Testing the effects of resource distribution on simultaneous predator and prey habitat selection using seven-spotted lady beetles (*Coccinella septempunctata* L., Coleoptera: Coccinellidae), pea aphids (*Acyrthosiphon pisum* (Harris), Hemiptera: Aphididae), and tic bean plants (*Vicia faba* L., Fabaceae)

By

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This thesis entitled:

Testing the effects of resource distribution on simultaneous predator and prey habitat selection using seven-spotted lady beetles (*Coccinella septempunctata* L., Coleoptera: Coccinellidae), pea aphids (*Acyrthosiphon pisum* (Harris), Hemiptera: Aphididae), and tic bean plants (*Vicia faba* L., Fabaceae)

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The final copy of this thesis has been examined by the signatories, and we find that

both the content and the form meet acceptable presentation standards of scholarly work

in the above mentioned discipline.

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Testing the effects of resource distribution on simultaneous predator and prey habitat

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Coleoptera: Coccinellidae), pea aphids (*Acyrthosiphon pisum* (Harris),

Hemiptera: Aphididae), and tic bean plants (*Vicia faba* L., Fabaceae)

Thesis directed by Assistant Professor Samuel M Flaxman

This study examined predator-prey interactions to determine which sources of

information available to individuals influenced their movement and habitat selection

across a heterogeneous landscape. I tested observed spatial distributions of organisms

against predictions of a general interference ideal free distribution model to determine

whether mobile predators, prey, or both achieve optimal distributions. To do so, I

incorporated habitat selection treatments in which there were (1) prey but no predators,

(2) predators but no prey, and (3) predators and prey simultaneously. For these

experiments, I used a tritrophic system in which seven-spotted lady beetles (*Coccinella

septempunctata* L., Coleoptera: Coccinellidae), pea aphids (*Acyrthosiphon pisum*

(Harris), Hemiptera: Aphididae), and tic bean plants (*Vicia faba* L., Fabaceae) were,

respectively, the predators, prey, and prey's resource. In microcosms, I created and

quantified patches of varying quality (from the perspective of the prey) among which

predators and prey were allowed to move freely. I also examined intraspecific

competition between beetle predators by determining the coefficient of interference for

the beetles.

Theoretical studies of tritrophic systems have given rise to the general prediction that predators should aggregate where prey's resource is of the highest quality, not necessarily where prey are most abundant. This suggests a general adaptive strategy of information use for predators: assess the quality of the prey's resource and spend more time where those resources are better. Empirically testing this and other predictions of models is important for advancing understanding of how spatial distributions are impacted by trophic interactions. My research quantified measures of individual fitness, intra-specific competition, and inter-species interactions in order to test predictions of a general interference model with mobile predators and prey. For this model, I integrate and systematically assess qualities important within a natural system, such as competition and intrinsic growth rates across patches.

My results show that predators were able to detect and respond to the quality of their prey's resource. Furthermore, both predators and prey followed predicted spatial distributions of simultaneous ideal free distribution. The joining of theoretical and empirical studies is critical for improving understanding of distributions and abundances of organisms in nature.

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Chapter 1 – Introduction
Animal Movement and Habitat Selection Mechanisms
in Tritrophic Systems

Understanding the movements of organisms in their environments is a central theme in basic and applied ecology because movement, whether passive or active, plays a fundamental role in all biological communities (Nathan et al. 2008). Organismal movement can be defined simply as a change in an organism's location in three-dimensional space. However, there are many complexities to understanding movement dynamics of individuals and their resulting patterns (Morales and Ellner 2002; Gibbs et al. 2010). Levin (2002) highlighted the difficulties inherent in connecting mechanisms with patterns in complex systems. Indeed, the result of multiple interactions occurring between large numbers of individuals is that even the simplest communities have complex dynamics (Bolker et al. 2003).

Understanding proximate cues that influence organismal movement is important for predicting spatial distributions and a population's response to change (Bowler and Benton 2005). Although historically underrepresented in ecology, analyzing movement at level of the individual organism can help to increase our understanding of larger-scale ecological patterns by teasing apart underlying building blocks of those patterns (Morales and Ellner 2002; Werner and Peacor 2003). For example, empirical and theoretical evidence suggest that adaptive movements by individuals have important consequences for larger scale ecological dynamics (Torney et al. 2010; Gouhier et al. 2010).

A frequent prediction across many theoretical studies—and one that has been relatively untested empirically—is that predators should assess and respond adaptively

to the quality of resources consumed by their prey – resources which the predators do not consume themselves (see Rosenheim 2004; Sih 2005; Hammond et al 2007; and Flaxman and Lou 2009 for reviews). In testing this prediction, few empirical studies have eliminated enough other cues to rigorously determine whether or not predators can detect and respond to the quality per se of their prey's resource (Lima 2002; Křivan et al. 2008). My research integrated theoretical predictions and empirical studies and elucidated the sources of information used in habitat selection by predators and prey.

Only a few studies (Bouskila 2001; Sih 2005; Hammond et al. 2007) have quantified patch quality for mobile prey and predators simultaneously and even fewer have done so with quantitative tests of explicit models (Lima 2002; Sih 2005; Křivan et al. 2008). To overcome this, I utilized a tritrophic system that incorporated i) patches of varying quality resource for the consumer, ii) a consumer that feeds exclusively on the resource, and iii) a predator that feeds exclusively upon the consumer. Furthermore, I also performed experiments that quantitatively measured the strength of intraspecific competition.

In one experiment, predator-prey interactions and their impacts on habitat selection by herbivores were assessed. My tritrophic system incorporated seven-spotted lady beetles (*Coccinella septempunctata* L., Coleoptera: Coccinellidae), pea aphids (*Acyrthosiphon pisum* (Harris), Hemiptera: Aphididae), and tic bean plants (*Vicia faba* L., Fabaceae) as, respectively, the predators, prey, and prey's resource. Using microcosms, I created patches of varying quality (from the perspective of the prey, following Hodge et al.'s (2005) methods), among which predators and prey were allowed to move freely. I used this to determine which sources of information influenced

movement and habitat selection in my system. The results of this study showed that predators were able to detect and respond to the quality of their prey's resource. While theory has frequently predicted such behavior, direct responses of predators to resource quality (rather than resource amounts, resource damage, or indirect cues of prey) have not previously been demonstrated. These results help to substantiate general predictions of ecological theory and have implications for predicting the behavior of biological control agents.

A second set of analyses used the same tritrophic system of lady beetles, pea aphids, and tic beans in order to test predictions of a general interference Ideal Free Distribution (IFD; Fretwell and Lucas 1969; Sutherland 1983; Sih 1998) model to determine whether mobile predators, prey, or both achieve IFDs when in the presence of one another. My research quantified measures of individual fitness, intra-specific competition, and inter-species interactions in order to fully parameterize and quantitatively test a general interference model of a multi-trophic ideal free distribution with mobile predators and prey. The results showed both predators and prey following predicted spatial distributions.

Organism Background: Distribution and Diversity

Insects are classic model organisms, often used to represent larger-scale systems in which empirical testing would be difficult or impossible. In order to test aspects of habitat selection and information use, the experimental system must be well established. Habitat selection studies utilizing insect models are widely accepted and have yielded substantial results for biological questions in many disciplines (e.g. Dixon

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1998, 2000; Flaxman and deRoos 2007; Hammond et al. 2007; Piñol et al. 2009). The well-known life histories studies of both pea aphids and seven-spotted lady beetles make this model system optimal for this study of habitat selection in a tritrophic system. The following is brief overview of relevant life history traits of these model organisms.

Acyrthosiphon pisum

Aphid population structure, traits, and dynamics have been extensively catalogued, specifically because of their importance as an agricultural pest species (Losey and Denno 1998; Caillaud and Via 2000; Abbot 2009; Piñol et al. 2009; Sarwar 2009). Aphididae are an extremely diverse family: an estimated 4000 species have been identified worldwide, mostly in temperate climates (Dixon 1998). Depending on the species, aphids can be generalists or specialists, although most species have a high rate of host specificity and are monophagus (Dixon 1998; Caillaud and Via 2000).

Aphids are small, soft-bodied, phloem feeding insects, which locate a potential food resource via antenna and feet chemoreception (Caillaud and Via 2000). A flexible stylet mouthpart penetrates the outer plant cell wall's extracellular material for phloem feeding and after penetrating the wall an enzyme is released to give rigidity to the stylet during feeding (Ma et al. 1990). A phloem feeder's diet consists of mostly sugars and low quantities of amino acids. As a result of this nutrient-poor diet, aphids are dependent upon gut endosymbionts (Dixon 1998), which are thought to provide amino acid supplementation (Douglas 1998).

Frequently, after arriving on a potential host plant, an aphid will probe the plant with its mouthparts several times prior to feeding as a means of host selection and

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location of a preferred site, usually near a new shoot (Dixon 1998). Interestingly, aphids

show little preference between hosts with regards to manipulated nutrient quality (e.g.

added fertilizer) and often require the presence of secondary plant compounds in

tissues to deter feeding (Givovich et al. 1994; Dixon 1998; Flaxman and DeRoos 2007).

Induced defenses that alter the phloem have been found to be most effective in

deterring aphid feeding (Givovich and Niemeyer 1995; Hodge et al. 2005; Ton et al.

2005). For instance, Hodge et al. (2005) found that manipulating plants using a non-

toxic, non-protein amino acid to induce greater extracellular material build up along

plant walls made the phloem more difficult to access by aphids.

Pea aphids have evolved several tactics for avoiding potential predators.

Dropping behavior, in which an aphid simply drops directly onto the soil or leaf beneath

it, occurs in response to disturbance by predators (and other stimuli as well: Piñol et al.

2009; Gish et al. 2010). An alarm pheromone, (E)-β-farnesene, is often produced by an

aphid just prior to dropping and alerts conspecifics (potential clones) to possible

predation risk (Dixon and Agarwala 1999). Dropping behavior increases an individual

aphid's risk of desiccation and contact with ground dwelling predators; however,

dropping behavior may be highly effective against an immediate risk of predation,

specifically against foliar and airborne predators (Piñol et al. 2009). Three factors that

are thought to impact dropping behavior are: i) risk of predation, ii) quality of the

resource being abandoned, and iii) risk of mortality in new habitat (Losey and Denno

1998). Interestingly, adult aphids are far more likely to react to the alarm pheromone by

dropping then nymphs, which is thought to be due to the higher mortality risk that a

nymph would encounter if removed from a plant (Losey and Denno 1998; movement on

the soil is slower and more difficult for nymphs is than adults). Frequent dropping

behavior increases risk of predation and desiccation as well as decreased feeding and

delayed development and reproduction (Dill et al. 1990). However, dropping also forces

an aphid into a habitat selection choice: it has to go back to a plant in order to survive.

Coccinella septempunctata

Lady beetles, known colloquially as ladybugs, are a widespread and successful

group of insects found throughout many regions of the world; approximately 4200

species have been described (Evans and Dixon 1986). As the most common predator

of aphids, lady beetles have been extensively examined in agricultural settings as

biocontrol agents (Dixon 2000; Piñol et al. 2009). However, lady beetles are extremely

dependent upon prey abundance and will quickly move away from patches with little or

no prey (Dixon 2000).

Predator-prey dynamics between aphids and lady beetles has been widely

researched (Evans and Dixon 1986; Dixon and Agarwala 1999; Weisser et al. 1999;

Dixon 2000; Křivan 2008; Piñol et al. 2009). Lady beetles are predators, but their ability

to find and capture prey, especially aphids, is limited as they are more efficient at

disturbing aphid feeding than capturing aphids, due in part to the dropping response by

the aphids (Weisser et al. 1999; Piñol et al. 2009). Lady beetles are generally

considered to be specialist predators of aphids as these make up the majority of their

diet (Dixon 2000). However, lady beetles will feed on other invertebrate species and

even nectar depending on current nutritional needs and aphid abundance (Soares et al.

2004). Predator responses to indirect cues about or from their prey, such as volatiles

emanating from plants damaged by herbivory, have been foci of a number of studies (e.g., De Moraes et al. 1998; De Moraes et al. 2000; Olson et al. 2009; Laundre 2010; Mauck et al. 2010). However, no empirical study to date has examined beetle predator's response to multiple patches of varying quality using a living resource.

My study examined predator-prey interactions to determine which sources of information influenced individuals in their movement and habitat selection within a heterogeneous landscape. Furthermore, I tested observed spatial distributions of organisms against predictions of a general interference ideal free distribution model to determine whether mobile predators, prey, or both achieve optimal distributions. For this model, I integrate and systematically assess qualities important within a natural system, such as competition and intrinsic growth rates across patches. Incorporating both theoretical and empirical studies is critical for improving understanding of distributions and abundances of organisms in nature.

Chapter 2
Can predators assess the quality of their prey's resource?

Movement by individual organisms affects patterns and processes at many levels of biological organization (e.g. Johnson et al. 1992; Morales and Ellner 2002; Levin 2002; Werner and Peacor 2003; Bowler and Benton 2005; Sih 2005; Kondoh 2007; Flaxman et al. 2011). An essential component in the study of movement ecology is the examination of mechanistic behavioral strategies—the algorithms governing real-time, individual movements—and how they influence ecological processes and patterns (Abrams 2001; Agrawal et al. 2007; Abrams 2008; Nathan et al. 2008). Accordingly, over the past several decades, movement strategies and habitat selection have been focus of many studies of animal behavior. However, we still lack a complete understanding of how individual-level movements impact and are shaped by larger scale processes, such as predator-prey dynamics (Nathan et al. 2008). Hence, the experiments presented here extend recent studies (Sih 1998; Rosenheim 2004; Sih 2005; Hammond et al. 2007; Piñol et al. 2009; Belovsky et al. 2011) by teasing apart the sources of information used by individuals selecting among heterogeneous patches of habitat in both the presence and absence of predator-prey interactions.

A rich body of theory has generated many predictions about movements of a single species considered in isolation. Fewer studies have examined the real-time dynamics of behavioral responses of predators in predator-prey interactions (reviewed by Lima 2002; Sih 2005; Abrams 2007; Hammond et al. 2007; Křivan 2008). Leaving out the behavior of predators ignores potentially important factors—such as the responsiveness of predators to prey as well as nonlethal interactions between predators

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and their prey—that can strongly influence the dynamics and patterns of predator-prey interactions (Hugie and Dill 1994; Lima 2002; Bolker et al. 2003; McCoy & Bolker 2008; Raffel et al. 2010; Belovsky et al. 2011).

The various spatially explicit theoretical models that have been developed on interacting predators and prey have consistently generated the same prediction about distributions of predators and prey that are simultaneously optimal for both species. Many of these models predict that the predators' spatial distribution should match the distribution of the prey's resource rather than matching that of the prey, whereas the prey are predicted to be more uniformly distributed than the resource. Sih (1998, 2005) coined the term "leapfrogging" to describe this prediction (see also Rosenheim 2004 and Flaxman and Lou 2009 for additional review and explanation). The generality of the leapfrogging prediction suggests a simple movement strategy that could be adaptive for predators in habitat selection: predators should use the prey's resource as a cue, and move preferentially to areas where that resource has higher abundance or quality.

Very few empirical studies have simultaneously manipulated predators, prey, and habitat quality simultaneously to examine the movement strategies that operate in the context of predator-prey interactions (Lima 2002). A few recent empirical studies have done so (see Bouskila 2001; Sih 2005; Hammond et al. 2007, Luttbeg et al. 2009), yielding some support for the leapfrogging prediction. However, no single empirical study to date has included all of the following features: i) predators and prey that are both free to move among patches, ii) simultaneous patch choice among three or more patches by both predators and prey, and iii) measured and manipulated patch quality using a living resource. I designed and conducted an empirical study including these

features to answer the following questions: What proximate cues affect the movement behavior of predators? Can predators detect the quality of a prey's resource? If so, do predators utilize that assessment as part of their movement strategy?

Answers to these questions will increase understanding of the information sources predators are using in real time to guide habitat selection. In turn, this understanding allows us to test general predictions from ecological theory about adaptive strategies and their consequences. Knowledge of this kind is also key if we are to reliably predict the responses of populations to rapidly changing habitats (Bowler and Benton 2005).

Methods

I utilized a tritrophic system that incorporated: i) patches of a plant resource of varied quality from the perspective of the prey, ii) prey that consume the resource, and iii) predators that consume the prey (but do not consume the plants). In my system, seven-spotted lady beetles (*Coccinella septempunctata* L., Coleoptera: Coccinellidae), pea aphids (*Acyrthosiphon pisum* (Harris), Hemiptera: Aphididae), and tic bean plants (*Vicia faba* L., Fabaceae) were, respectively, the predators, prey, and plant resources. I manipulated plant quality from the aphids' perspective with a previously tested nontoxic method, described in detail below. Here I report the results of three different habitat selection experiments involving manipulation of this tritrophic system in laboratory enclosures. In the first of trials there were predators and plants (of varying quality) but no prey. In a second set of trials there were prey and plants (of varying quality) but no predators. Lastly, in the third trial all three species were present. These different

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scenarios allowed us to tease apart the relative contributions of different sources of information to the conditional movements of predators and prey in a straightforward manner.

Organisms and Rearing Techniques

Tic bean plants were grown in an environmentally controlled greenhouse with 16:8 hour daily light:dark cycles. To ensure even growth, plants were illuminated by 32-watt fluorescent bulbs (Philips "Daylight Deluxe", color temperature 6500K) during the 16-hour light cycle throughout the experiment. The average daily temperature was 20±2°C (mean ± 1 SD) and average nightly temperature was 17±2°C. Plants were grown from seed in 10cm-diameter round plastic pots (one seed per pot; seeds obtained from Harris Seeds, Rochester, NY; variety = "Broad Bean Improved Long Pod"). All plants were grown in Fafard Growing Mix F-15 (Canadian Sphagnum Peat (85%) Perlite) and were watered as needed. No fertilizers or pesticides were applied.

Pea aphids (hereafter, "aphids") utilized in this study were clone "5A red" and were provided (under USDA permit number P526P-09-03859) by the laboratory of Dr. Nancy Moran. Details about this clone's original collection and genetics are described by The International Aphid Genomics Consortium (2010). Following the rearing techniques of Flaxman and DeRoos (2007), aphids utilized for trials were raised at low to moderate densities—no more than 50 adults per plant—on 14-21 day old tic bean plants within ventilated 8 L plastic tubs.

Seven-spotted lady beetles (hereafter, "beetles") were field collected on the campus of the University of Colorado at Boulder starting in May 2010 through

September 2010. Beetles were raised in enclosures containing tic bean plants and aphids, replenished as needed.

Creating and Quantifying Variation in Plant Quality

To create patches of varying quality from the perspective of the prey, I used the methods of Hodge et al. (2005) in order to manipulate the quality of tic bean plants. Fourteen day-old tic bean plants were treated with a single 25 mL application of either a 50 mM, 25 mM, or 0 mM (control) solution of DL-β-aminobutyric acid (BABA), applied as a soil drench. BABA is a non-protein amino acid and a single soil drench has been shown to be effective in reducing plant quality for phloem-feeding herbivores, such as aphids, by increasing a plant's defenses (Hodge et al. 2005). I anticipated (and validated, below) that the three different concentrations of BABA used (control = 0 mM, 25 mM, and 50 mM) would create three different levels of plant quality, with the control being the highest quality and the 50 mM being the lowest (Hodge et al. 2005). BABA (purity > 95%) was obtained from The Lab Depot, Inc. (Dawsonville, GA). To ensure uptake and distribution of the BABA throughout a plant's tissues, tic bean plants were not watered or used for the study until 72 hours following the soil drench application of BABA.

To validate that BABA did indeed change plant quality from the perspective of the aphids, I performed a bioassay, similar to that performed by Hodge et al. (2005). For this I utilized enclosures (30cm high x 15cm width x 15cm length) containing a single plant that had been subjected to one of the three treatments described above (N = 25 plants per treatment). The enclosures were constructed from transparent, colorless

acrylic glazing (walls) with openings for ventilation on the top and sides covered by fine-mesh organza. Each plant remained in its pot, which was sunk into a hole in the floor of the enclosure such that the top of the pot was flush with the enclosure's floor. The floor of the enclosure was covered with a thin layer of (untreated) soil to create a continuous, natural surface on which organisms could walk; this layer of soil also prevented organisms from contacting any BABA treated soil. Additionally, to prevent organisms from climbing up the walls of the enclosures, the bottom 2 cm of the walls of the enclosure were coated on the inside with Fluon® (Northern Products, Woonsocket, RI), a substance with an extremely low coefficient of friction.

To quantify plant quality in these bioassay trials, I measured the intrinsic rate of increase of the aphids on plants grown in the different BABA treatments. To do so, a single adult, apterous aphid, the "foundress," was placed on each plant for 24 hours. After 24 hours, the foundress and all but one nymph were removed and the remaining nymph, the "secondary foundress," was allowed to mature and produce nymphs. As soon as the secondary foundress began to produce nymphs, 120 hours (five days) were allowed to pass. I then used the number of nymphs produced by the secondary foundress in the 120 hour time period to quantify the intrinsic rate of increase of the aphids on the different treatments. For the latter, I utilized the following formula, modified from Wyatt and White (1977; as applied to aphids by Hodge et al. 2005):

$$r_m = 0.74 \, [\log_e (\text{\# nymphs produced})] / 120 \text{ hours}$$

In addition, survival of the adult aphids and nymph production were calculated to determine other quantitative impacts of BABA on survival and fecundity of aphids.

General Setup of Habitat Selection Experiments

For the habitat selection trials, enclosures were constructed in a similar manner to those above but with four plants (instead of one) inside a larger enclosure (30cm high x 30cm wide x 30cm long; Figure 2.1). Each enclosure contained one control plant, two 25 mM plants (denoted 25 mM A and 25 mM B) and one 50 mM plant. All four plants were of equal size at the start of a replicate. Plants were arranged in a pattern as shown in Figure 2.1, with a barrier preventing movement across the middle of the enclosure. With this arrangement, any focal plant has two neighbors whose qualities are different than that of the focal plant. Each replicate (N=70; details below) of the habitat selection trials lasted 120-hours (five days) from the initial addition of organisms to an enclosure.
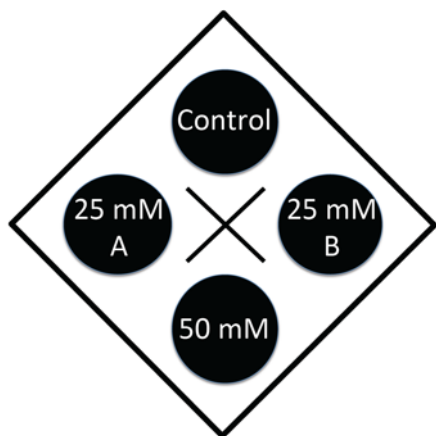
Figure 2.1 Overhead schematic view of the laboratory enclosures used for habitat selection experiments. Circles with abbreviations represent plants and their BABA treatments (see Methods). Lines indicate the placement of barriers to movement.

Habitat Selection by Predators without Prey

Trials incorporating predators only (N=20 replicates; henceforth referred to as "predators only trials") used tic bean plants and predators only; prey were never present in these enclosures, eliminating any direct or indirect cues (e.g., responses of plants to herbivory) that arise from the presence of herbivorous prey.

Four beetles were added to each enclosure with different, naïve individuals used for each replicate. Four beetles were added to each enclosure with different, naïve individuals used for each replicate. Preliminary work (ACW & SMF, personal observations) suggested that this density of beetles (average of 1 per plant) would allow us to observe many predator-prey interactions but would still be low enough to allow many of the aphids to survive to the end of a trial (in the trials below using both predators and prey). When added to the enclosure, beetles were placed individually on the soil between plants. Prior to all trials, beetles had access to aphids *ad libitum* (in rearing chambers) on tic bean plants. In order to quantify habitat selection and spatial distributions of beetles proportion of time spent on a plant for predators were recorded for one hour during each of the five days that a replicate lasted. A beetle was defined as being in one of the four "patches" if it was on the given plant; otherwise it was recorded as being on the soil or wall of the enclosure (i.e., it was not assigned to a patch of habitat). To capture predators at their most active time period (1100-1400 hours; ACW, personal observation), as well as for consistency across replicates, all observation periods used for calculating beetle activity budgets took place between 1200h and 1300h, Mountain Standard Daylight time. Beetle habitat use and spatial

distributions are presented below as the proportion of time the beetles in a trial spent overall in each patch.

Habitat Selection by Prey without Predators

Trials incorporating prey only (N=20 replicates; henceforth referred to as "prey only trials") used tic bean plants and adult, apterous (wingless) aphids only; lady beetle predators were never present in these enclosures, eliminating any direct or indirect cues that arise from the presence of predators.

A total of 160 aphids were introduced to an enclosure by placing an equal number of aphids on the upper leaves of each of the four plants (40 aphids per plant). This number of aphids represents natural infestation levels of aphids on a young plant (Dixon 1998; Losey and Denno 1998). The locations of all aphids in a trial were recorded once each day at 24-hour intervals from the starting time. An aphid was defined as being in one of the four "patches" if it was on the given plant; otherwise it was recorded as being on the soil or wall of the enclosure (i.e., it was not assigned to a patch of habitat). Aphid habitat use and spatial distributions are presented below as the proportion of all aphids present in each patch.

Habitat Selection by Predators with Prey

For trials incorporating both predators and prey (N=30 replicates; henceforth referred to as trials with "predators and prey together"), enclosures as described above utilized four beetle predators, 160 adult, apterous aphids, and four tic bean plants. All

these trials started with a uniform distribution of aphids (40 aphids/plant). The aphids

were allowed to settle for 24 hours before the beetles were introduced to the enclosure.

These trials again lasted for 120 hours (from the initial addition of aphids) with

counts of all organisms and recording of proportion of time spent in a "patch" by a beetle

(as above) once every 24 hours. The counts tallied all of the remaining original 160

aphids, those not consumed by the beetle predators, as well as any new nymphs

produced by the aphids. Aphid distributions reported below are for the adults aphids.

Statistical Analyses

All statistical analyses were performed in JMP (JMP 9.0.2, SAS Institute, Cary,

NC). In order to determine the relationship between BABA treatment and the intrinsic

rate of increase for aphids, a one-way analysis of variance (ANOVA) and χ^2 analysis

were performed (all data were normally distributed). Similarly, in order to make

comparisons between patches (i.e. if proportions of organisms differed between two

patches), a comparison of means, either t-test or Wilcoxon ranked test as appropriate,

were performed.

Regression Analyses and Model Selection

Due to the nature of our study, the data for the habitat selection trials were right

skewed towards the small counts (zeros for numbers of organisms in some patches at

some times of observation), and thus the proportion of time spent in each patch was

fitted with a logistic regression for binomial counts (0 for not in a patch, 1 for in a patch)

within using the Generalized Linear Model (GLM) procedure in JMP (version 9.0.2, ©

SAS Institute, Cary, NC). Trial ID was included as a random effect to account for repeated observations on a single replicate. Day of replicate (1, 2, 3, 4, or 5), plant treatment (50mM, 25mM, or control), and proportion of heterospecifics in a given patch were considered as predictors. To determine which of the fixed effects most impacted habitat selection by both predators and prey I used the model selection approach based on Akaike Information Criterion ("AIC"; Burnham and Anderson 2002) as well as the resulting odds-ratios. In order to define which model(s) show the best the support we compared ΔAICc values and focused on models with lower ΔAICc values. As ΔAIC increases there is considerably less evidence that a model is the best model of the models considered in explaining observed data; for example when a ΔAIC reaches a value of four or greater there is considerably less support while values over ten essentially have no evidence in support of that model (Burnham and Anderson 2002). Furthermore, in comparing models with ΔAIC ≤ 2 and different numbers of predictors, we checked the goodness of fit for each model to see if the addition of a variable changed the deviations between models. If the goodness of fit of a model was improved by the addition of a variable (and the ΔAIC value was still ≤ 2), then the variable was kept as a predictor variable (i.e., we did not throw it out as being "pretending variable", sensu Anderson 2008).

To determine if insects' use of the two patches of equivalent quality ("25mM A" and "25 mM B"; see above and Figure 2.1) differed, a separate GLM analysis was performed for each of the three habitat selection experiments (i.e., predators only, prey only, and predators and prey together). For both predators and prey, these analyses revealed no significant difference between use of the 25 mM A and B plants in any of

the three habitat selection experiments and thus I subsequently pooled data from 25 mM A and B for analyses. To pool these I took all data points from both patches (A and B) from a specific replicate (predators and prey, predators only, and prey only; done independently for each trial) and randomly subsampled from within the replicate to create a data set that is equal in number to that of the other two patches. The newly created data set acted as the data points used in subsequent analyses and created a balanced design (across the different patch types) for statistical analyses.

Results

Creating and Quantifying Variation in Plant Quality

The different plant treatments had significant effects on the performance of the aphids in terms of survival, nymph production, and intrinsic rate of increase with the control treatment being the most favorable and the 50mM treatment being the least favorable for aphid performance (Table 2.1). These results provide the quantitative basis for my claims of differences in "resource quality from the perspective of the aphids" among the differently treated plants. Specifically, survival to reproductive age (by the secondary foundress) was 100% for the control plant treatment, 80% on the 25mM treatment, and 69% on the 50mM treatment (Table 2.1).

Table 2.1

Results of bioassay of methods utilized to create variation in plant quality in which primary foundress experience on an individual plant was quantified.

	Plant Treatment				
	0 mM	**25 mM**	**50 mM**		
Primary Foundress Survival (%, n=16)				χ^2	P
1st 24 hours	100	100	100	-	NS
Until day 7	100	92	84	4.33	NS
Until reproduction	100	80	69	9.05	<0.05
Nymph Production by Primary Foundress (mean±SE, (n))				*F*	*P*
Nymphs produced [a]	4.15±1.7	4.07±2.9	4.23±2.7	0.02	NS
	(26)	(26)	(26)		
Nymph Production by Secondary Foundress (mean±SE, (n))				*F*	*P*
Days until 1st nymph	8.84±0.7	10.0±1.0	11.0±1.1	26.31	<0.0001
	(26)	(21)	(18)		
Total Nymphs [b]	32.15±10.5	15.69±11.5	6.15±7.3	45.41	<0.0001
	(26)	(21)	(18)		
r_m [c]	0.50±0.04	0.33±0.18	0.18±0.17	30.67	<0.0001
	(26)	(21)	(18)		

[a] during a 24-hour period
[b] Average total nymphs produced by secondary foundress over 120 hour trial
[c] Intrinsic rate of increase

The average numbers of nymphs produced by a secondary foundress were significantly different among patch treatments (Table 2.1). Finally, the intrinsic rates of increase of secondary foundress strongly differed by plant treatment (Table 2.1).

Additional survival and nymph production results in Table 2.1 support the control patch as most favorable and the 50 mM patch as least favorable, from the perspective of the aphids. In sum, all results were very similar to those reported by Hodge et al. (2005). Hence, my main purpose for reporting them here is to validate the usage of these methods for the purpose of creating variation in patch quality in the habitat selection experiments, and also to put quantitative estimates on plant quality for this and future studies.

Habitat Selection by Predators in the Absence of Prey: Predators Only Trials

In examining all alternative models in the model selection analyses (Table 2.2), data were most consistent with predators basing their habitat selection on resource quality; the predictor "day" showed little support within the model selection. Furthermore, the addition of the variable "day" to the less complex model, treatment, did not significantly impact the model and thus was dismissed as pretending variable (Anderson 2008). Using the top model with the strongest support (lowest ΔAICc) shows that in the complete absence of prey, or prey cues, predator habitat use was significantly influenced by different plant treatments (F (2,297) = 59.07, p<0.0001; Figure 2.2). The small error bars around the mean proportions indicate that there was little variability in the spatial distributions of predators across replicates (Figure 2.2).

Table 2.2

Model selection based on AICc of the probability of predators or prey being on a treatment patch when heterospecifics are absent from the enclosure.

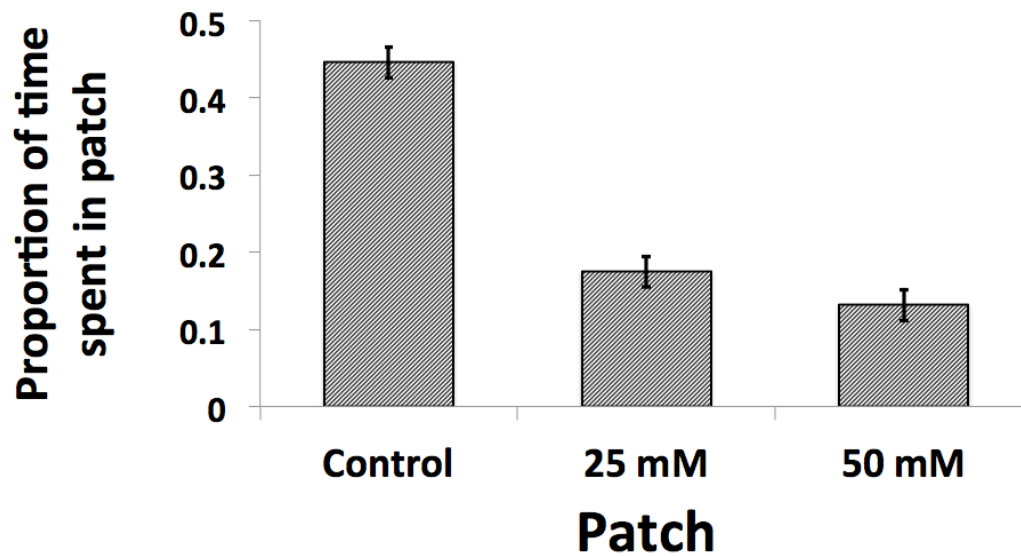| Factor(s) in Model		Predator Only		Prey Only	
		ΔAICc	Akaike Weight	ΔAICc	Akaike Weight
	Treatment	0.00	1	0.00	1
Day	Treatment	3.84	0.15	4.82	0.09
Day		59.55	0.00	38.22	0.00

Figure 2.2 Variation in the proportion of time spent by predators in each patch based on BABA treatment (means ± SE) in the predators-only trials in which there were no prey (or prey cues) at any time within the enclosure. Patches 25 mM A and 25 mM B were pooled for analysis (see methods). See methods and Figure 2.1 for explanation of plant treatments and spatial arrangement.

The GLM and resulting odds-ratios from the model indicate predators spent the greatest amount of time in the control patch, followed by the 25 mM patches, followed by the 50 mM patch (control vs. 25 mM: $F_{(2,297)} = 4.63$, p = 0.0314; control vs. 50 mM: $F_{(2,297)} = 22.40$, p < 0.0001; 25 mM vs 50 mM: $F_{(2,297)} = 9.72$, p = 0.0018; Table 2.3).

Habitat Selection by Prey in the Absence of Predators: Prey Only Trials

The alternatives in the model selection analyses (Table 2.2) show that prey appear to base their habitat selection on resource quality as the predictor "day" showed little support within the model selection. In the model with the strongest support (lowest ΔAICc), prey habitat use was significantly influenced by different plant treatments ($F_{(2,297)} = 323.04$, p <0.0001; Figure 2.3). The small error bars seen around the mean proportions of prey allocation of time indicate little variability in the spatial distribution across replicates (Figure 2.3). The GLM and resulting odds-ratios from the model indicate prey in the absence of predators were found significantly more often in the control and 25 mM patches than in the 50 mM patch (control vs. 25 mM: $F_{(2,297)} = 2.12$, p = 0.1456; control vs. 50 mM: $F_{(2,297)} = 100.41$, p < 0.0001; 25 mM vs 50 mM: $F_{(2,297)} = 39.78$, p < 0.0001; Table 2.3).

Table 2.3
Results of logistic regression model odds-ratios for all trials after stepwise selection of variables and with p ≤ 0.05. "OR" = odds-ratio, "95% CI" = 95% confidence interval, "P" = p-value.

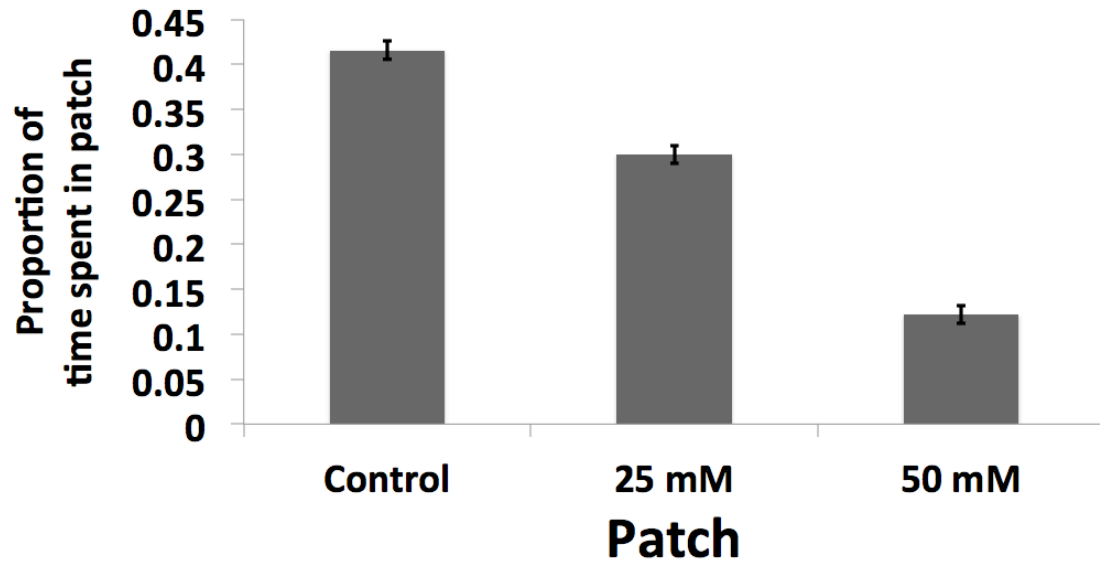| Comparison	Predator			Prey		
	OR	95% CI	P	OR	95% CI	P
Each species alone						
Control vs 50 mM	9.21	4.9-17.94	<0.0001	20.57	15.69-24.01	<0.0001
Control vs 25 mM	5.45	3.00-10.12	0.0314	1.83	0.95-3.48	0.1456
25 mM vs 50 mM	1.69	0.89-3.24	0.0018	3.53	1.91-5.17	<0.0001
Predators and prey together						
Control vs 50 mM	2.61	1.64-4.18	0.0001	2.99	1.83-4.68	0.0166
Control vs 25 mM	1.75	1.11-2.78	0.0021	3.07	1.98-5.12	0.0028
25 mM vs 50 mM	1.48	0.93-2.38	0.411	1.08	0.68-1.73	0.7225

Figure 2.3 Variation in the proportion of prey in each patch based on BABA treatment (means ± SE) in the prey-only trials in which there were no predators (or predator cues) at any time within the enclosure. Patches 25 mM A and 25 mM B were pooled for analysis. See methods and Figure 2.1 for explanation of plant treatments and spatial arrangement.

Habitat Selection in Trials with Predators and Prey Together

Utilizing all three organisms - tic bean plants, aphids, and beetles - I examined alternative models to determine which factor(s) influence habitat choice (Table 2.4). Model analysis showed that plant treatment and proportion of heterospecifics were the strongest factors for both predators and prey, as the predictor "day" (and any combination with day) showed little support within the model selection.

In the presence of prey, predator patch choice was still significantly influenced by plant treatment (F (2,447) = 16.84, p = 0.0002). The GLM and resulting odds-ratios from the model indicate predators spent significantly more time in the control patch as compared to the 25 mM and 50 mM patches (control vs. 25 mM F (2,447) = 16.84, p = 0.0021; control vs. 50 mM F (2,447) = 16.84, p = 0.0001; 25 mM vs 50 mM F (2,447) = 16.84, p = 0.411; Table 2.3). In examining alternative models incorporating treatment and heterospecifics (i.e., prey) both top models have ΔAICc values less than two and show considerable support as predictor variables and thus are both important factors in predator habitat selection (Table 2.4).

In the presence of predators, prey habitat choice was still strongly influenced by plant treatment (F (2,447) = 29.68, p <0.0001). The GLM and resulting odds-ratios from the model indicate prey spent significantly more time in the control patch than in the 25 mM and 50 mM patches (Figure 2.4; control vs. 25 mM F (2,447) = 8.96, p = 0.0028; control vs. 50 mM F (2,447) = 5.73, p = 0.0166; 25 mM vs. 50 mM F (2,447) = 0.63, p = 0.7225; Tables 2.3 and 2.4). The odds-ratios results reveal that prey, when in the presence of predators, are almost equally as likely to stay in the control or 25 mM patches and less likely to stay in the 50 mM patches (Table 2.3).

Table 2.4
Model selection based on AICc of the probability of predators or prey being on a treatment patch when heterospecifics are present in the enclosure.

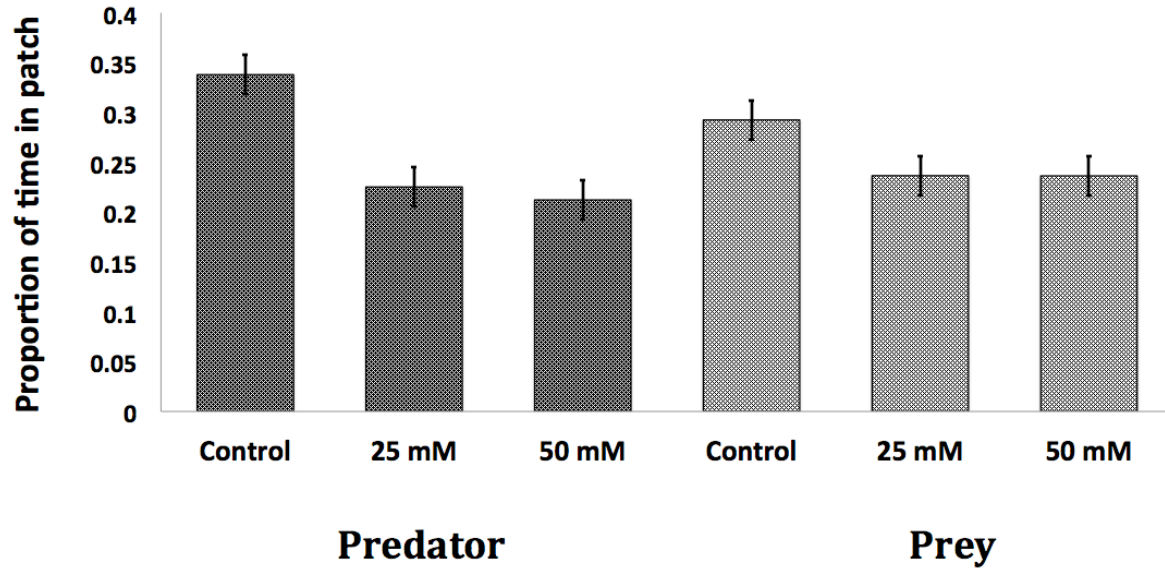| Factor(s) in Model			Predator		Prey	
			ΔAICc	Akaike Weight	ΔAICc	Akaike Weight
	Treatment		0.00	0.51	0.00	0.69
	Treatment	Heterospecific	0.32	0.44	2	0.25
Day	Treatment		6.21	0.02	5.63	0.04
Day	Treatment	Heterospecific	6.53	0.00	7.66	0.01
		Heterospecific	14.7	0.00	26.18	0.00
Day			18.98	0.00	31.34	0.00
Day		Heterospecific	20.94	0.00	31.97	0.00

Figure 2.4. The proportion of time spent in treatment patch based on BABA treatment (means ± SE) by predators and prey in trials in which all organisms were free to move among patches of habitat. Patches 25 mM A and 25 mM B were pooled for analyses; see methods and Figure 2.1 for explanation of plant treatments and spatial arrangement.

I then compared prey distributions in the presence and absence of predators and found prey habitat use was changed significantly by the presence of predators. Compared to the absence of predators, prey in the presence of predators were more uniformly distributed (compare Figures 2.3 and 2.4). Specifically, comparing proportions of prey by patch type in the presence versus the absence of predators I found that prey modify use of two of the patches, control and 50 mM: in the presence of predators (compared to absence of predators), prey densities are greater on the 50 mM plant and lesser on the control plant (F (1,248) = 5.99, p= 0.0144; F (1,248) = 25.56, p<0.001, respectively). However prey use of the 25 mM patches was statistically unchanged (F (1,248) = 0.132, p=0.4338). By contrast, predator habitat use across all patches was not significantly different between trials with and without prey (F (1,187) = 0.096, p = 0.7562).

Additionally, we compared best quality and worst quality patch use between predators and prey. When predators and prey were both present, predators still preferred the higher quality patch and aggregated there more strongly than did the prey (Paired t test: t_{210} = 1.9482, P = 0.05). Similarly prey in the presence of predators aggregated more strongly towards the lower quality patch (Wilcoxon signed-ranks test: T = 8819.5, N = 150, P = 0.0012).

Discussion

A great deal of theory suggests that it would be adaptive for predators to use the quality of their prey's resource as a cue in habitat selection (reviewed by Flaxman and Lou 2009). Predator responses to indirect cues about or from their prey, such as

volatiles emanating from plants damaged by herbivory, have been foci of a number of studies (e.g., De Moraes et al. 1998; De Moraes et al. 2000; Olson et al. 2009; Laundre 2010; Mauck et al. 2010). As no empirical study to date has included free mobile predators and prey across multiple patches of varying quality using a living resource, these findings provide novel insight into habitat selection mechanisms. This study was designed to determine if predators could respond to patch profitability (from the prey's perspective) per se, apart from any direct or indirect cues of prey presence. To determine what proximate cues predators are using, I studied model predators, seven-spotted lady beetles, and their pea aphid prey. I additionally used my experiments to explore what proximate factors influence the habitat selection behavior of the prey.

Based upon the "leapfrogging" prediction made by many habitat selection models (reviewed above), I made the following four predictions about the habitat use patterns that predators and prey were expected to show. First, if predators utilize patch quality as an information source in habitat selection, I would expect predators to aggregate most strongly in the highest quality patch. This should hold in both the presence and absence of prey. Second, in the absence of predators, prey should aggregate most strongly in the highest quality patch. Third, when predators are present, the prey should be more uniformly distributed than when predators are absent. Fourth, when predators and prey are both present, predators should aggregate more strongly than the prey in the highest quality patch; and conversely, the proportion of prey in the lower quality patches should be greater than the proportion of predators there.

To test these predictions, I used model selection based on ΔAICc to compare habitat selection by predators and prey under a variety of conditions. This has

previously been shown to be an effective approach in discerning underlying patterns in organism's space use under similar conditions (Hammond et al. 2007, Luttbeg et al. 2009). Collectively, my results (Figures 2.2-2.4, Tables 2.2-2.4) provided strong support for these predictions. Specifically, in both the presence and absence of prey, predators aggregated in the highest quality patch (Figures 2.2 and 2.4), and patch quality was the best single predictor of predator distributions (Tables 2.2-2.4), supporting the first prediction. In the absence of predators, patch quality strongly predicted the prey distribution as well (second prediction; Tables 2.2 and 2.3, Figure 2.3). However, as described above (see Results), when in the presence of predators, the prey's distribution shifted significantly toward less use of the control patch and greater use of the 50mM patch, resulting in a more uniform distribution of prey (third prediction; compare Figures 2.3 and 2.4). Based on this we can say that (i) predator aggregation towards the highest quality patch was greater than that of prey (though predators appeared to assume a more uniform distribution in the presence of prey than in their absence, the change was not significant), and (ii) prey assume a more uniform distribution which results in a higher proportion of prey on the lowest quality patch (fourth prediction; compare Figures 2, 3, and 4).

These results support the hypothesis that many predators may assess and adaptively use information about prey's resources, in addition to information on the location of prey, in order to "predict" what location may potentially have the greatest success in prey capture. Indeed a recent study of a generalist arthropod predator larva (*Coleomegilla maculata ssp.*) has shown assessment of potential prey and subsequent adaptive learning by predators as a mechanism for food choice behavior (Boivin et al.

2010). Of course, the results beg the question: How did beetles assess patch quality?

While many insects have the ability to assess quality of plant through chemoreceptors located on the mouthparts (Lundgren 2009) or on the tarsi (Städler and Reifenrath 2009), our experiments did not address the precise sensory mechanisms that enabled beetles to discriminate among the patches. A potential concern might be that BABA itself was a toxic stimulus to the beetles. However, we can exclude this concern for several reasons. First, BABA was previously shown to be non-toxic when applied directly in concentrated form to other insects (Hodge et al. 2005). Second, throughout the trials, beetles spent a fair amount of time on BABA-treated plants regardless of the presence or absence of prey (Figures 2, 4). Third, the greatest concentration of BABA would be found in the BABA-drenched soil around the treated plants, which we took care to cover with a layer of non-treated soil (see Methods). Though we observed beetles over many periods of time, we never observed any behaviors suggesting that beetles responded differently to soil around treated versus non-treated plant. Finally, in trials in which aphids were present, beetles frequently consumed aphids that had fed on the BABA-treated plants with no signs of harm to the beetles (ACW personal observation).

While expected from theory, it is nonetheless surprising that the arthropod predators I studied were actually able to detect and use information about the quality of a resource they do not consume. In trials with only predators and resources (Figure 2.2), (i) there were no aphids present at any time, (ii) there was no damage from herbivory to any of the plants, (iii) the manipulation of plant quality is nontoxic (Hodge et al. 2005), and (iv) the plants were statistically all equivalent in size, and hence the only

source of information available was the quality of the plants. While theory has frequently predicted that predators will use this information, limited empirical research (e.g., Sih 2005; Hammond et al. 2007) has tested this prediction, and no previous studies have tested it in a way that eliminates the possibility of predators responding either to the amount of a resource or to indirect cues of prey presence (e.g., chemical cues left by prey or induced defenses of the resource). Hence, the results of the predator only trials allow for a better understanding of what specific proximate cues can actually influence the movements of real predators and thus play a fundamental role in determining spatial distributions of predators in a heterogeneous landscape.

Likewise, prey in the absence of predators preferred the higher quality habitat patch as well (Figure 2.3). Theory and experiments have shown that prey should prefer a higher quality patch when predators are either absent or fixed in space (e.g. Sih 1998; Hammond et al. 2007). Hence, the results on prey behavior in the absence of predators were as expected and are consistent with several previous studies (Flaxman and DeRoos 2007; McCoy and Bolker 2008; Belovsky et al. 2011). While expected, these results (Figure 2.3) still merit reporting for at least two reasons. First, aphids are often characterized as "sessile", yet these results support the idea that even apterous (wingless) aphids employ active habitat selection behaviors moving from a starting uniform distribution toward the higher quality patch (see also Flaxman and DeRoos 2007). Second, these results validate that aphids, as the model prey species, can actually detect and respond to the variation in resource quality that I created experimentally.

When predators and prey are both present and both free to move simultaneously, theory most often predicts that predators should adopt the "leapfrogging" distribution (discussed above) while prey should balance foraging and predation risk (Sih 1998; Luttbeg and Sih 2004; Sih 2005). In my experimental trials, incorporating predators and prey together, both predators and prey significantly preferred the higher quality patch (Figure 2.4). Through model selection (Table 2.4) I see that both predators and prey are influenced by the same factors—plant treatment and proportion of heterospecifics—in making their habitat selection. However, as predicted, prey use of the best patch was decreased by the presence of predators (discussed above). It is expected that predators and prey should impact each other's movement, and thus predators and prey that are all free to move among patches of habitat may display different patterns of habitat selection compared to either species considered in isolation (Lima and Dill 1990; Lima 2002). During the trials both predators and prey utilized multiple proximate cues— location of one another and quality of resource—in habitat choice.

Understanding proximate cues that influence organismal movement is immensely important for predicting spatial distributions, populations' response to change, effectiveness of biological control agents, and more (Bowler and Benton 2005; Nathan et al. 2008). The results of this study are novel are applicable to not only future predator-prey interaction studies but also are of general interest to behavioral ecologists examining how organisms assess the environment and make movement decisions. My results have implications that extend beyond the single species of predator I studied. The seven-spotted lady beetle is a generalist, foliar foraging predator, and the behavior of this and other coccinellid beetles is of great importance for biological control.

Furthermore, variation in the quality of resources is a universal feature of biological systems, and I thus expect it to be both a relevant and available source of information for many predators.

Chapter 3
Quantitative Tests of Ideal Free Distribution Theory

Understanding the spatial distributions of predators and prey in response to one another is a fundamental topic in behavioral ecology (Sih 2005). Accordingly, small-scale spatial distributions and habitat selection have been the foci of numerous studies, both theoretical and empirical (reviewed by Tregenza 1995; Lima 2002; Křivan et al. 2008). Traditionally, the vast majority of spatial distribution studies have focused on analyzing how just one or two factors (considered in isolation) impact habitat selection, for example considering how resource quality and competition affect habitat selection by a single species of consumer. This simplified approach is often utilized for pragmatic reasons: the consideration of additional factors (e.g. more species and their interactions) leads to substantially increased complexity of both theory and experiments. My research quantified measures of individual fitness, intraspecific competition, and inter-species interactions in order to parameterize and quantitatively test a general, widely used model (explicitly defined below) of a multi-trophic ideal free distribution with mobile predators, mobile prey, and interference competition within species.

The ideal free distribution (Fretwell and Lucas 1969; henceforth "IFD") is frequently used as a springboard for studies of habitat selection and small-scale spatial distributions. In a heterogeneous, patchy environment, an IFD is achieved when the average per capita fitness of consumers is equal across patches. Viewed another way, when a population reaches an IFD, the negative effects of competition between consumers in the same patch are balanced by the positive effects of resources in the

patch. Thus, intuitively, at an IFD there will be more consumers in higher quality patches and fewer consumers in lower quality patches.

IFD theory has served as a logical starting point for a large number of habitat selection models (Tregenza 1996a,b; Křivan et al. 2008). When applied to only one species of consumer, IFD predictions are frequently supported, at least qualitatively (tests of fully parameterized interference models are rare: Flaxman and DeRoos 2007). However, when additional variables, such as multi-species interactions, are added to IFD models, spatial distribution equilibria and simultaneous IFDs for all species are not necessarily predicted (Cressman and Křivan 2006; Křivan et al. 2008).

Recent studies have begun empirically testing quantitative predictions of general IFD models in multispecies contexts (e.g. Hammond et al. 2007; Dupach et al. 2009; Luttbeg et al. 2009). However, frequently these studies omit measurement of important parameters, such as quantified measures of (i) individual fitness across patches of multiple, different qualities and (ii) intra-specific competition, which is necessary for rigorous testing of IFD models. Additionally, predators are often restricted to a patch, commonly the highest quality patch, creating inherent riskiness in certain patches (e.g. Peacor and Werner 2004; Raffel et al. 2010). For example, Peacor and Werner (2004) observed modified patch foraging by prey in the presence of caged predators; this however is intuitive, as prey have been shown to avoid fixed sources of predation risk (Lima 2002). Furthermore, frequently an inanimate resource of varying quantity but not quality is used (e.g. Hammond et al. 2007; Dupach et al. 2009). Changing resource amount per se can have very different effects than changing resource quality or density (Flaxman and DeRoos 2007).

Sih (1998) developed and explored theory treating simultaneous IFDs of mobile

predators and mobile prey. His model incorporated (1) foraging success of both species,

(2) competition within species, and (3) variation in the intrinsic qualities of patches (from

the perspective of the prey). Sih's (1998) model is a straightforward multi-trophic

extension of a broad, general class of single-species models known as "interference"

IFD models (Tregenza 1995). Indeed, the same or very similar functional forms used by

Sih have appeared in a variety of predator-prey IFD models (Alonzo 2002; Brown 1998;

Cressman et al. 2004; Heithaus 2001; Jackson et al. 2004; Křivan 1997; Křivan and

Schmitz 2004; Morris 2003; see also Rosenheim 2004, Sih 2005, and van Baalen and

Sabelis 1993). I parameterize and test the predictions of Sih's (1998) model (which, as

just noted, is one general version of a large number of mathematically similar models). I

also attempt to explain deviations from the IFD predictions in terms of behavioral

mechanisms (such as those discussed in Chapter 2).

The Models

My general interference model examines patch profitability such that

consumption of resources within a patch depends upon both the density of consumers

present in the patch as well as competition between the consumers in order to

determine patch profitability from an individual consumer. In the basic interference IFD

model (see Parker and Sutherland 1986), per capita resource gain in patch *i* is modeled

as

$$W_i = R_i/N_i^x \qquad\qquad (1)$$

where R_i is the quality of patch i (measured as the intrinsic rate of increase of prey would have in the patch), N_i is the density of consumers in patch i, and x is the coefficient of interference, a measure of the degree of competition between consumers (Hassell and Varley 1969; Sutherland 1983; Tregenza et al. 1996b). Small values of the coefficient of interference, (0 - 1), indicate weak to moderate competition, whereas values less than zero indicate Allee effects and values greater than one indicate harsh competition between individuals. In this model, an IFD is achieved when payoffs are equal across patches, in other words when $W_a = W_b$ for any two patches a and b. From equation (1), the latter will satisfied when the ratio of consumers in any two patches is such that

$$\frac{N_a}{N_b} = \left(\frac{R_a}{R_b}\right)^{1/x} \tag{2}$$

I modified the basic interference IFD model for predators *when in the absence of prey* (one of my experimental treatments, described below), because the quality of a patch with no prey (i.e., nothing for predators to consume) is zero to a predator. Using the measurement of the quality of a patch from the perspective of the prey, I solved for predicted predator spatial distributions. Simply put, even in the absence of prey, predators should aggregate more strongly to patches that prey find more profitable since, in natural settings, higher quality patches should be more likely to recruit prey (for more rationale, see review by Flaxman and Lou 2009). Thus, in the absence of prey, the distribution of adaptively behaving predators that assess the quality of the prey's resource (see Chapter 2) would thus be expected to follow

$$\frac{P_a}{P_b} = \left(\frac{R_a}{R_b}\right)^{1/m} \tag{3}$$

for any two patches, *a* and *b*. In equation (3), P_i is the predator density in patch *i*, and *m* is the coefficient of interference for predators.

Finally, I tested the full model considering the case where predators and prey are together and simultaneously selecting among multiple patches of habitat. I assume that each patch is characterized by its patch quality from the perspective of the prey for both predators and prey. For predators, per capita payoff in patch *i* was measured as patch quality (from the perspective of the prey). Patch quality for prey was a measured as the intrinsic rate of increase that a lone consumer would be expected to have (see Chapter 2). From Sih (1998), the simultaneous interference IFD model for predators and prey is achieved when both of the following are satisfied for any two patches, *a* and *b*:

$$\frac{N_a}{N_b} = \left[\left(\frac{R_a}{R_b} \right) \left(\frac{cN_b}{cN_a} \right)^{\frac{1}{m}} \right]^{\frac{m}{(m(x-1)+1)}} \tag{4}$$

$$\frac{P_a}{P_b} = \left[\left(\frac{R_a}{R_b} \right) \left(\frac{cN_a}{cN_b} \right)^{1-x} \right]^{\frac{1}{(m(x-1)+1)}} \tag{5}$$

where $c(N_i)$ is the functional response of predators (i.e., the per capita success rate of predators as a function of prey density).

My prior work (Chapter 2) showed that resource quality is a significant predictor of both predator and prey spatial distribution with predators qualitatively matching the distribution of resource qualities while prey assumed a more uniform distribution (although the latter still had a slight preference for the higher quality patch; Figures 2.2 and 2.3). However, no single study to date has quantified measures of individual fitness, intra-specific competition, and inter-species interactions in order to fully parameterize and quantitatively test a general, multitrophic interference IFD model with mobile

predators and prey. After doing so, I also examined mechanisms causing departures

from the predicted spatial distributions and their importance in predator and prey habitat

selection. IFD models comprise some of the most widely empirically applied and

accepted models from theoretical ecology (Earn and Johnstone 1997; Jackson et al.

2004; Tregenza 1995); rigorous, quantitative testing of them in multitrophic contexts is

thus important for improving understanding of how organisms are expected to be

distributed at small spatial scales in nature.

Empirical Methods

      I utilized a tritrophic system that incorporated: i) patches of a plant resource of

varied quality from the perspective of the prey, ii) prey that consume the resource, and

iii) predators that consume the prey (but do not consume the plants). In my system,

seven-spotted lady beetles (*Coccinella septempunctata* (L.), Coleoptera: Coccinellidae),

pea aphids (*Acyrthosiphon pisum* (Harris), Hemiptera: Aphididae), and tic bean plants

(*Vicia faba* L., Fabaceae) were, respectively, the predators, prey, and plant resources. I

use the previously reported (Chapter 2) results of three different habitat selection

experiments involving manipulation of this tritrophic system in laboratory enclosures. In

one set of trials there were predators and plants (of varying quality) but no prey. In a

second set of trials there were prey and plants (of varying quality) but no predators.

Lastly, in the third trial all three species were present.

      Data from these three habitat selection experiments are the same as those

reported in Chapter 2. However, here I also (1) report data from additional experiments

aimed at quantifying the strength of competition (the coefficient of interference: Hassell

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and Varley 1969; Sutherland 1983; Sutherland and Parker 1985; Parker and Sutherland 1986) in the predators, and (2) use the habitat selection data for a different set of analyses aimed at answering different questions.

Quantifying Interference Competition of Lady Beetles

To determine the extent to which beetles within the same patch impact each other's success in foraging for prey, I determined the coefficient of interference for the beetles (Hassell and Varley 1969, Sutherland 1983, Sutherland and Parker 1985). To quantify the coefficient of interference I followed Flaxman and DeRoos' (2007) on pea aphids. For this I utilized enclosures (30cm high x 15cm width x 15cm length) containing a single plant. The enclosures were constructed from transparent, colorless acrylic glazing (walls) with openings for ventilation on the top and sides covered by fine-mesh organza. Each plant remained in its pot, which was sunk into a hole in the floor of the enclosure such that the top of the pot was flush with the enclosure's floor. The floor of the enclosure was covered with a thin layer of (untreated) soil to create a continuous, natural surface on which organisms could walk. Additionally, to prevent organisms from climbing up the walls of the enclosures, the bottom 2 cm of the walls of the enclosure were coated on the inside with Fluon[®] (Northern Products, Woonsocket, RI), a substance with an extremely low coefficient of friction.

Using 14 day-old tic bean plants, I put 40 adult, apterous aphids on the plant, and then, after a brief twenty minute adjustment period in which the aphids were allowed to settle on the plant and begin feeding, I added 1, 2, 3, 4, 8, 12, or 16 beetles on the soil of the enclosure (N=20 replicates per beetle density). Beetle success was quantified as

the per capita encounter rate with aphids during a 20-minute observation period. For the latter, an "encounter" was defined as physical contact between a beetle and an aphid, resulting in aphid movement, aphid dropping from plant, or consumption of the aphid (i.e., a predation event).

The coefficient of interference, m, in this case is obtained as the negative value of the slope of a log-log plot (Sutherland and Parker 1985; Parker and Sutherland 1986) of beetle success regressed on beetle density. If this relationship is linear, that implies that m is constant and does not vary with beetle density; if non-linear, then m is a function of beetle density (see also Moody and Ruxton 1996).

Statistical Analyses

All statistical analyses were performed in JMP (version 9.0.2, SAS Institute, Cary, NC). See Chapter 2 for results of bioassay and observed spatial distributions of predators and prey. The functional response of beetles was assumed using a Type 1 linear functional response for the general interference model. The quantified intraspecific competition and quantified patch quality variables, along with the mean proportions of predator and prey from each patch, were further analyzed to test predictions of the IFD models used (equations 2, 3, 4, 5).

In any habitat selection experiment, the number of degrees of freedom in patch choice is one less than the number of patches. For example, in my experiment, since there were four patches (Chapter 2, Figure 2.1), there are only three degrees of freedom in the spatial distributions: once the proportions of individuals in three patches are observed, the proportion of organisms in the fourth patch is already determined.

Thus, in statistical testing of observed distributions against expected IFDs, I use data from three patches (control, 50, and one of the 25 patches) in a nested analysis of variance (nested ANOVA). Specifically, to account for repeated observations of the same trial, trial identity was viewed as a factor nested under plant treatment. All nested ANOVA assumptions were met.

In order to compare the spatial distributions of organisms in each patch to the predicted spatial distributions of the interference IFD model I took the observed values and subtracted them from the predicted values to give us values that were comparable across trials and patches. For example, if prey were more uniformly distributed than predicted by their IFD, then when observed minus expected differences are calculated across patches, those differences would be (1) significantly less than zero for the highest quality (Control) patch and (2) significantly greater than zero for the lowest quality (50mM) patch. In such a case, the differences calculated for the 50mM patch would also be significantly larger than the differences for the control patch. I thus compared the observed minus expected differences to zero and to one another to determine departures from the predicted spatial distributions. If a departure existed, I performed post hoc analyses to see which patch(es) deviated from predictions. Deviations from the predicted interference model distributions could include "overmatching" or "undermatching" (Tregenza 1995). Overmatching occurs when, compared to predictions, organisms are more strongly aggregated in the highest quality patch; undermatching occurs when organisms are more uniform than predicted.

Results

Validation of the efficacy of using BABA to manipulate plant quality

As described in Chapter 2, the different plant treatments had significant effects on the performance of the aphids in terms of survival, nymph production, and intrinsic rate of increase with the control treatment being the most favorable and the 50mM treatment being the least favorable for aphid performance (Chapter 2, Table 2.1). These results provide the quantitative basis for my claims of differences in "resource quality from the perspective of the aphids" among the differently treated plants.

Quantifying Interference of Lady beetles

There was a significant negative relationship between the density of beetles present and their per capita encounter rate with aphids: as beetle density increased, per capita encounter rates with aphids decreased (Figure 3.1). The best-fit model to the data had a linear term only, indicating that the strength of competition was approximately constant over the densities we used. The negative value of the slope of this regression was 0.475 (95% confidence interval: [0.390, 0.559]), which is my point estimate of the coefficient of interference, m, for the beetles (note that this measure is unitless). A value of 0.475 indicates moderate competition between individuals (Sih 1998). From the above regression, I also obtained an estimate of the success of a lone beetle (i.e., in the absence of competition) in a patch with 40 aphids. This estimate is given by the antilogarithm of the y-intercept, i.e., $10^{0.585} = 3.85$ aphid encounters per 20 minutes (95% CI: [3.29, 4.49]).
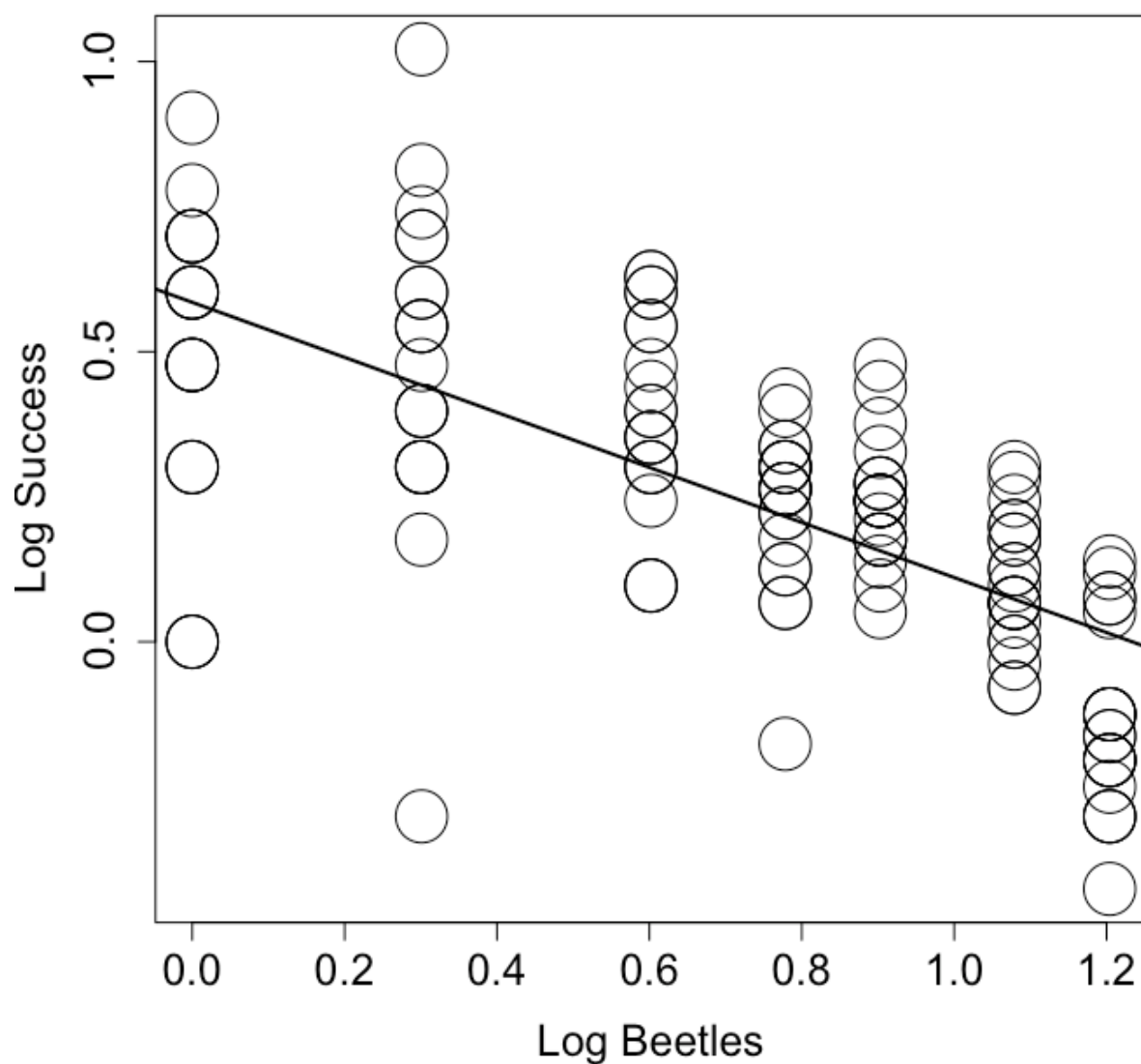
Figure 3.1. The regression the per capita success rate of beetles on beetle density (N = 140 trials total, with 20 replicates per density). The line is the equation of the linear regression: $\log_{10}(\text{per capita success}) = -0.475 \log_{10}(\text{beetle density}) + 0.585$.

As the IFD predictions relied on prey competition as well, I utilized Flaxman and DeRoos's (2007) prior work with pea aphids. Flaxman and DeRoos explored pea aphid competition in terms of reproductive success over a period of five days. Their results indicate that the coefficient of interference for aphids is 0.0852, indicating very weak competition (Tregenza 1995).

Testing the Ideal Free Distribution

Data on observed predator and prey distributions is given in Chapter 2 (Figures 2.2-2.4). The observed spatial distributions of both predator and prey were tested against the generated predictions from the general interference IFD model as described above (equations 1-5 and associated text).

Trials with Predators and Prey Together

The predicted IFDs were as follows. For predators in the presence of prey, the model predicted 0.36 of the predators in the Control patch, 0.24 in each of the 25mM patches, and 0.15 in the 50mM patch. Likewise, for prey in the presence of predators, the model predicted 0.49 of the predators in the Control patch, 0.18 in each of the 25mM patches, and 0.14 in the 50mM patch.

Predators, in the presence of prey, had distributions that were not significantly different from the predictions of the simultaneous IFD ($F_{(43, 449)} = 1.3281$, $p = 0.1872$; Figure 3.2). I then tested the observed spatial distributions against a uniform distribution (i.e., 25% of time spent in each patch). The uniform distribution represents a null hypothesis of equal proportions of consumers in each patch. The results showed that

predators differ significantly from the uniform distribution ($F_{(43, 449)}$ = 20.5661, p <0.0001).

Examining the prey component of the simultaneous IFD model, the proportion of prey had observed distributions that were also not significantly different from the predictions of the simultaneous IFD ($F_{(43, 449)}$ = 1.5027, p = 0.0879; Figure 3.2). Interestingly, prey deviated, though not significantly, from predicted distributions as prey slightly undermatched the best quality patch (Control) and slightly overmatching the lower quality patch (50 mM patches) (Figure 3.2). I then tested the observed spatial distributions against a uniform distribution (i.e., 25% of aphids in each patch). The results showed that prey differ significantly from the uniform distribution ($F_{(43, 449)}$ = 1.7894, p = 0.0014).

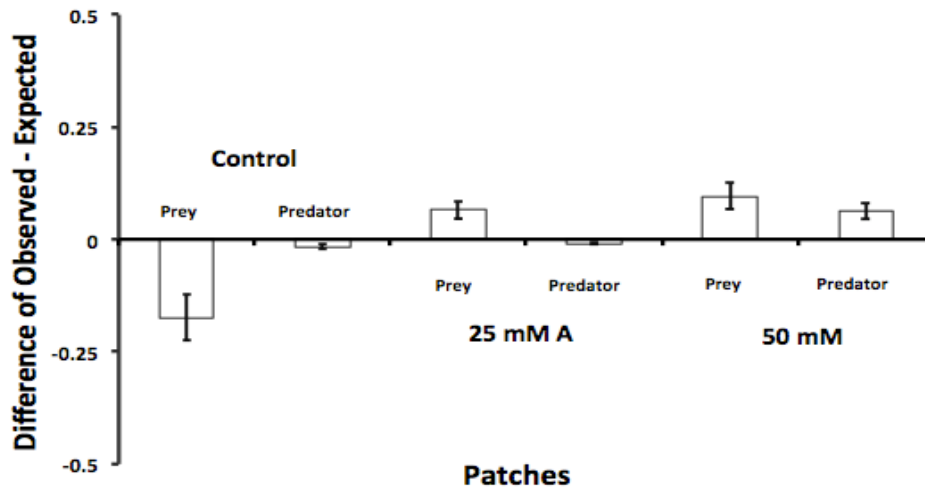*Predators in the Absence of Prey: Predators Only Trials*

For predators in the absence of prey, the model predicted 0.38 of the predators in the Control patch, 0.24 in each of the 25mM patches, and 0.13 in the 50mM patch. In the absence of prey, predators had distributions that were not significantly different from the predictions of the IFD ($F_{(28, 299)}$ = 1.0640, p = 0.3827; Figure 3.3). I then tested the observed spatial distributions against a uniform distribution (i.e., 25% of time spent in each patch). The results showed that predators differ significantly from the uniform distribution ($F_{(28, 299)}$ = 40.7188, p < 0.0001).

Prey in the Absence of Predators: Prey Only Trials

For predators in the absence of prey, the model predicted 0.97 of the predators in the Control patch, 0.01 in each of the 25mM patches, and 0.0001 in the 50mM patch.

In the absence of predators, prey spatial distributions were not significantly different from the predictions of the simultaneous IFD, albeit weakly, (F (28, 299) = 3.9456, p = 0.0562; Figure 3.4). As prey only weakly matched interference IFD predictions when alone in the enclosure, I then tested the observed spatial distributions against a uniform distribution (i.e., 25% of aphids in each patch). The uniform distribution represents a null hypothesis of equal proportions of consumers in each patch. The results showed that prey did not differ significantly from the uniform distribution (F (28, 299) = 1.4987, p = 0.0678).
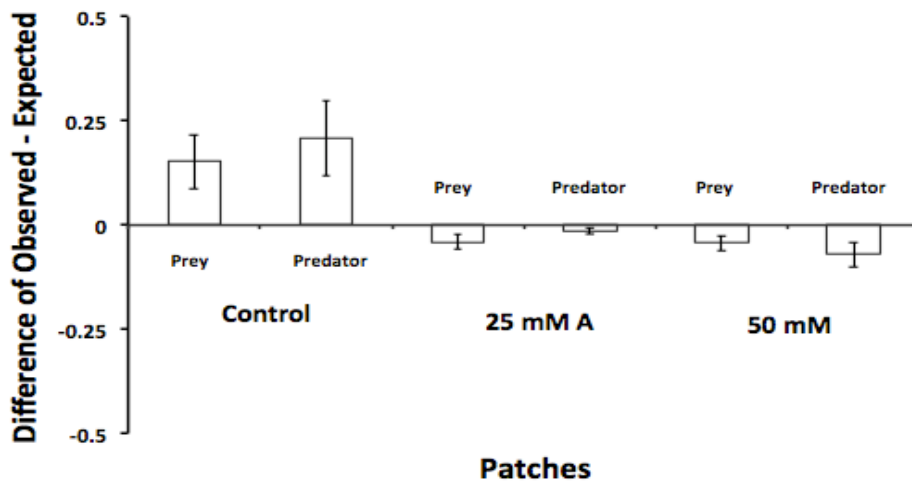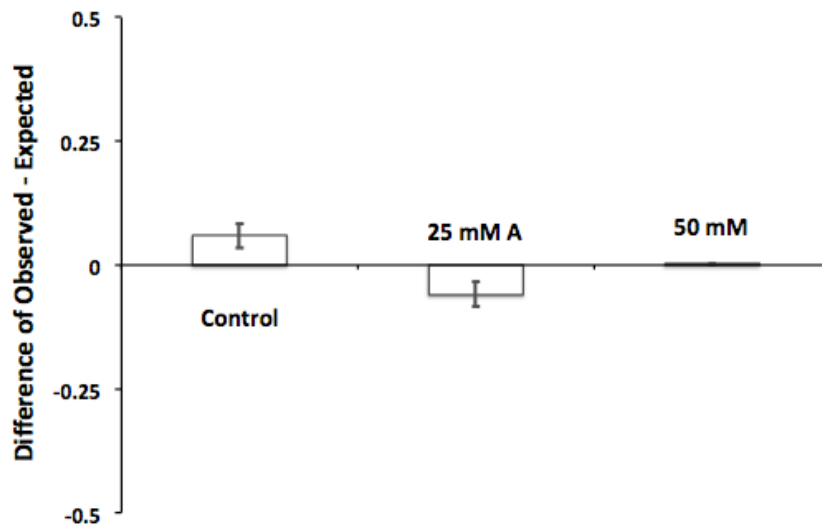
A.

B.

Figure 3.2. A. Variation of predators and prey between observed spatial distributions and predicted simultaneous spatial distributions (mean±SE) when both predators and prey were together in an enclosure. B. Variation of predators and prey between observed spatial distribution and uniform spatial distribution (mean±SE). The horizontal line at 0 indicates the predicted ideal free distribution of both predators and prey (Observed = Predicted) with deviations from the prediction going above (overmatching) or below (undermatching) in a given patch.
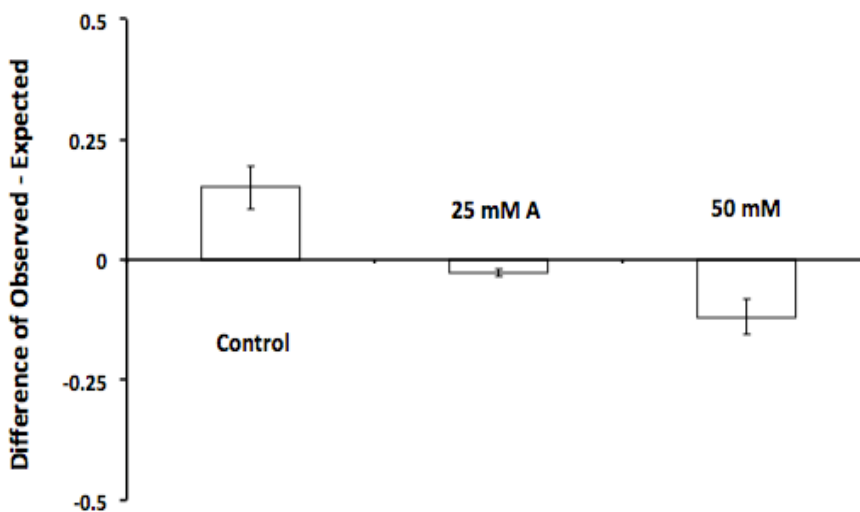
A.

B.

Figure 3.3. A. Deviations from IFD predictions by predators when in the absence of prey (mean±SE). B. Deviation from uniform distribution when in the absence of prey (mean±SE). The horizontal line at 0 indicates the predicted ideal free distribution of both predators and prey (Observed = Predicted) with positive (or negative) deviations from predictions indicating more (or less) predators than predicted in a given patch.

A.

B.

Figure 3.4. A. Variation of prey when alone in enclosure between observed spatial distributions and predicted IFD spatial distributions (mean±SE). B. Variation of prey observed spatial distributions and a uniform distribution in the absence of predators (mean±SE). The horizontal line at 0 indicates the predicted ideal free distribution of both predators and prey (Observed = Predicted) with deviations from the prediction going above (overmatching) or below (undermatching) in a given patch.
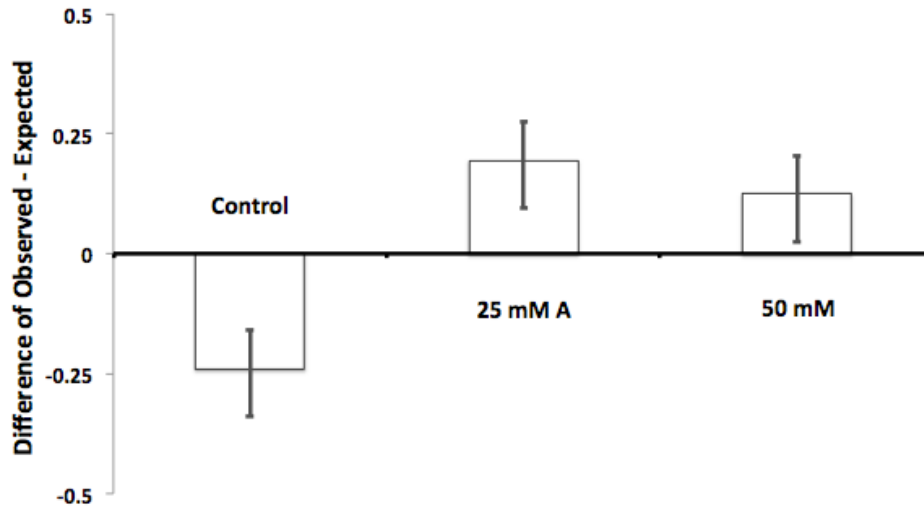
Discussion

      Empirically testing theoretical predictions of ideal free distribution models is important for understanding how trophic interactions (e.g., between predators and their prey) impact small-scale spatial distributions and abundances of organisms. Indeed, recent reviews have highlighted the need for robust tests of IFD models in multi-trophic scenarios (Lima 2002; Sih 2005; Hunsicker et al. 2011). However, testing simultaneous IFD predictions can be quite complex when considering variability in the strengths of intraspecific competition for predators and prey (Sih 1998). Accordingly, recent reviews of current models and empirical studies of IFD theory have indicated that previous studies fall short in critical areas, such as fully parameterizing models and incorporating treatments with and without heterospecifics (Křivan et al. 2008; Matsumara et al. 2010). In order to overcome these limitations, I quantified measures of competition and habitat selection payoffs across a multi-patch, predator-prey-resource system. This was a true tritrophic system, in which a living resource for prey was experimentally manipulated to yield multiple similar-sized patches of varying quality, which more accurately models a natural system than using inanimate resources (as has been done in the few, previous similar experimental tests).

      Interestingly, though my results provide only partial support of the model's predictions (Figures 3.2-3.4), deviations from the predictions may be the result of prey behavior in the absence of predators. Here I suggest that predators act as an instigator of prey movement—and thus, habitat selection by prey—resulting in prey distributions that are closer to the predicted IFD (as compared to prey in the absence of predators).

In the absence of predators, the low competition levels between aphids (Flaxman and DeRoos 2007) may mean that prey have little reason to move between patches.

Although all observed spatial distributions were not significantly different from the predicted IFDs, I tested the observed spatial distributions against a uniform distribution. The uniform distribution represents the null hypothesis, or equal proportions of consumers in each patch, which would be expected if consumers lacked adaptive habitat selection abilities. The results indicated that observed spatial distributions of predators or prey together were significantly different than uniform. Likewise, predators in the absence of prey were significantly different than uniform distribution; prey, however, when alone in the enclosure did not differ from uniform distribution. Thus, while prey in the absence of prey matched both IFD predictions as well as uniform distribution, the results of predators alone and predators and prey together show that predators and prey were much closer to the IFD than they were to being randomly distributed. As prey in the absence of predators showed the largest deviations from predicted IFDs (Figure 3.4), this supports my contention of predators as instigators of prey movement.

In intuitive, qualitative terms, the model (equations 4, 5) predicted that in a tritrophic system, in which both predators and prey are mobile and present, predators distributions should overmatch prey distributions and aggregate most strongly in the patch with the highest quality resource, while prey should also aggregate in that patch but to a lesser degree, balancing predation risk and foraging. Both predators and prey slightly undermatched, though not significantly, the highest quality patch while overmatching, again not significantly, the lowest quality patch (Figure 3.2). Prior

research has shown that predators prefer prey-rich habitat (Lima 1998; Křivan et al. 2008); naturally, beetle predators in my system preferred the prey rich patches. Indeed predators overmatched the lower quality patch more than what was predicted, potentially as a result of prey overmatching that patch. This supports the idea of prey abundance influencing predator patch choice (Figure 3.2). Despite this however, predators still preferred the higher quality patch as predicted. Chapter 2 results indicate that predators utilized both density of heterospecifics and quality of patch in their habitat selection strategies. Thus, I suggest that this deviation, though not significant, may be the result of a shift in predator spatial distributions to accommodate both patch quality and prey density.

Intuitively prey in the absence of predators were predicted to strongly aggregate to the highest quality patch. However, prey matched the predicted spatial distributions weakly (Figure 3.4). Prey's departure, though not significant, from the predicted distribution may be the result of consumers historically undermatching resources in both theoretical and empirical studies (e.g. Kennedy and Gray 1993; Jackson et al. 2004; Křivan 2008; Luttbeg et al. 2009). Several factors have been shown to influence pea aphid movement between patches: i) risk of predation, ii) quality of the resource being abandoned, and iii) risk of mortality in new habitat (Losey and Denno 1998). Given the gregarious nature of pea aphids (Dixon 1998) and low level of competition between individuals (Tregenza 1995), prey movement between patches may have been constrained in the absence of the predators. Furthermore, aphids have been shown to benefit from higher densities of conspecifics as an anti-predator tactic (Dixon 1998, 2000) potentially leading to a higher number of prey in each patch than my model

predicted (i.e., dilution or Allee effects are not considered in equations 1-5). Interestingly, prey in the presence of predators were closer to their predicted IFD than prey in the absence of predators. Prior studies have shown that predators could induce prey movement as a nonconsumptive effect (reviewed by Peckarsky et al. 2008). However, recent studies have suggested predator influence on prey as a driving force of prey movement (Orrock et al. 2008; Sih et al. 2010). Without the proxy of predator stimulus, prey in the absence of predators may have been unlikely to switch patches until resources quality diminished more drastically. This suggests that predators spurred movement of their pea aphid prey, and that these movements by aphids were often subsequently adaptive for the prey.

My tritrophic system used patches of varying quality but not varying size, a parameterized model, and uniform starting distributions of all organisms to quantitatively test predator-prey models of ideal free distribution. These quantitative results support the model predictions of mobile predators and prey achieving simultaneous ideal free distributions in a tritrophic system. The observed spatial distributions of predators and prey matching predicted spatial distributions of a general interference model is contingent on assessment of patch quality by both predators and prey as well as density of heterospecifics. However, when predators and prey were alone in the enclosure, predators overmatched the best quality patch while prey undermatched the best quality patch. Thus, predictions of a single consumer model often does not account for the driving forces of predator-prey interactions, which are essential in realistic models of the natural world.

Incorporating trials of predators and prey with both the presence and absence of heterospecifics provides a more detailed examination of the potential outcomes and responses of organisms to one another. The joining of theoretical and empirical studies is critical for improving understanding of distributions and abundances of organisms. This study represents perhaps the most rigorous test to date of a fully parameterized general interference ideal free distribution model. The results of this study will assist in facilitating in future empirical tests of IFD models as well as a better understanding of spatial distributions of organisms.

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