Feeding bout lengths were log transformed prior to the analysis to meet the assumption of normality. Larval age class had no significant effects on the duration of either feeding bouts or feeding intervals (Tables 3.4 , 3.5, and 3.6). The powers of these tests are low (0.09 for bout length and 0.25 for interval length, $\alpha = 0.05$,

Table 3.2- Results of linear regression of feeding interval length on feeding bout length in fifth-instar *Pieris rapae* larvae.

Linear Regression	R^2	**F Ratio**	**P**
Bout Length x Interval Length	0.259	14.329	<.001

Table 3.3- Mean feeding bout and feeding interval lengths for fifth-instar *Pieris rapae* larvae, obtained in the field.

Mean Bout Length± SE (in min.)	**Mean Interval Length± SE** (in min.)
4.79 ± .42	47.26 ± 3.40

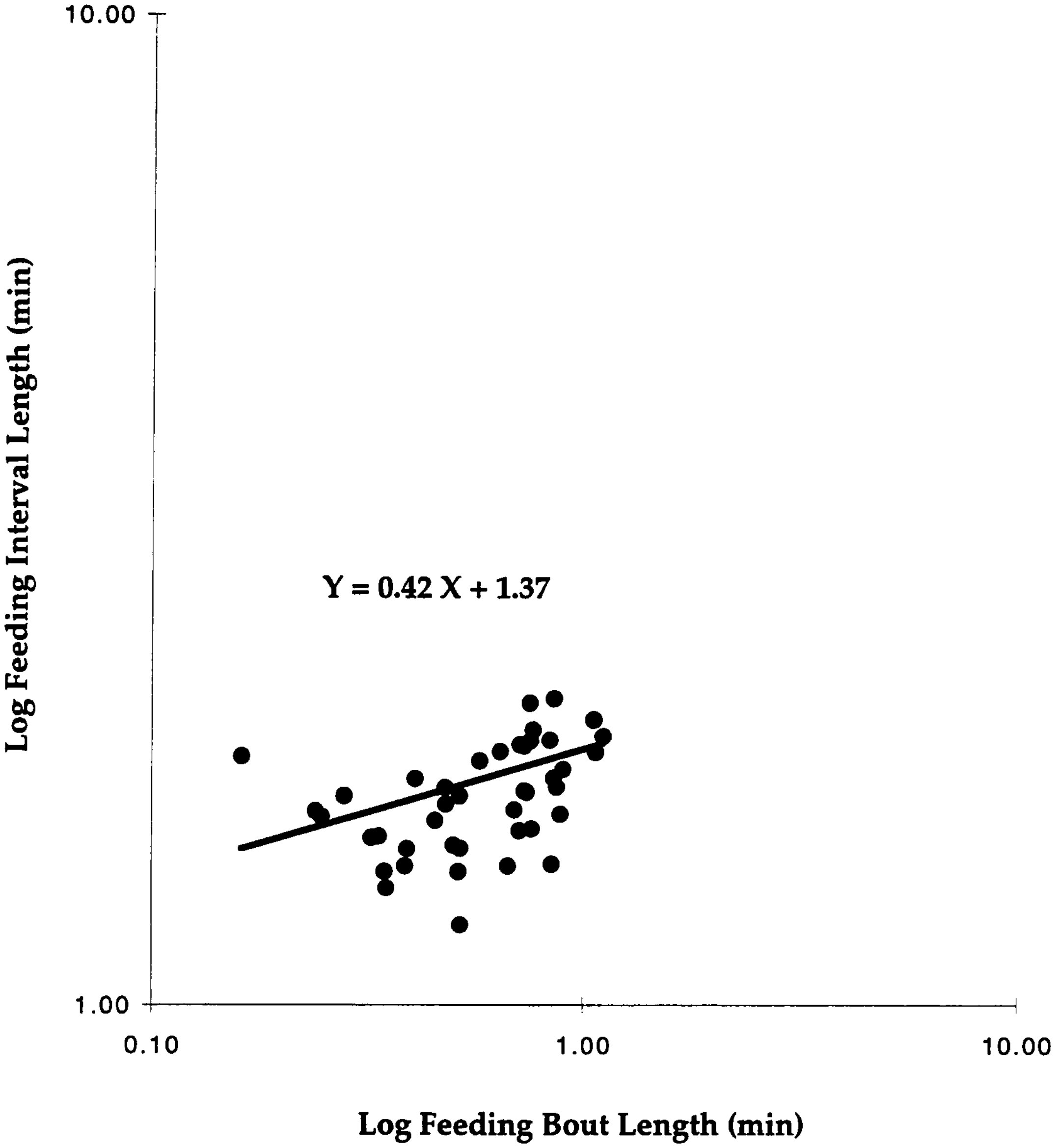


Figure 3.3- Linear relationship between feeding bout length and feeding interval length. Data are from control observations, described under *Lost Feeding Time.*

Table 3.4- Results of two-way ANOVA partitioning the sources of variation associated with feeding bout length in fifth-instar *P. rapae* larvae. Larval age classes were early (< 12 h old), middle (approx. 36 h old) and late (approx. 60 h old) instar.

Source of Variation	***df***	**SS**	**MS**	**F Ratio**	**P**
Larval Age Class	2	1.45×10^{-2}	0.116	0.276	>.75
Individual	30	1.14	2.37×10^{-2}	1.44	>.10
Error	60	1.58	3.00×10^{-2}		

Table 3.5- Mean (± SE) feeding bout and feeding interval measurements for fifth instar *P. rapae* larvae in early, middle and late-instar age classes. There are no significant differences between the means at $\alpha = .05$.

	Larval Age		
	Early Instar (< 12 h old)	Middle Instar (≅ 36 h old)	Late Instar (≅ 60 h old)
Feeding Bout Duration (Mean ± SE)	3.86. ± .28 min	3.95 ± .27 min	3.77 ± .31 min
Feeding Interval Duration (Mean ± SE)	59.4 ± 3.2 min	54.8 ± 2.0 min	52.9 ± .4.7 min

Table 3.6- Results of two-way ANOVA partitioning the sources of variation associated with feeding interval length in fifth-instar *P. rapae* larvae. Larval age classes were early (< 12 h old), middle (approx. 36 h old) and late (approx. 60 h old) instar.

Source of Variation	***df***	**SS**	**MS**	**F Ratio**	**P**
Larval Age Class	2	1.74 x 10^4	5.79 x 10^2	1.24	>.25
Individual	30	6.91 x 10^2	3.46 x 10^2	2.07	>.01
Error	60	1.68 x 10^2	2.79 x 10^2		

n= 31), such that the probability of commiting a Type II error by concluding that there is no effect is quite high. However, I believe that the apparent absence of a strong effect justifies the exclusion of this variable from the simulation._

Effect of Temperature

Regression analysis of the data revealed that the observed variation associated with feeding bout and feeding interval lengths could not be explained by variation in temperature (Table 3.7). In addition, data obtained in the laboratory at a constant temperature show similar levels of variability in feeding bout and feeding interval length (Table 3.8). Thus, temperature was not included as a parameter in the simulation.

Weight Gain Equivalents of Feeding Time

Values used for converting feeding time to weight gain in the simulation ranged from 0.0002 g/min to 0.0008 g/min. Again, this reflects the middle 80% of the total data set to minimize the impact of outliers.

Threshold Weight for Pupation

Threshold weight for pupation was estimated to be 0.16 g. Based on calculations using these data, pupal weight is approximately 5% of the threshold weight which makes this value consistent with the results of Gilbert (1984a) who found that more than 85% of individuals in a given population had pupal weights greater than 0.15 g.

Table 3.7- Results of linear regression of feeding bout and feeding interval lengths on temperature.

Linear Regression	**R^2**	**F Ratio**	**P**
Temperature x Feeding Bout	0.006	.225	>.60
Temperature x Feeding Interval	0.037	1.573	>.20

Table 3.8- Results of F-test comparing variances of data sets obtained in the laboratory at a constant temperature and in the field under fluctuating temperatures.

Variable	**Laboratory** (n=93)	**Field** (n=43)	**F Ratio**	**P**
Feeding Bout	2.60	7.55	0.34	>.95
Feeding Interval	378.6	496.4	1.31	>.10

Dislodgement Experiment

Of the 34 larvae tested, 14 (41.2%) returned to plants within the experimental plot during the allotted 48 h period. Of those 14, five returned to the plants within three hours, an additional three had returned within six hours and and the remaining six were not found until after 24 h. Eight of the 14 returning larvae (57.1%) were found on plants other than those on which they started, indicating that the animal traveled some distance to obtain another host. These distances varied from 1 to 6 m.

Lost Feeding Time

Air-disturbance attacks typically resulted in cessation of feeding followed by withdrawal of the head capsule and first few body segments from the site of feeding (Table 3.9). Capture-release attacks typically elicited stronger anti-predator responses including thrashing, regurgitation of fluids, and dislodgement (Table 3.9). Latency to feed, feeding bout, and interval length were log-transformed to meet the assumptions of ANOVA and Student's t-test (Sokal and Rohlf 1981). Latency to feed was significantly longer in capture-release simulations than in air-disturbance simulations (Table 3.10). There was no difference in feeding bout or interval length in control, air disturbance and capture-release simulations (Table 3.11; Table 3.12). Power analysis revealed a 46% chance of committing a Type II error by concluding that there is no statistically significant difference in feeding bout length and a 27% chance of making the same conclusion regarding feeding interval length.

Table 3.9- Outcomes of simulated predator attacks on fifth-instar *P. rapae* larvae. Air disturbance simulations were performed by administering a puff of air at the head capsule with a lens duster. Capture-release simulations were performed by gently squeezing the larvae behind the head capsule with broad-tipped entomological forceps.

Response Type	**Type of Predator Simulation** Air Disturbance (n=29)	Capture-Release (n=20)
None	3.4%	0.0%
Cease Foraging	96.6%	67.7%
Dislodge	0.0%	27.3%
Injury	0.0%	5.0%

Table 3.10- Feeding time lost by of P. *rapae* larvae following air-disturbance and capture-release predator simulations. Differences are significant at P <.001 (Student's t-test).

Simulation Type	**Mean Time Lost ± SE** (min)	**Sample Size** (n)
Air-Disturbance	2.78 ± 0.61	29
Capture-Release	34.94 ± 5.23	20

Table 3.11- Feeding bout and interval lengths of P. *rapae* larvae in control, air-disturbance and capture-release treatments. Univariate ANOVAs showed no effect of simulation type on either bout or interval length.

Simulation Type	**Mean Bout Length± SE** (in min)	**Mean Interval Length± SE** (in min)
Control (n=43)	4.79 ± 0.42	47.26 ± 3.40
Air-Disturbance (n=39)	6.62 ± 0.72	55.96 ± 4.97
Capture-Release (n=20)	4.55 ± 0.50	49.24 ± 3.22

Table 3.12- Results of univariate ANOVAs on feeding bout and feeding interval length in control, air-disturbance and capture-release treatments.

Source	**d.f.**	**SS**	**F Ratio**	**P**
Bout Length				
Simulation Type	2	0.367	2.856	>.05
Error	89	5.716		
Interval Length				
Simulation Type	2	9.297×10^{-2}	1.312	>.25
Error	89	2.870		

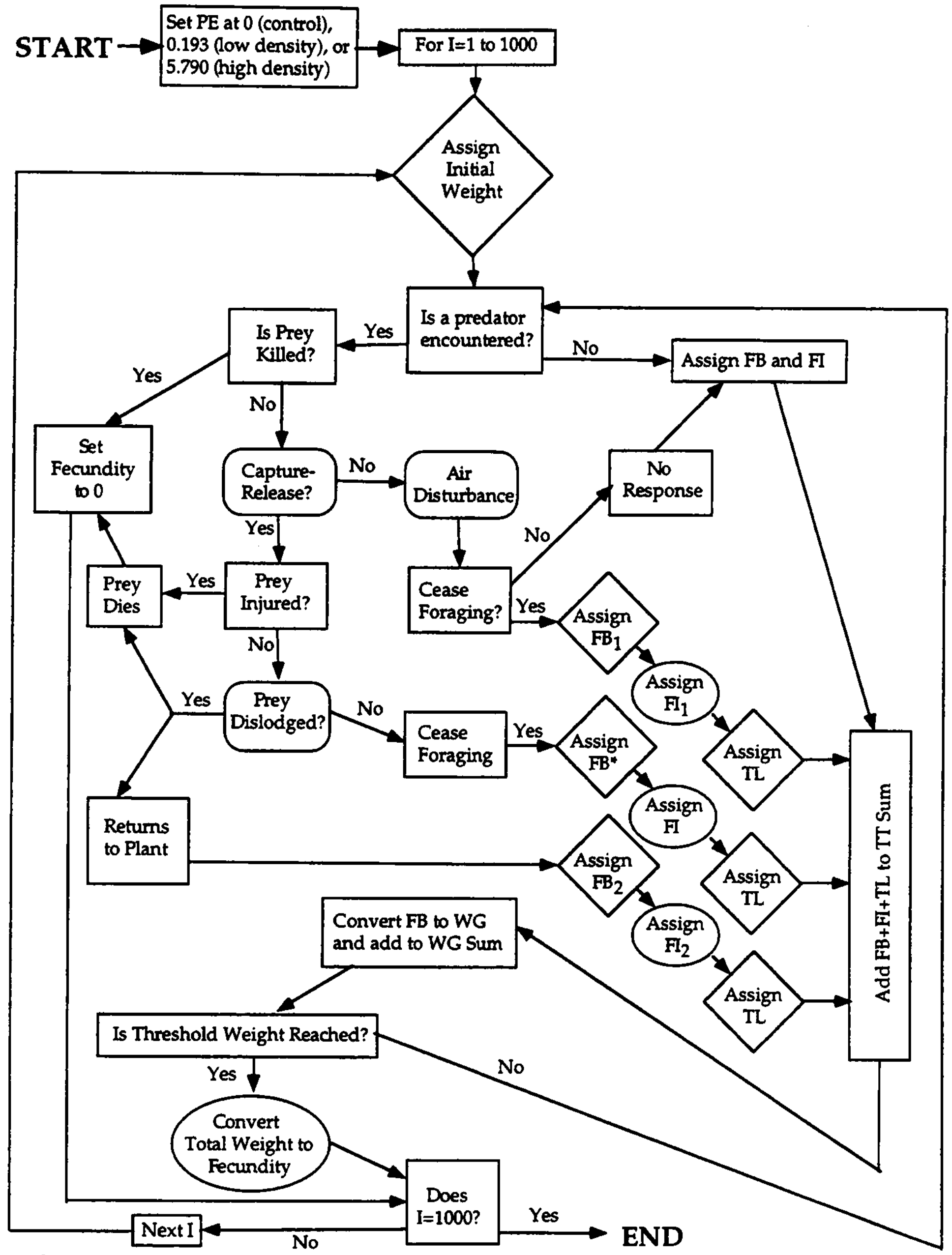
Relationship between Pupal Weight and Fecundity

The equation of the regression line used to convert pupal weight to fecundity for this simulation was $Y = 3.72 X - 222.53$ where X is equal to pupal weight and fecundity (Y) is the number of eggs produced by a female.

Simulation Structure

The computer simulation was developed in collaboration with Dr. Gary Huxel of the University of California at Davis. The code for the program, which is written in Matlab, appears in Appendix I. The simulation proceeds as follows:

For populations of 1000 individuals each, a predator encounter rate is assigned. This predator encounter reflects the probability that any given larva will encounter a predator. For control simulations (i.e., those in which no predators are encountered), this encounter rate is zero. For the low predator density simulation, the encounter rate is 0.19 (based on the calculations described previously). For the high predator density simulation, the encounter rate is 5.79. An encounter is presented to individuals at random points in the feeding-growth cycle presented in Fig. 3.6, such that the entire simulated population conforms to these encounter rates. Each individual enters the simulation at the beginning of the fifth instar and is immediately assigned a starting weight, selected from a uniform distribution of values (range: 0.04 g - 0.06 g) using a random number generator. If the animal does not encounter a predator, it proceeds through the following loop. The animal is assigned a feeding bout length, selected from a uniform distribution of



◇ Value selected from data set using random number generator

▢ Probability function

◯ Dependent variable

PE=Predator encounter rate
FB=Feeding bout length
FI=Feeding interval length
WG=Weight gain
TL=Feeding time lost due to encounter with predator.
TT=Total time spent as juvenile prior to pupation (or maturation time)

Figure 3.4- Schematic representation of simulation model investigating predator-presence effects on *P. rapae*. * Data set is the same as FB because values are the same.

values (1.77 min- 7.90 min) using a random number generator. A feeding interval was then assigned using the equation $Y = 4.35\ X + 26.42$ where X is feeding bout length. Feeding time is converted to weight gain by multiplying the feeding bout length by a weight gain conversion factor selected from a range of normally distributed values (0.0002 g/min to 0.0008 g/min, mean= 0.0004 g/min) using a random number generator. The resulting weight gain is then added to the individual's starting weight. If the sum is greater than or equal to the threshold weight of 0.16 g, the resulting weight (which is an estimate of the pupal weight) and the time to maturation (the sum of the feeding time and the feeding interval) is recorded. Pupal weight is converted to fecundity using the equation $Y = 3.72\ X - 222.53$ where X is equal to pupal weight and fecundity (Y) is the number of eggs produced by a female (Gilbert 1984a). The next individual then enters the simulation and these steps are repeated beginning with the assignment of starting weight.

If the sum of the starting weight and weight gained is less than the threshold weight, then the animal goes back to the beginning of the feeding loop and repeats it. If the individual encounters a predator, then the loop changes as follows. A chance event based on the empirical probability function of predation rate (0.24) determines whether or not the individual survives. If the individual dies, it receives a 0 for fecundity. If the individual is not killed, then the type of encounter is assigned, again based on probability functions (0.83 for air-disturbance types and 0.17 for capture-release types).

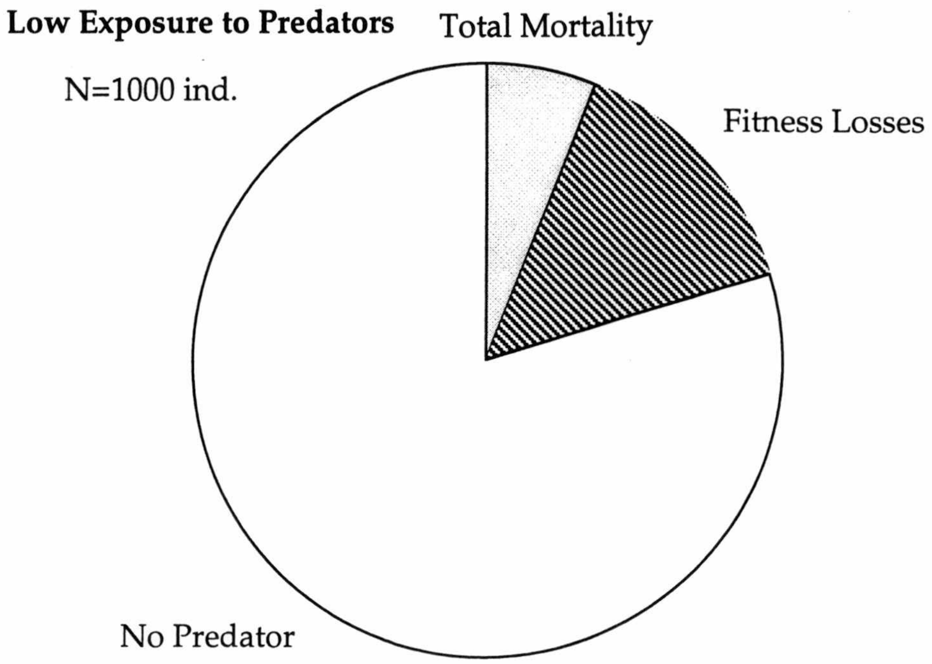
If the encounter is of an air-disturbance type, then the animal is assigned a feeding bout length from a specified data set using a random number generator. Because feeding bout and feeding interval lengths tend to be longer following air-disturbance encounters, a data set obtained from simulated air-disturbance encounters is used. In this case, the range of values for feeding bout length is 1.82 min to 15.45 min (drawn the middle 80% of the total data set) and the values are normally distributed with a mean of 6.62 min. Feeding interval length is assigned using the equation $Y = 4.35 X + 26.42$ where X equals feeding bout length in minutes. Feeding bout length is converted to weight gain, again using a conversion factor selected from a range of normally distributed values (0.0002 g/min to 0.0008 g/min, mean= 0.0004 g/min) using a random number generator. In addition, a value for lost feeding time is added to the sum of the feeding bout and feeding interval to reflect the consequences of the disturbance. The value for this time lost was selected from a uniform distribution of values (0.10 min to 11.89 min) using a random number generator. The weight gain for this loop is added to the individual's starting weight. If the sum is greater than or equal to the threshold weight then the resulting weight and the time to maturation (the sum of the feeding bout, feeding interval and time lost) is recorded. The weight of the animal is converted to fecundity.

If the encounter is of a squeeze type, the outcome is determined by probability functions: the individual is injured and, therefore, dies (0.14), the individual dislodges from the plant (0.27) or the individual simply loses feeding time (0.58). The fate of the larva that dislodge from the plant is also determined by probability functions: the individual dies (0.59), or the individual returns to the plant (0.41). All the animals that die are assigned a fecundity of 0. Those that do not die are assigned feeding times and feeding intervals. Since feeding bout and feeding interval lengths following capture-release simulations are not significantly different from controls, the same data set used for the controls is used here. A value for feeding bout length is randomly generated and then a corresponding interval length is assigned using the equation $Y = 4.35 X + 26.42$ where X equals feeding bout length in minutes. Feeding bout lengths are converted to weight gain using another randomly selected conversion factor (taken from the normal distribution of values with a range of 0.0002 g/min to 0.0008 g/min and a mean= 0.0004 g/min). A value for time lost is selected from a uniform distribution of values (10.33 min - 76.62 min for non-droppers; 120 min - 1440 min for droppers) using a random number generator. The assigned value is added to the sum of the feeding bout and feeding interval length and the weight gain is added to the individual's starting weight. If the sum of the weight is greater than or equal to the threshold weight then the animal is finished and the pupal weight, fecundity, and time to maturation are recorded. The next individual enters the model and these steps are repeated from the beginning. If the sum is less than the threshold weight then the animal goes back to the feeding loop and proceeds through it again until the threshold weight is reached.

The simulation was run four times. The first two populations served as control populations in which no predators were encountered. Generating two control data sets made it possible to determine where differences between populations might be due to random variation in the parameter measures used by the computer. The second two populations were generated using two different measures for predator encounter rate. The first (hereafter referred to as the low predator density simulation) incorporated the predator encounter measure obtained experimentally, as described under Encounter Rate. This measurement was made in a plot in which crop rows were alternated with bare ground, in a manner consistent with most conventional farming practices. The second (hereafter referred to as the high predator density simulation) used a predator encounter rate of 30 times that number, consistent with plots in which predator densities are elevated due to habitat manipulation (Riechert and Bishop 1990).

Simulation Outcomes

In the low predator density simulation (where the predator encounter rate was 0.19), 939 of the 1000 individuals in the population survived to reproduce. Of those 939, 141 encountered a predator during the fifth instar (Fig. 3.7). In the high predator density simulation (where the predator encounter rate was 5.79), 718 of the 1000 individuals in the population survived to reproduce (Fig. 3.7). All of the surviving individuals encountered at least one predator during the fifth instar.



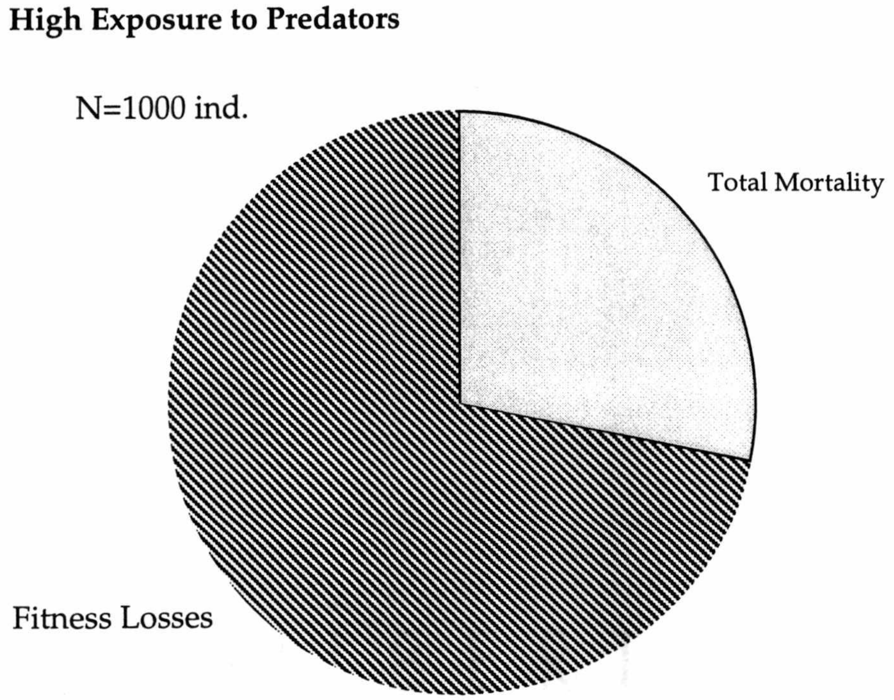


Figure 3.5- Comparison of mortality in simulated populations of *P. rapae* under low and high predator densities. Mortality is due to predation, predator induced injury, and dislodgement.

The data for fecundity and maturation time failed to meet the assumptions of parametric ANOVA despite numerous transformations. A Kruskal-Wallis test on untransformed data was used in its place. Because the Kruskal-Wallis test requires equal sample sizes, values were randomly excluded from the two control and low predator density simulations to equalize the sample sizes (as in Ball and Baker 1996). This analysis was repeated three times, excluding a new set of randomly chosen values each time, in order to verify that the results were unaffected by the excluded data. For both variables, the results were consistent between the three analyses, so I report only the first analysis of each variable here.

Fecundity did not differ significantly among the four simulated populations (Kruskal-Wallis Test, $\chi^2 = 2.20$, df = 3, $P > .50$). Mean values for all four populations were considerably lower than those typically observed in field populations (Table 3.13). The populations also showed less variability than one would expect to see in the field (Jones et al. 1982; Gilbert 1984a).

Maturation times differed significantly between the four populations (Kruskal-Wallis Test, $\chi^2 = 100.54$, df = 3, $P < .0001$). Maturation times for all four populations were shorter than those observed by Slansky (1974) and were the longest in the population exposed to high densities of predators (Table 3.14). The two control populations were not significantly different from one another, indicating that significant differences are probably not due to the effects of random variable selection by the computer. Low predator densities did not significantly affect maturation times (Table 3.15).

Table 3.13- Mean fecundity estimates for *P. rapae* obtained for four simulated populations in this study and compared with values obtained from the literature.

Population	**Mean Fecundity ± SE**
This Study	
No Predator 1	377.53 ± 0.12
No Predator 2	377.49 ± 0.11
Low Predator Density	377.38 ± 0.11
High Predator Density	377.26 ± 0.13
Gilbert 1984*	
Vancouver, Canada	443.05 ± 32.41
Jones et al. 1982*	
Canberra, Australia	468.85 ± 22.78

* indicates that data were obtained from figures published in these papers.

Table 3.14- Mean maturation times for the four simulated populations of *P. rapae* in this study. The four populations compared include two control populations in which no predators were encountered, a population that was exposed to low predator densities and a population that was exposed to high densities. A measurements taken from Slansky 1974 in a laboratory population is reported for comparison.

Population	**Maturation Time (in h) ± SE**
This Study	
No Predator 1	46.60 ± 0.10
No Predator 2	46.82 ± 0.10
Low Predator Density	46.75 ± 0.10
High Predator Density	47.46 ± 0.15
Slansky 1974	
Laboratory (no predator exposure)	66.0 ± 3.8

Table 3.15- Results of mean comparisons performed on maturation times of *P. rapae* larvae, generated in a computer simulation. The four populations compared include two control populations in which no predators were encountered, a population that was exposed to low predator densities and a population that was exposed to high densities.

Comparison	χ^2	**P**
No Predator 1 vs. No Predator 2	.5569	>.45
No Predator vs. Low Predator Density	.5660	>.45
No Predator vs. High Predator Density	72.824	<.005
High Predator Density vs. Low Predator Density	8.520	<.0001

F. Discussion

Predator-presence effects accumulated during the fifth instar of larval development appear to significantly impact at least one fitness parameter in *P. rapae*: time to maturation. When predator densities are high, mean maturation times are significantly greater than when no predators are present and when predator densities are low. Maturation time is strongly coupled to fitness in several ways. It determines the "window of vulnerability" (*sensu* Benrey and Denno 1997) to predator, parasites, and pathogens of the larval stage (all of which are significant sources of mortality for *P. rapae* - Pimentel 1961; Harcourt 1966; Dempster 1967; Baker 1970). It also has the potential to influence competitive dynamics. Individuals who mature, find mates, and lay eggs at an accelerated rate may have competitive advantages over those who lag behind. Studies have shown that females of the genus *Pieris* are deterred from ovipositing on plants where congeneric eggs are already present. This interaction is mediated by a pheromone which actually inhibits egg-laying (Schoonhoven 1991). Thus, when oviposition sites are not abundant, late-maturing individuals may not be able to lay eggs or may only have access to oviposition sites of lower quality.

Early maturation times also increase the likelihood that an individual will complete the life cycle when habitats are ephemeral. For insects inhabiting agroecosytems, crop duration is an important determinant of larval survivorship. Individuals whose maturation is delayed are at increased risk for mortality as the season progresses. Host plant quality decreases with age, such that older plants yield only a fraction of the nutrients of younger plants (Slansky 1974). Age-induced toughening of the leaves mean that larvae must spend increased amounts of energy chewing and digesting plant material (Slansky 1974). Falling temperatures further reduce growth rate (Scriber and Slansky 1981), compounding the negative effects of reduced food quality and lost foraging time. Delayed pupation may pose a special threat to the overwintering generation of larvae. Individuals may be forced to pupate at such low weights that they do not survive diapause (Gilbert 1984a) or they may simply be killed by exposure to frost. Host plants may die or be harvested. Cumulatively, these effects may be quite significant at the level of the population because the overwintering generation provides the "breeding stock" with which the population is reconstituted from year to year. Maturation time also has a strong effect on the intrinsic rate of growth of a population (or r), such that even small reductions can slow population growth considerably (Belk 1998).

The values for maturation time obtained in the simulations are considerably shorter than those recorded by Slansky (1974). This is probably due, in part, to the absence of temperature effects in the simulation. Although temperature effects on feeding bout or feeding interval length were not detected by this study, temperatures below a certain threshold may play a role in larval foraging patterns. Most of the feeding bouts and feeding intervals measured took place at temperatures within a relatively narrow range (i.e., between 22-28 °C). Preliminary observations made at much cooler temperatures (< 16° C) revealed that feeding interval length tended to be considerably longer (frequently over 2 hours), and larval movement was much slower, possibly due to reduced temperatures (Joos 1992). This suggests that it would be important to measure feeding bout and feeding interval lengths over the entire range of temperatures to which these animals are exposed. Doing so may reveal the existence a threshold below which larval motor ability is impaired and feeding bouts and intervals are lengthened. A simulation that included some temperature-based constraints for the larvae would be more realistic and would probably generate maturation times that were more consistent with those observed in real populations. If such a threshold does exist, it further strengthens the argument that predator-presence effects will be particularly important for overwintering populations. These larvae may already be constrained by their physiology with respect to available time for feeding.

Unfortunately, this simulation study does not adequately measure predator-presence effects on the fecundity of *Pieris rapae.* This was an unforseen artifact of the simulation's design and not reflective of any biological phenomenon. In the simulation, the larval period ends as soon as the larva reaches the threshold size. This causes the values for pupal weight (which are the determinants of fecundity) to cluster around the threshold weight with less variance than is observed in nature. In the tobacco hornworm, *Manduca sexta,* the hormone that initiates pupation is regulated by a circadian clock (Nijhout 1975). Although achieving the threshold weight renders the larva developmentally competent for the neurohormonal decision initiating pupation, larvae may have to wait for hormonal release to actually occur. This gives the larvae additional feeding time after the critical weight is reached (Nijhout 1975). Ultimately, fecundity may depend quite heavily on other variables, such as the amount and quality of food consumed or temperature during the period between the attainment of critical weight and pupation (Stamp and Bowers 1991). Clearly, the simulation needs to be adjusted if it is to be useful for examining predator-presence effects on fecundity.

A potentially simple modification to the simulation might include the addition of a counter that would designate 24 h periods. Thus, it might be possible to have the larva reach the critical weight, but not be able to pupate until some specified point in time (consistent with the time of hormonal release). Larvae in this type of simulation would have post-critical weight opportunities to feed and be disrupted by predators. My simulation suggests that this post-critical weight period may be quite important in accounting for the observed variability of pupal weights in *Pieris rapae* populations. Thus, it would be very interesting to look at the impact of predator-presence effects during this period. Not only are they potentially important for fecundity, but also for other fitness parameters if larger females get more matings, as is true for many invertebrate species (Svensson et al. 1989; Miyashita 1994; Uhl 1998).

The simulation, and the parameters I measured to formulate it, also shed light on the role of predator-presence effects in regulating population growth. My observations of predator-prey encounters suggest that, for fifth instar imported cabbageworms, 83.7% of the mortality associated with predators comes from predation. The remaining 16.3% comes from the combined effects of predator-induced injury and dislodgement. The overall mortality estimates derived in this study are undoubtedly conservative. This study probably underestimates the effect of predator-induced injury, as these data came from the simulated predator attacks in which no attempt was made to injure the larvae. Predator attacks in the field, primarily by vespid wasps, commonly result in injury to the larvae and, in most cases, subsequent mortality. Thus, predator-induced injury is an additional source of mortality that needs to be better quantified in future studies. Additional sources of mortality that were not quantified, but may be important, include starvation (due to reduced feeding) and increase susceptability of larvae to predation due to poor nutrition. I know of no studies that have specifically examined the latter. However, a significant body of evidence (e.g., Slansky and Feeny 1977; Loader and Damman 1991; Benrey and Denno 1997) has demonstrated that the vulnerability of *P. rapae* to mortality from natural enemies increases when growth rate is slow. Although this may be due primarily to an increased window of time in a vulnerable size class, it may also be due to nutrition-mediated effects on predator-prey encounters. It certainly stands to reason that animals in a nutrient-depleted state might be less successful at mounting defenses against predators than those that are well nourished. In contrast, the fact that starvation can result from predator-induced feeding losses was well established by Schmitz et al. (1997) in an old-ecosystem. Their findings suggest that predation was actually compensatory to predator-induced starvation as a source of mortality for grasshoppers, who foraged less in the presence of the spider *Pisaurina mira.* Starvation effects were not examined in this simulation, and thus, overall mortality is probably significantly underestimated.

The simulation also suggests that most non-lethal predator encounters are not particularly costly to the imported cabbageworm. Eighty-three percent of the encounters are of the air disturbance type, which occasionally fail to induce any response from the larvae at all (3.4% of the time). Larvae that do respond lose relatively short periods of feeding time (i.e. between a few seconds and a few minutes) due to disruption by a predator. For an organism that lives approximately 66 hours (Slansky 1974), a loss of 3 min of foraging time is not likely to make much of a difference from a fitness perspective. In contrast, a relatively small percentage of the encounters (i.e., 16.6%) appear to be quite costly to the larvae, in terms of subsequent mortality and long lapses in foraging. For larvae that are forced to dislodge from the plant, high probability of mortality and foraging delays of 2-24 h probably have significant implications for individual fitness. This further supports the assertion that foraging strategy of the predator is paramount in determining the magnitude of predator-presence effects. Further research in this area may reveal that some predators have impacts on larval behavior that result in significant reductions in *P. rapae* fitness while others do not.

Another important follow-up question is whether larvae can compensate for feeding time lost due to predator disruptions over the course of an instar or a lifetime. Mean feeding bout and feeding interval length are longer following an air disturbance encounter than in control observations or following a capture-release encounter. This result, although not statistically significant, suggests that perhaps larvae lengthen their feeding bout lengths slightly to compensate for the lost feeding opportunity associated with predator disturbance. Although this would not save them any time toward maturation (since that time is already lost), they may make up time by foraging longer at an already established feeding site, rather than using time to travel to a new site. If host plant quality at the established site is high, this may provide a mechanism for the larvae to compensate for the effects of predator presence.

Such increases in feeding bout length are not observed following capture-release encounters. If the larvae are able to compensate for lost feeding time as described above, they may elect not to following a capture-release encounter because of differences in the level of perceived risk. If a capture-release encounter conveys strongly that the present site is risky, larvae may elect to cut their losses and move on. I observed that following air-disturbance encounters, the larvae seem to be in a heightened state of vigilance, such that wind or investigator movements that are normally not detected by the larvae induce subsequent interruptions in a feeding bout. Although I did not quantify this phenomenon (nor did I include these observations in the data set for the simulation), I noticed that it does not seem to occur following capture-release simulations. If larval decision-making is playing a role in these responses, it may be that air disturbance encounters stimulate the larvae to continue sampling its current environment for degree of predation risk. In contrast, larvae that were subjected to a capture-release encounter may not need additional information to conclude that the environment is risky enough to leave following the completion of a feeding bout. Relocation to a new feeding site did appear to be more common following a capture-release simulation.

In conclusion, it appears that high encounter rates between insects and their predators are required for predator-presence effects to be important. From a biological control perspective, this finding supports the idea that natural enemy populations in agroecosystems must be augmented using habitat manipulations before we can expect them to exert significant control of pest insects (Riechert and Bishop 1990). Because some of the important effects of predators are presence effects (i.e., the slowing of population growth due to predator-induced changes in prey behavior), evaluations of biological control agents based on predation events or predation rates are underestimating the cumulative effects of the predator assemblage. An additional application of this simulation would be to determine the lowest encounter rate that produces statistically significant differences between maturation times of populations. This would give pest managers a predator-prey ratio to aim for as they develop conservation and augmentation strategies for natural enemies.

PART IV

CONCLUDING REMARKS AND FUTURE DIRECTIONS

This study suggests that the predator-presence effects that play such an important role in aquatic systems are also important in agroecosystems. Spiders, which are the predominant predators in agroecosystems, may be reducing damage to crop plants by 20-40% by influencing the feeding activity of insect herbivores. In some cases, the impact of spiders on prey behavior exceeds their impacts on insect densities. Thus, we may be underestimating the potential contributions of natural enemies if we do not assess their impact on insect behavior.

In addition, this study demonstrates that predator-induced reductions in feeding activity can have negative fitness consequences for pest insects. For *Pieris rapae*, high predator densities result in significantly delays in maturation time which leads to slowed population growth. This is a mechanism for limiting populations which has not yet been widely reported in the literature.

An additional implication of these findings is that predator-presence effects might be used to our benefit in the development of new pest control strategies. The identification of the cues that insects use to detect predators should become a research priority. If we know what cues trigger antipredator responses, we may be able to manipulate those cues to induce reductions in feeding activity. Visions of "spider scent", tiny spider "scarecrows" and generators emitting wasp-like vibrations dance in my head.

Undoubtedly, future studies will find that predator-presence effects are important in many terrestrial systems. However, I disagree with the assertion that the sublethal costs of predator presence are nearly universal consequences of foraging under predation risk (Peckarsky et al. 1993). In my study, I found that some predators appear to produce stronger effects than other predators, and some prey appear to be more affected than others. Even the same predator can induce responses of varying magnitudes (e.g. wasps can produce relatively innocuous air-disturbance encounters or injurious capture-release encounters that result in mortality). Thus, it may be possible for an organism to encounter multiple predators over the course of a lifetime and still experience relatively little consequence, if those encounters are sufficiently infrequent or of short duration.

Other authors (e.g., Stamp and Bowers 1991) have come to similar conclusions suggesting that predator foraging mode will ultimately determine the magnitude of the effects. This is an important area for future research. It should be possible to begin to systematically look at the foraging modes of predators with the expressed purpose of developing predictive theory about predator qualities that generate strong presence effects on their prey. It would also be important to look at what qualities make some prey more susceptible to predator presence than others. For example, one might predict that animals that are well-defended by morphological or chemical defenses might be less likely to exhibit strong behavioral responses to predator-presence than those that do not possess such alternative defenses.

One must also consider the possibility that in some cases, predator presence effects are not important. Small modifications in behavior are potentially less costly than investment in morphological and chemical defenses and may represent default, reactive strategies when other defenses fail. Especially for organisms that can correctly evaluate the riskiness of their habitat, short lapses in foraging time may be compensated for over the life cycle of the individual. Ultimately, selection should only act to maintain these behaviors if the relative consequences of lost foraging time are less severe than the benefit gained by escaping a predator.

Several authors (Clancy and Price 1987; Damman 1987; Skelly and Werner 1990; Belk 1998) have demonstrated that slowed growth resulting from predator presence can actually be beneficial to prey. These authors have suggested that some organisms engage in facultative life-history shifts to protect them from predation pressure. Although I don't believe that is what is happening with insects in agroecosystems (insects are probably constrained in their ability to shift life-history strategies because they do not grow as adults), I believe that more studies (like that of Ball and Baker 1996) are needed to rule out the possibility that there are hidden benefits to predator-induced changes in prey behavior. The critical issue here is whether or not it is possible to predict the circumstances under which organisms will be able to compensate for predator-presence effects and when predator encounters can be safely assumed to reduce fitness.

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APPENDIX

APPENDIX

COMPUTER PROGRAM FOR CABBAGEWORM SIMULATION
(WRITTEN IN MATLAB BY DR. GARY HUXEL, UNIVERSITY OF CALIFORNIA-DAVIS)

```
clear
rand('state',sum(100*clock));
randn('state',sum(100*clock));
pop1 = zeros(1000,4); % first # is weight & second is fecundity & 3 is time
% & 4 is zero if still living larvae
pop2 = zeros(1000,5); % if 5 = 0 then no predator inaction else interaction
encounters=0;
for i = 1:1000;

% Create a normally distributed random # with mean .04963 from .0410
% to .0597 - this is the weight of the prey
% do this for both populations
 rndinwgt = random('norm',.04963,.005);
 if rndinwgt < .0410;
  rndinwgt = .0410;
 end
 if rndinwgt > .0597;
  rndinwgt = .0597;
 end
 pop1(i,1) = rndinwgt;
 rndinwgt = random('norm',.04963,.005);
 if rndinwgt < .0410;
  rndinwgt = .0410;
 end
 if rndinwgt > .0597;
  rndinwgt = .0597;
 end
 pop2(i,1) = rndinwgt;
 pop1(i,3) = 0;
 pop2(i,3) = 0;
 pop1(i,4) = 0;
 pop2(i,4) = 0;
 rndenc = rand;
 if rndenc < .193;  % predator encountered at some time
  pop2(i,5) = 1;
   encounters = encounters+1;
 end;
end;
```

```
for pops = 1:2;
 dead = 0;
 while dead < 1000;
  for prey = 1:1000;
   if pops == 1;
     if pop1(prey,4) == 0;  % still living larvae
      % rndft feeding time 1.7667 - 7.900 min uniform distribution
      rndft = rand*(7.900-1.7667)+1.7667;
      fi = 4.35*rndft + 26.42; % feeding interval
      pop1(prey,3) = pop1(prey,3) + rndft + fi; % total time
      % rndwg normally dist random # .00017 - .00079g/min w/ mean .00043
      rndwg = random('norm',.00043,.00013);
     if rndwg < .00017;
        rndwg = .00017;
     end
     if rndwg > .00079;
        rndwg = .00079;
     end
     wategain = rndft * rndwg;
     pop1(prey,1) = pop1(prey,1) + wategain;
     if pop1(prey,1) > .16;  % pupate
       pop1(prey,2) = 1000*3.72*pop1(prey,1)-222.53; % # of eggs
       pop1(prey,4) = 1; % pupate
       dead = dead + 1;
     end;
    end;
   else; %  pop2
    if pop2(prey,4) == 0;
      if pop2(prey,5)==1; % then encounter could occu
       rndenc2 = rand;
        if rndenc2 < .1; % if predator enc, then this is prob of enc
        pop2(prey,5)=2; % encounter has occurred
        rnddeath = rand;
        if rnddeath < .236;  % death occurs
        pop2(prey,1) = 0; % weight goes:0
        pop2(prey,2) = 0; % fecundity goes:0
        pop2(prey,4) = 2; % death
        dead = dead + 1;
       else;
        rndb = rand;
         if rndb > .166;  % buzz encounter
           % normal dist feeding time 1.82 - 15.45 with mean of 6.62 mins
           rndbft = random('norm',6.62,2.4);
          if rndbft < 1.82;
            rndbft = 1.82;
```

```
    end
    if rndbft > 15.45;
      rndbft = 15.45;
    end
     fi = 4.35*rndbft + 26.42; % feeding interval
     rndlt = rand*(11.89-.10)+.10; % lost time 0.10 - 11.89 min
    pop2(prey,3) = pop2(prey,3)+rndbft+fi+rndlt;
      rndwg = random('norm',.00043,.00013);% normally dist random #
         .00017 - .00079g/min w/ mean .00043
    if rndwg < .00017;
         rndwg = .00017;
end
   if rndwg > .00079;
         rndwg = .00079;
   end
    wategain = rndft * rndwg;
   pop2(prey,1) = pop2(prey,1)+wategain;
   if pop2(prey,1) > .16;  % pupate
     pop2(prey,2) = 1000*3.72*pop2(prey,1)-222.53; % # eggs
     pop2(prey,4) = 1; % pupate
     dead = dead + 1;
   end
  else %  squeeze
     rndinj = rand; % .143 die due:injury
    if rndinj < .143;
     pop2(prey,4) = 2; % death
     pop2(prey,1) = 0;
     pop2(prey,2) = 0;
     dead = dead + 1;
   else
      rnddrop = rand; % prob of dropping off
     if rnddrop > .273 % drop
       rnddie = rand; % prob droppers die
       if rnddie < .588;
        pop2(prey,4) = 2; % death
        pop2(prey,1) = 0;
        pop2(prey,2) = 0;
        dead = dead + 1;
      else
          % rndft feeding time 1.7667 - 7.900 min uniform distribution
         rndft = rand*(7.900-1.7667)+1.7667;
         fi = 4.35*rndft+26.42;
          rndslt = rand*(1440-120)+120; % lost time 120 - 1440 min
         pop2(prey,3) = pop2(prey,3)+rndft+fi+rndslt;
```

```
       rndwg = random('norm',.00043,.00013); % normally dist random
     # .00017 - .00079g/min w/mean .00043
     if rndwg < .00017;
       rndwg = .00017;
     end
     if rndwg > .00079;
       rndwg = .00079;
     end
     wategain = rnddft * rndwg;
     pop2(prey,1) = pop2(prey,1)+wategain;
     if pop2(prey,1) > .16  % pupate
      pop2(prey,2) = 1000*3.72*pop2(prey,1)-222.53; % # eggs
      pop2(prey,4) = 1 % pupate
      dead = dead + 1
     end
    end % ends if rnddie < .588;
   else % did not drop off
     rndsft = rand*(7.900-1.7667)+1.7667; % squeeze feeding time
    fi = 4.35*rndsft+26.42;
     rndslt = rand*(76.62-10.33)+10.33; % lost time 76.62 - 10.33 min
    pop2(prey,3) = pop2(prey,3)+rndsft+fi+rndslt;
      rndwg = random('norm',.00043,.00013); % normally dist random
    # .00017 - .00079g/min w/ mean .00043
    if rndwg < .00017;
      rndwg = .00017;
    end
    if rndwg > .00079;
      rndwg = .00079;
    end
     wategain = rndft * rndwg;
    pop2(prey,1) = pop2(prey,1)+wategain;
    if pop2(prey,1) > .16;  % pupate
      pop2(prey,2) = 1000*3.72*pop2(prey,1)-222.53 % # eggs
      pop2(prey,4) = 1; % pupate
     dead = dead + 1;
    end
   end % ends if rnddrop < .273; % drop
  end % ends if rndinj < .143;
 end % ends if rnddb > .166
 end % ends if rnddeath < .236
else
  rndft = rand*(7.900-1.7667)+1.7667; % feeding time
 fi = 4.35*rndft+26.42;
 pop2(prey,3) = pop2(prey,3)+rndft+fi;
```

```
               rndwg = random('norm',.00043,.00013); % normally dist random #
                  .00017 - .00079g/min w/ mean .00043
             if rndwg < .00017;
              rndwg = .00017;
             end
             if rndwg > .00079;
              rndwg = .00079;
             end
             wategain = rndft * rndwg;
             pop2(prey,1) = pop2(prey,1)+wategain;
             if pop2(prey,1) > .16;  % pupate
               pop2(prey,2) = 1000*3.72*pop2(prey,1)-222.53; % # eggs
               pop2(prey,4) = 1; % pupate
               dead = dead + 1;
             end
            end % ends if rndenc2 < .1
        else % no encounter
         rndft = rand*(7.900-1.7667)+1.7667; % feeding time
         fi = 4.35*rndft+26.42;
         pop2(prey,3) = pop2(prey,3)+rndft+fi;
         rndwg = random('norm',.00043,.00013); % normally dist random #
         .00017 - .00079g/min w/ mean .00043
        if rndwg < .00017;
          rndwg = .00017;
        end
        if rndwg > .00079;
          rndwg = .00079;
        end
         wategain = rndft * rndwg;
         pop2(prey,1) = pop2(prey,1)+wategain;
         if pop2(prey,1) > .16;  % pupate
           pop2(prey,2) = 1000*3.72*pop2(prey,1)-222.53; % # eggs
           pop2(prey,4) = 1; % pupate
           dead = dead + 1;
         end
       end % ends if pop2(prey,5)==1
     end % ends pop2(prey,4)==0
    end % ends if pop = 1
   end % ends for prey=1:1000
  end % while

if pops == 1;
  fid = fopen('pop1.txt','w');
        for pp = 1:1000;
```

```
         fprintf(fid,'%1.4f\t %1.4f\t %3.1f\t
%3.0f\n',pop1(pp,1),pop1(pp,2),pop1(pp,3),pop1(pp,4));
       end
  st = fclose(fid);
else
  fid = fopen('pop2.txt','w');
         for pp = 1:1000;
         fprintf(fid,'%1.4f\t %1.4f\t %3.1f\t %3.0f\t
%3.0f\n',pop2(pp,1),pop2(pp,2),pop2(pp,3),pop2(pp,4),pop2(pp,5));
       end
  st = fclose(fid);
end

end % pops
```

VITA

Rebecca Young Rivers was born on April 11, 1966 in New York, New York. In 1988, she received her Bachelor of Arts degree in psychobiology from Wellesley College in Wellesley, Massachusetts. Following graduation, she studied sustainable agriculture at the New Alchemy Institute in East Falmouth, Massachusetts. She then became a research assistant at the Cranberry Experiment Station, a branch campus of the University of Massachusetts that focuses on cranberry research and extension. It was there that she developed an interest in the impact of spiders as biological control agents. She entered the graduate program in Ecology and Evolutionary Biology at the University of Tennessee in the fall of 1991. In 1996, she married William Petty Rivers and their daughter, Sarah, was born in 1997. She is presently on the faculty of the Environmental Studies Program at St. Lawrence University in Canton, N.Y.