THE ROLE OF GRAIN SORGHUM IN CONSERVATION OF PREDATORY ARTHROPODS OF TEXAS COTTON

A Dissertation

by

JARRAD REED PRASIFKA

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2003

Major Subject: Entomology

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Approved as to style and content by:

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ABSTRACT

The Role of Grain Sorghum in Conservation of Predatory Arthropods of Texas Cotton.
(May 2003)
Jarrad Reed Prasifka, B.S., The University of Texas at Austin
Chair of Advisory Committee: Dr. Kevin M. Heinz

Four separate but complimentary studies investigated the role of grain sorghum as a predator source for Southern Rolling Plains cotton in 2001 and 2002. Objectives were to: (1) determine the timing and magnitude of predator movement between crops, (2) test putative causes of movement by manipulating prey levels at different stages of crop phenology, (3) explore the feeding and reproductive behavior of a common predator colonizing cotton, and (4) examine the effects of grain sorghum and uncultivated areas on cotton predator abundance at an area-wide scale. Rubidium mark-recapture experiments indicated grain sorghum fields produced a net predator gain for adjacent cotton. Analysis suggested two coccinellids, *Hippodamia convergens* Guérin-Méneville and *Scymnus loewii* Mulsant, were responsible for the overall pattern of predator movement. Predator movement into cotton did not appear to be concentrated at specific stages of sorghum phenology. Manipulations of aphid levels in field cages were used to determine if prey abundance or phenology influenced the movement of *H. convergens* into cotton. In both years, more lady beetle adults were collected on cotton during the latest stages of sorghum phenology. In the second year, relatively low aphid densities (15 per plant) appeared to influence the movement of beetles onto caged cotton. Carbon isotope ratios of *H. convergens* were used to assess adult feeding behavior after colonizing cotton and to determine if prey consumed in sorghum contributed to egg production in cotton. Though aphids were absent 2001, *H. convergens* adults stayed in cotton, did not produce eggs and apparently consumed few prey. Cotton aphids were present in 2002 and *H. convergens* isotope ratios changed from prey consumed in cotton. The isotope ratios of egg masses collected in 2002 indicated prey consumed in grain sorghum contributed very little to egg production in cotton. An area-wide pattern analysis suggested the abundance of grain sorghum and uncultivated areas both positively influenced cotton predator levels. While these landscape effects were less important overall than prey levels and cotton planting dates, in some sampling periods landscape composition appeared to be the most important factor in determining cotton predator levels.

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CHAPTER I

GENERAL INTRODUCTION

Predator conservation is a method of biological pest control whereby human efforts are used to increase the abundance and effectiveness of predatory arthropods, and by extension, to reduce the levels of arthropod pests. Among the many predator conservation strategies, diversification and alteration of cropping patterns have been successfully used in a number of different systems (see Altieri and Letourneau 1982). Diversified cropping patterns can help to achieve enhanced pest suppression by providing predator populations for early colonization of other nearby crops, by contributing food or temporary shelter, or other mechanisms (Van Driesche and Bellows 1996).

Fye (1971) increased interest in using cropping diversification for cotton pest suppression by suggesting that alternating large strips of cotton and grain sorghum would result in earlier and more abundant predator populations in cotton. Noting that both crops shared a number of common generalist predators, Fye claimed that predators feeding on aphids in grain sorghum would reproduce to create large populations capable of colonizing cotton. Support for this assertion was provided by weekly density estimates of predators in both crops during their coincident period of cultivation.

Several subsequent publications dealt with the possibility of using grain sorghum as part of a diversified cotton cropping system. Fye and Carranza (1972) examined

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This dissertation follows the style and format of Environmental Entomology.

predator densities over time in a manner similar to that of Fye (1971), concluding that predators from grain sorghum were able to traverse a distance of at least 160 m into a cotton crop, and that the timing of plant maturity (phenology) was probably important for encouraging predator movement. Robinson et al. (1972a, 1972b) tested the effects of planting cotton in strips with several crops, including grain sorghum, versus a control over a two-year period. Results indicated greater predator abundance and greater overall yields in cotton plots associated with grain sorghum, but also greater damage from larvae of the moths *Helicoverpa zea* (Boddie) and *Heliothis virescens* (Fabricius). Massey and Young (1975) explored strip-cropping cotton with both corn and grain sorghum, and in concordance with Robinson et al. (1972a), showed somewhat paradoxically that both plant damage and yields were greater. Lopez and Teetes (1976) used two different strategies to examine the validity of possible predator colonization of cotton from grain sorghum. First, a sampling of predators in adjacent strips of cotton and grain sorghum showed a steady increase in the relative similarity of predators in the two crops, suggesting continued colonization of cotton from the more mature grain sorghum. Second, a fluorescent dust was used to mark predators collected in grain sorghum, which were re-released into grain sorghum strips. Of an estimated 500,000 predators released in grain sorghum, 51 were recaptured in cotton, indicating they had colonized cotton after their release into grain sorghum.

Papers published in the five years after Fye (1971) generally supported the use of grain sorghum as a source for enemies of cotton pests, but were insufficient to warrant adoption of this crop association as a pest control technique. Previous studies provided little direct evidence of predator movement between the two crops, and the strip sizes used were impractical or inconvenient for many growers. In an attempt to further validate the role of grain sorghum as a possible contributor in cotton pest control, Prasifka et al. (1999) explored the relationship of adjacent fields of cotton and grain sorghum in the Southern Rolling Plains of Texas.

By mass-marking predators in both cotton and grain sorghum, Prasifka et al. (1999) examined net movement between pairs of cotton and grain sorghum fields and showed that while predators sometimes moved into grain sorghum from cotton (an undesirable result for cotton producers), the number of predators cotton gained from grain sorghum was greater, with a ratio of approximately 2:1. Repeating predator mark-and-recapture experiments several times a season, Prasifka et al. (1999) showed that predator movement varied over distinct stages of grain sorghum phenology. Collection of various biotic and abiotic factors also showed a positive correlation between predator movement and temperature, and a negative correlation between predator movement and local aphid abundance, suggesting that predators may move in response to increasing temperature and decreasing food availability.

Although data from Prasifka et al. (1999) added to the base of knowledge of a proposed cotton and grain sorghum cropping system, the low number of marked predator recaptures and lack of a mechanistic explanation suggest further research is needed. While there are many possible questions to be answered, the objectives detailed below represent directed goals to test the validity of and search for possible improvements to the proposed predator conservation system.

Objective 1

All field research was conducted with cooperating cotton and sorghum growers in Texas' Southern Rolling Plains, with efforts focused on the Ballinger (Runnels Co.) area. The first objective sought to improve on the data collected by Prasifka et al. (1999) by using an elemental marker to determine the timing and magnitude of predator movement between adjacent cotton and grain sorghum.

Two treatments were applied to measure predator movement between adjacent cotton and grain sorghum plots. In one treatment, a rubidium chloride (RbCl) solution was applied to mark arthropods in a grain sorghum plot, and predators were later collected in a corresponding area in the adjacent cotton field. This arrangement measured total predator movement into cotton. The reciprocal treatment, application of the rubidium (Rb) marker in cotton and predator collections in sorghum, measured total movement from cotton into sorghum. Each treatment was replicated in three pairs of cotton and grain sorghum fields. Predator collections in unmarked areas were made two to four days after RbCl application. Predators were frozen, and later analyzed by Atomic Absorption Spectroscopy for rubidium content. Because preliminary results indicated different levels of predator movement over time, this routine was repeated three times over the growing season, separated by two weeks so that the preceding Rb application could degrade.

Analysis examined whether predators collectively moved into cotton in greater numbers than they moved from cotton into sorghum, and if this movement was concentrated at one or more stages of plant maturity. Which specific predator groups may have generated the overall patterns of predator movement was subsequently examined. The net benefits to cotton predator levels were quantified, and the rates at which various predator groups moved into the cotton crop were compared.

Objective 2

Measuring the pattern of predator movement between cotton and grain sorghum gives potentially valuable information for pest management but does not address the fundamental causes of predator movement. Because previous research suggested both prey levels and plant maturity may bring about predator immigration into cotton (Fye 1972, Prasifka et al. 1999), the second objective evaluated putative causes of movement by manipulating prey levels at different stages of crop phenology.

To test the hypothesis that low aphid levels cause predator movement out of cotton or grain sorghum plots, field inclusion cages were used to create experimental subplots isolated from the outside environment. Cotton and sorghum plants were grown on opposite sides of the cages. Selected plants received an artificial infestation of greenbug *Schizaphis graminum* (Rodani), or the cotton aphid *Aphis gossypii* (Glover), as appropriate for each crop. To ensure that these infestations reflected actual insect densities, cages were treated with an insecticide a week before aphids were added. Adults of a lady beetle predator, *Hippodamia convergens* Guérin-Méneville, were subsequently placed in all cages alternately on either cotton or sorghum. Beetles were collected one day later, with the location of collection noted for all beetles recovered. Three replicates of the eight treatment combinations were used (24 cages), with the experiment repeated at three different stages of crop phenology.

A three-factor analysis of variance was used to explore the effects of aphid treatment, release location, and crop phenology on the proportion of beetles collected on cotton plants one day after their release. Two-way interactions between all factors were also tested. In cases where main effects were detected, a means separation procedure was used to examine the nature of treatment effects.

Objective 3

To support the results of the rubidium mark-recapture study and to further explore the feeding and reproductive behavior of *H. convergens* colonizing cotton, stable carbon isotopes were used. This technique allowed evaluation of the interval during which adult *H. convergens* move from sorghum into cotton, if beetles feed after colonization of cotton, and if resources consumed in grain sorghum contribute to the production of the subsequent generation of lady beetles in cotton.

Adults and eggs of *H. convergens* were collected from four cotton fields for six or seven weeks after plants reached the two to four-leaf stage of maturity. Because cotton and grain sorghum use different photosynthetic pathways to fix inorganic carbon, they show distinctly different ratios of two carbon isotopes (^{13}C:^{12}C). These isotope ratios (expressed at $\delta^{13}C$) are transferred by feeding to herbivores and their predator or parasitoid natural enemies with little distortion (Edwards and Walker 1983). Predators colonizing cotton from grain sorghum should show higher $\delta^{13}C$ values than long-time cotton residents, with intermediate $\delta^{13}C$ values (between cotton and grain sorghum isotope ratios) found for predators feeding after moving into cotton.

Isotope ratios of individual beetle adults were examined to determine if *H. convergens* moved into cotton during all weeks sampled, or if immigration was confined to a shorter period. Because samples of beetles and eggs taken each week were not independent, mean carbon isotope ratios of adults and eggs over time were compared using a repeated-measures analysis. Decreases in the mean isotope ratios of *H. convergens* indicated active feeding of beetles in cotton. Lastly, isotope ratios of lady beetle eggs were used to indicate if resources in cotton or grain sorghum were used to produce eggs collected in cotton. General results of this method were also compared to the rubidium mark-recapture experiment.

Objective 4

This objective examined the effects of landscape design, prey levels and agronomic factors on cotton predator abundance in a three-county area. While experiments using strip-cropping have shown some benefits of growing cotton and grain sorghum together, these studies probably do not represent a practical method of crop production because of necessary changes in crop management (irrigation, planting, weed and pest control) when these crops are grown in strips. This study addresses whether the arrangement of cotton, sorghum and uncultivated areas over a large scale impacts predator abundance in area cotton fields. Additionally, if landscape composition is related to predator abundance, its importance relative to other factors can be compared.

To explore these issues, a pattern analysis was conducted on 63-70 cotton fields over two years. Data on the abundance of predators and pests were collected for 10-11 weeks from each field. Additional data on cultural practices (planting date for cotton and nearby sorghum fields, cotton field shape) and landscape composition (amount of sorghum or uncultivated land) were collected relative to each cotton field. Because the scale at which landscape composition acts on predator populations is of interest, these data were collected at three different spatial scales.

To parallel the other objectives, data analysis was conducted at three different periods during the growing season in each year. At each time period, a separate stepwise regression was conducted to select from prey levels, landscape, and agronomic factors those most closely related to cotton predator abundance. If at least one measure of landscape composition was included in a model, that factor was suggested as a parameter that influenced predator abundance. Based on the fraction of total explanatory power (R^2), the relative importance of landscape factors in determining cotton predator abundance was assessed.

CHAPTER II

TIMING, MAGNITUDE, RATES AND PUTATIVE CAUSES OF PREDATOR MOVEMENT BETWEEN COTTON AND GRAIN SORGHUM FIELDS

Surrounding vegetation directly influences the abundance of generalist predators in agricultural fields (Altieri and Letourneau 1982). This connection to neighboring habitats is particularly important for annual crops, where standing vegetation is routinely destroyed and renewed according to a yearly cycle. Predators moving from these habitats act as the initial colonists to recently planted agricultural crops (Wissinger 1997), but surrounding areas may also be sources of recolonization when predator populations are decimated by the use of pesticides (Wratten and Thomas 1990). Though attention has generally been focused on the benefits of uncultivated habitats as sources of predatory arthropods (Thomas et al. 1991, Landis et al. 2000), predators may also move from one crop to another, particularly when the phenologies of the crops are not synchronized (Wratten and Thomas 1990, Bommarco and Fagan 2002).

One reported example of such predator movement between crops involves contiguously grown cotton, *Gossypium hirsutum* L., and grain sorghum, *Sorghum bicolor* (L.) Moench. Both crops are common across broad geographic ranges of the United States, with cotton grown across the southern states while grain sorghum spans the central region from South Dakota to Mexico. This results in overlapping production ranges in several states, but most extensively in Texas, which typically ranks first and second in the production of cotton and grain sorghum, respectively (Texas Agricultural Statistics Service 1998, 2000, 2002). Several factors noted by Fye (1971, 1972) suggest that in areas where both crops are produced, grain sorghum could serve as a source of predators to cotton. First, cotton and grain sorghum support similar groups of predator taxa, the adults of which are generally very mobile. Second, grain sorghum is not usually treated with pesticides, in part because it is a relatively pest tolerant crop. Lastly, grain sorghum reaches maturity early relative to nearby cotton fields. Fye (1972) hypothesized that this would result in large predator populations produced in grain sorghum that move into cotton during the late stages of grain sorghum phenology. The corollary noted by subsequent researchers (Robinson et al. 1972b, Lopez and Teetes 1976, Prasifka et al. 1999) is that such predator movement would improve biological control in cotton.

Several studies have explored the issue of predator movement from grain sorghum to cotton using different methods. Studies have examined predator densities in cotton at increasing distances from adjacent strips of grain sorghum (Burleigh et al. 1973, Massey and Young 1975), compared predator densities over time in both cotton and sorghum (Fye 1971, Fye and Carranza 1972), or compared isolated cotton plots to those planted near grain sorghum (Robinson et al. 1972b, Parajulee et al. 1997). Lopez and Teetes (1976) used fluorescent dust marking to examine predator movement into cotton, and Prasifka et al. (1999) also used dusts to mark predators in both crops, attempting to assess predator movement into and out of cotton.

Though most of these studies support the premise that grain sorghum acts as a source of predators to colonize nearby cotton, a basic understanding of predator movement in this system has not been achieved. For example, direct measurement of predator movement using mark-recapture methods has only been attempted twice. In both cases inadequate numbers of predators were recovered to support generalizations about the timing, magnitude, or rates of predator movement between cotton and sorghum. Further, while Fye (1971, 1972) asserted that plant maturity was the cause of movement, only one study (Prasifka et al. 1999) has examined the possibility that other factors may motivate predator movement. Results indicated that predator movement was correlated with high temperatures and low levels of aphid prey. However, because this study relied on correlations and not experimental manipulation, causality cannot be inferred directly.

To correct these shortcomings, modifications to previous research were necessary. First, protocols for the use of a trace element marker, rubidium, were developed for use in cotton and sorghum (Prasifka et al. 2001). This allowed relatively easy predator marking and assured an increase in the number of marked predators recovered. Second, experimental manipulations of the putative causes of predator movement were made under field conditions. With these changes in methodology, the following objectives were pursued: (1) to measure the timing, magnitude, and rates of predator movement between cotton and grain sorghum, and (2) to test possible causes of movement for a common predator in both crops.

Materials and Methods

Complementary field studies were conducted in the Southern Rolling Plains of Texas (study area ≅ 31.3 – 32.1° N, 99.6 – 100.6° W) during 2001 and 2002. The first study was designed to measure directly the movement of predatory arthropods between adjacent fields of cotton and grain sorghum. A second study was conducted to test putative causes of predator movement between cotton and grain sorghum. In both cases, three study periods per season were timed to the soft-dough, hard-dough, and physiological maturity stages of grain sorghum phenology (Vanderlip 1972). At these stages, cotton development had reached roughly five to six true leaf, first 1/3 grown square, and first bloom stages, respectively. The sorghum stages selected span the processes of grain maturation and leaf senescence hypothesized to cause predator dispersal (Fye 1972).

Measuring Predator Movement. Each year six sites were selected in Runnels County, TX. A site consisted of one cotton field and one grain sorghum field oriented with their rows parallel. Within each field, a plot 100 m long by 40 m wide (0.4 ha) was flagged. Plots began 10 m from the crop interface of cotton and grain sorghum and were inset at least 100 m from the adjacent field edge. At each site, one plot was further divided into three subplots 10, 20 and 50 m from the interface of the cotton and grain sorghum fields (Fig. 1). The study sites were organized spatially into three pairs, in which the distance between paired sites was less than that between unpaired sites. For example, in 2001 the distance between paired sites ranged from 3.7 – 5.2 km and 16.8 – 32.5 km for unpaired sites. Weather conditions (temperature, relative humidity, precipitation, wind speed, wind direction, barometric pressure) were monitored at one site within each site-pair with a PortLog™ weather station (RainWise Inc., Bar Harbor, ME) recording at 1 h intervals.

At the onset of the three grain sorghum phenological stages noted above, foliar sprays of rubidium chloride (RbCl) were applied to mark predators. Rubidium is a

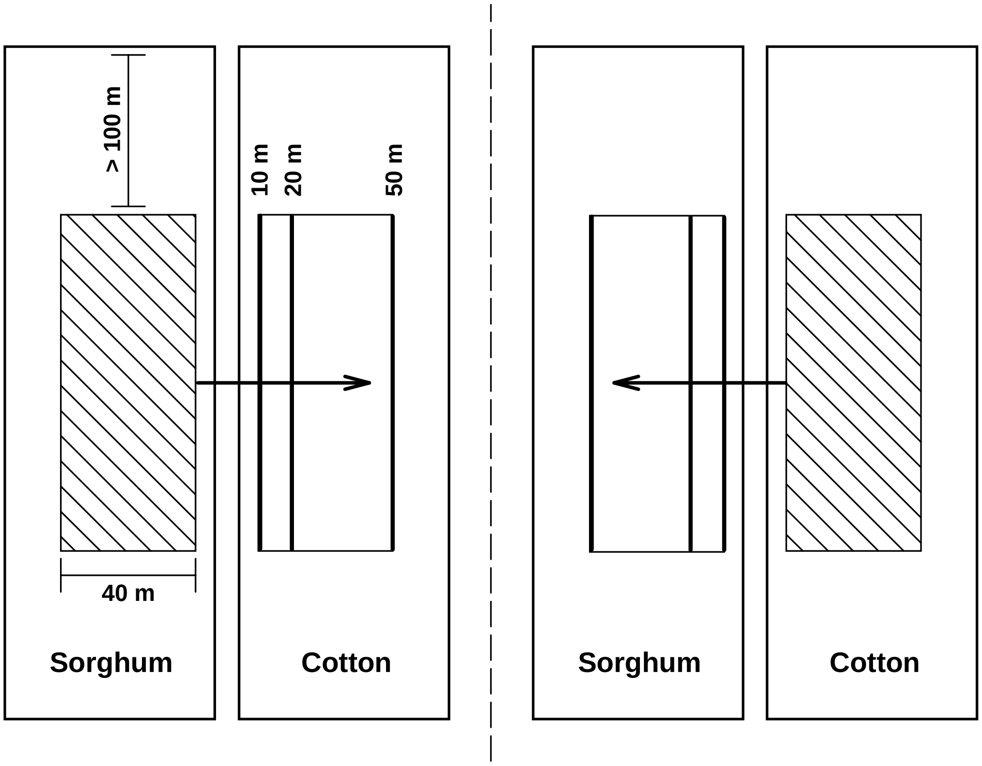

Fig. 1. Field plot arrangements for predator movement studies, 2001-2002. Dashed line separates sites where rubidium was applied to sorghum or cotton. Rubidium-treated plots are indicated by shading. Arrows indicate the predator movement measured. Numbers above unsprayed plots indicate the distance of sampling areas from the interface of fields. Diagram is not to scale.

ubiquitous element chemically similar to potassium, but usually found at very low concentrations. This similarity allows rubidium to be incorporated into biological systems at moderate levels without harmful effects (Stimmann 1974, Knight et al. 1989, Johnson and Reeves 1995) and results in its vertical transmission between trophic levels (Graham et al. 1978, Johnson and Reeves 1995, Corbett et al. 1996). These properties permit augmentation of background rubidium levels to internally mark plants, herbivores and natural enemies. Because rubidium is replaced by potassium in the diet, the mark is temporary for actively feeding insects (Shepard and Waddill 1976, Graham et al. 1978, Fleischer et al. 1986) and may allow multiple mark-recapture experiments to be conducted at a location in one season. To measure movement both into and out of cotton, three cotton fields (one site within each pair) and three grain sorghum fields were selected to receive a RbCl spray. In the selected fields, RbCl sprays were made with equipment as described in Prasifka et al. (2001), applying of 200 g RbCl dissolved in 68 l water per 0.4 hectare plot.

Predator sampling to recover rubidium-marked predators was conducted in the unsprayed plots two, three and four days after the RbCl sprays in the adjacent plot. Each subplot (one row × 100 m) was sampled for 40 person-minutes per day using visual searches of plants. Only adults of insect predators were collected, but both immature and adult spiders were sampled. Predators were collected with double-chambered inhalation-type aspirators, and aspirator inner chambers (2-dram screw cap vials) were capped and separated after completion of each subplot. Vials were then preserved in dry ice until they could be transported to the Biological Control Facility in College Station, TX, and placed in freezers prior to analysis.

In the laboratory, predators were sorted taxonomically into nine groups. Species (*Hippodamia convergens* Guérin-Méneville, *Scymnus loewii* Mulsant), genus (*Orius* spp., *Notoxus* spp., *Collops* spp., *Geocoris* spp., *Nabis* spp.), family (Chrysopidae) and order (Araneae) level groupings were used as needed, and all predators were separated as individual samples. Predators were then digested and analyzed for total rubidium content via atomic absorption spectrometry (AAS) as described in Prasifka et al. (2001) with two exceptions as noted below. The AAS technique measures the amount of light absorbed (at element-specific wavelengths) when a sample is heated to a temperature sufficient to generate free atoms of the element of interest. As made customary by Stimmann (1974), a predator was considered marked if its rubidium content in parts per million (PPM = μg Rb/g predator dry mass) was at least three standard deviations above a control mean. Samples previously collected from the study area (Prasifka et al. 2001) were used as controls.

Changes made to the rubidium analysis were intended to improve accuracy and simplify methods. First, to minimize error, all samples were massed to μg accuracy instead of using an average mass value for predators of the same group. Establishing precise mass values for each sample allowed an additional change in the methods used to test the rubidium mark status of spiders. Prasifka et al. (2001) used a size index to estimate mass values for non-control samples of spiders and regressed the rubidium content of controls onto estimated mass values to construct an adjustable rubidium-mark threshold for spiders of various sizes. However, because the rubidium content per gram of spider mass (regardless of overall size) appeared constant, a single threshold was established using mass values and rubidium content of control samples from Prasifka et al. (2001). Consequently, spiders collected in 2001 and 2002 were evaluated using the same type of threshold (mean background plus three standard deviations) as other predator groups. The interpretation of individual marked samples from spiders and the insect predators was straightforward; because predators were collected only from areas not treated with rubidium chloride sprays, all marked individuals were assumed to have recently moved from the adjacent field.

Statistical analyses were made using SAS software (SAS Institute Inc. 1999) with specific procedures as indicated. A two-factor analysis of variance (PROC ANOVA, including the two-way interaction) was conducted to assess if the magnitude of predator movement (sum of marked predators across all taxonomic groups) was explained by the time (phenology) and location (crop) of the collection. If main effects were found, additional analyses were used to determine which predator groups contributed to the main effects indicated by the ANOVA. Data from individual predator groups could not be transformed to meet normality or variance expectations of parametric statistics, so an $r \times c$ contingency table was used. This test was conducted once for each predator group (PROC FREQ, CHISQ option) and was based on both the number of marked individuals and the total number collected. For predator groups that moved into cotton in sufficient numbers ($n \geq 20$), mean dispersal rates (m/d) were compared using a one-way analysis of variance (PROC GLM). For these estimates, predators were assumed to have originated in the center of rubidium-treated plots, and were collected from a known location in the untreated plots. Accordingly, the distance between the middle row of the nearby rubidium-treated plot and the row in which a predator collected was divided by the number of days since the rubidium spray to obtain an estimated dispersal rate.

Testing Causes of Movement. One site in Runnels County, TX, was selected each year to test putative causes of predator movement between crops. Fye (1971, 1972) and Prasifka et al. (1999) identified plant phenology, ambient temperature and aphid density as putative causes of predator movement. Because manipulation of these variables could not be produced and replicated at full-scale, inclusion cages were used to simulate field conditions. These cages were used to test for effects of phenology and prey density on predator movement while temperature was monitored as an uncontrolled variable.

Alternating four row strips of cotton and grain sorghum were planted (1 m row spacing), with cotton planted 40 to 45 days after grain sorghum. Shortly after cotton emergence, field cages measuring 3.0 by 3.0 by 2.0 m (l×w×h) were placed over the crops. The cages were covered with a Lumite mesh (20×20 holes/cm^2, Synthetic Industries, Gainesville, GA) tight enough to prohibit the ingress or egress of the herbivores and natural enemies studied. Six cages placed only over cotton or sorghum were used for rearing of cotton aphid, *Aphis gossypii* Glover, or greenbug, *Schizaphis graminum* (Rodani), respectively. Another 24 cages were placed over three planted rows (two cotton, one sorghum). The middle row was removed and the remaining plants were thinned to 10 of each crop at opposite sides of the cage (Fig. 2). To examine if climate differences caused by the cages might influence the behavior of predators released, ambient temperature and relative humidity were measured during 2002 both inside and outside the cages by two HOBO® H8 Pro Series data loggers (Onset Computer Corporation, Bourne, MA) set to record at 1 h intervals.

Prior to the start of the soft-dough, hard-dough and physiological maturity stages of grain sorghum phenology, cages were treated with chlorpyrifos (Lorsban-4E, Dow AgroSciences, LLC, Indianapolis, IN) at 1100 g (AI)/ha to eliminate existing pest and predator populations in the experimental cages. Seven days later each experimental cage received one of four randomly assigned aphid treatments: aphids (*Schizaphis graminum*) on sorghum only, aphids (*Aphis gossypii*) on cotton only, aphids on both crops, or aphids on neither crop. On plants selected to receive aphids, a cut section of leaf with 15 of the appropriate aphid species (obtained from the aphid rearing cages) was pinned to one of the upper leaves with the aphids facing upward. This number of aphids was selected as representing a non-outbreak aphid infestation level from field data collected during 1998 (Prasifka and Heinz, unpublished data). Within the next 24 hours, both aphid species moved off the cut leaf sections and onto their intended host plants.

One day later, insectary-bought predators (Rincon-Vitova, Inc., Ventura, CA) of unknown age were released into the cages. Predators were shipped with cold-packs but without food or water. Prior to release, all predators were held under refrigeration without food for a maximum of five days and provided with moisture using a small piece of dental wick saturated with revere-osmosis treated water. In 2001, 30 *Hippodamia convergens* and 40 *Orius insidiosus* (Say) adults were released into each cage. No effort

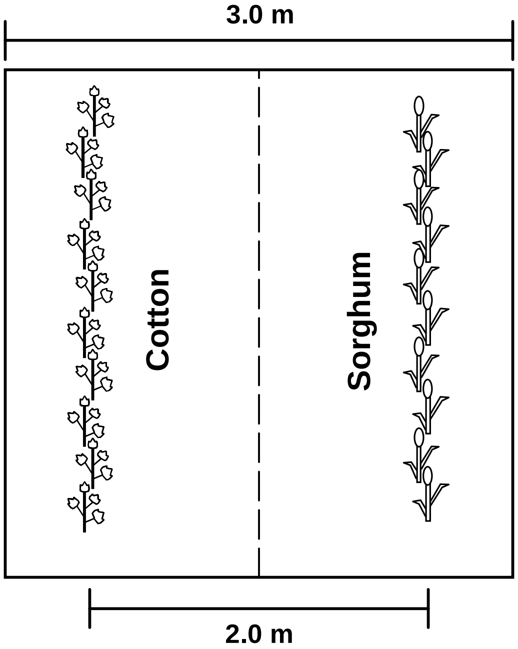

Fig. 2. Representation of cages and crops for assessing causes of movement, 2001-2002. Dashed line indicates the center of field cages. Dimensions indicated are to scale.

was made to measure or control sex ratio of the predators released. High mortality and small size contributed to inadequate recovery of *O. insidiosus* in 2001, so only *H. convergens* was used in 2002. Predator releases were made onto the upper leaves of plants, either cotton or grain sorghum, within each cage. Assignment of release location was made randomly within an aphid treatment so that three replicates of each of the eight aphid treatment × predator release combinations were created. Sampling of predators started one day after predator release. Predators collected from visual searches on cotton or grain sorghum plants were aspirated into separate vials. To detect excessive mortality or escapes, live predators found on the ground or other locations of the cage were aspirated into a third vial. Vials from each cage were placed in dry ice until transport to College Station, TX, where the number of recovered predators in each vial was counted.

As with the previous experiment, analyses of data from this experiment were made using SAS software (SAS Institute Inc. 1999). For data from each year, a three-way ANOVA (PROC GLM, including all two-way interactions) was used to test for the effects of crop phenology, aphid treatment, and predator release location on the recovery of *H. convergens* from caged cotton plants. To homogenize variance across treatments, recovery of *H. convergens* was assessed as the proportion of lady beetles collected on cotton (relative to the total number of beetles recovered) in each cage, and this independent variable was arcsine square root transformed to meet assumptions of normality. When ANOVA results indicated an effect of phenology or treatment, Fisher's Least Significant Difference (LSD) procedure was conducted to separate means. To determine if weather conditions inside the cages were similar to those outside, mean temperature and humidity values (n = 30 days) were compared at six evenly-spaced times during the day using a paired t-test.

Results

Measuring Predator Movement. The new rubidium mark threshold for spiders (based on 185 control samples) was 9.25 PPM. This value is intermediate to the thresholds established by Prasifka et al. (2001) that were used for other predator taxa in this study (range = 2.15 – 12.60 PPM). Overall, predator collections during 2001 yielded a total of 3,715 predators. Of these, 609 predators were marked with rubidium, indicating recent movement from an adjacent rubidium-treated plot. Cotton gained far more predators (443) than it lost (166) via an association with grain sorghum. The total numbers of predators collected and marked recoveries in each crop are shown sorted by taxonomic group in Table 1.

A two-way ANOVA indicated that the stage of phenology and crop in which collections were made did not adequately explain the variability in the number of marked predators recovered ($F = 1.11$; df = 5,12 ; $P = 0.407$), but the F-test for the crop component only ($F = 4.88$; df = 1,12 ; $P = 0.047$) was significant (Fig. 3). Analysis of separate predator groups indicated that two groups moved preferentially into cotton, *H. convergens* ($\chi^2 = 57.87$, df = 1, $P < 0.001$) and *S. loewii* ($\chi^2 = 22.27$, df = 1, $P < 0.001$). For all other groups the hypothesis that the proportion of predators entering cotton was equal to the proportion leaving for adjacent plots of grain sorghum could not be rejected. Estimated dispersal rates of predators entering cotton fields ranged from 15.8 – 19.9 m/d

Table 1: Predators collected and marked in cotton and grain sorghum, 2001

	Cotton		Sorghum	
Predators	Collected (*n* = 2331)	Marked (*n* = 443)	Collected (*n* = 1384)	Marked (*n* = 166)
Hippodamia convergens	1040	195	430	15
Araneae	498	52	363	38
Scymnus loewii	357	98	139	11
Orius spp.	88	24	344	91
Notoxus spp.	114	10	25	0
Chrysopidae	108	35	11	1
Collops spp.	78	25	30	8
Geocoris spp.	36	1	24	0
Nabidae	12	3	18	2

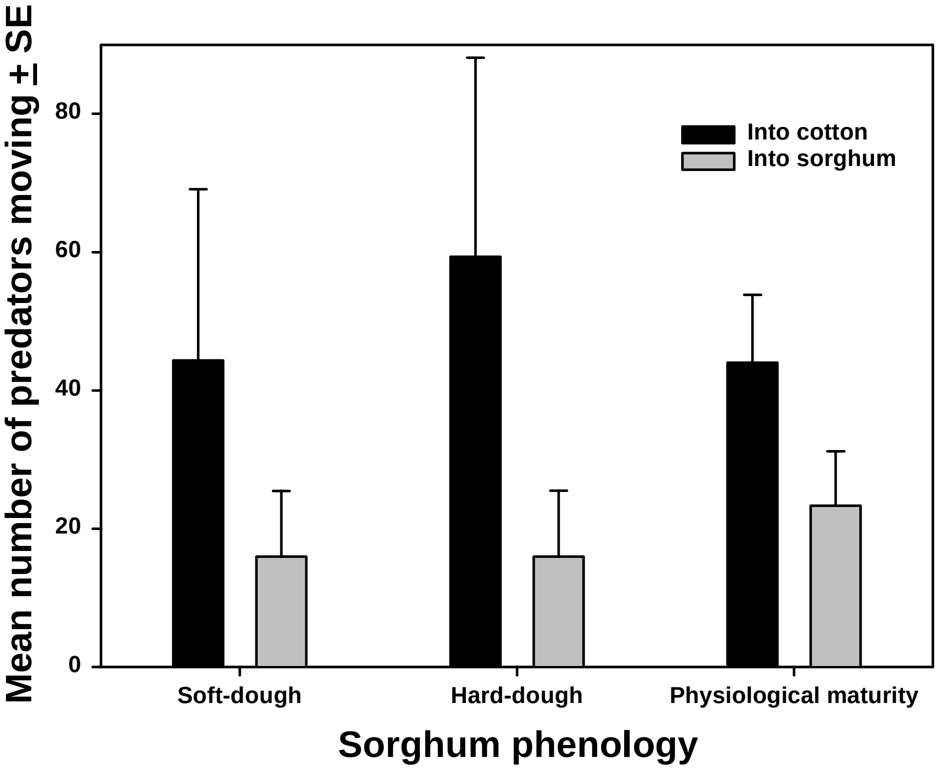

Fig. 3. Mean number of predators (± SE) moving into cotton or sorghum at indicated stages of sorghum phenology, 2001. A two-way ANOVA found differences ($P < 0.05$) between the number entering cotton and sorghum but not between stages of phenology.

(Table 2), but did not vary among taxa according to an ANOVA ($F = 1.17$; df = 5, 423 ; $P = 0.324$).

Predator collections from 2002 produced 580 total predators, of which 34 were found to be rubidium-marked. Rainfall collected by our weather stations ranged from 5.62 – 17.95 cm during the sampling dates at sorghum's soft dough stage. This caused extensive flooding in the region and prohibited any field collections of predators. When sorghum had reached maturity, additional rains of 1.58 – 3.68 cm created conditions unsuitable for rubidium spraying in three of the six locations. Compared to typical rainfall (mean ± SE) for July in the Ballinger area over the previous 10 years (2.59 ± 0.66 cm, Office of the State Climatologist, Texas A&M University), these periods represented unusually high levels of precipitation. The resulting low sample sizes and unbalanced design prohibited statistical analysis of 2002 movement data.

Testing Causes of Movement. The temperature ($t = 1.31$, df =5, $P = 0.25$) and relative humidity ($t = -0.12$, df =5, $P = 0.91$) profiles inside and outside the field cages were similar during the duration of the study (Fig. 4). ANOVA results from 2001 indicated that phenology affected the recapture of *H. convergens* on cotton ($F = 13.96$; df = 2,54 ; $P < 0.001$). Means separation using Fisher's LSD showed that a greater proportion of *H. convergens* was recovered from cotton during the hard dough and maturity stages of grain sorghum than at the soft dough stage. No other factors or interactions were significant during 2001 (Table 3).

Phenology was also significant during 2002 ($F = 36.01$; df = 2,54 ; $P < 0.001$), again with a greater proportion of *H. convergens* collected on cotton during sorghum's

Table 2: Estimated mean dispersal rates for predators immigrating into cotton, 2001

Taxon	Mean dispersal rate (m/d) ± 1 SD	Sample size (*n*)
Hippodamia convergens	18.3 ± 7.9	195
Scymnus loweii	17.3 ± 7.2	98
Araneae	17.7 ± 5.2	52
Chrysopidae	19.9 ± 8.3	35
Collops spp.	19.0 ± 7.9	25
Orius spp.	15.8 ± 7.8	24

Estimates assume direct linear movement from center-line of rubidium-treated plots to collection point.

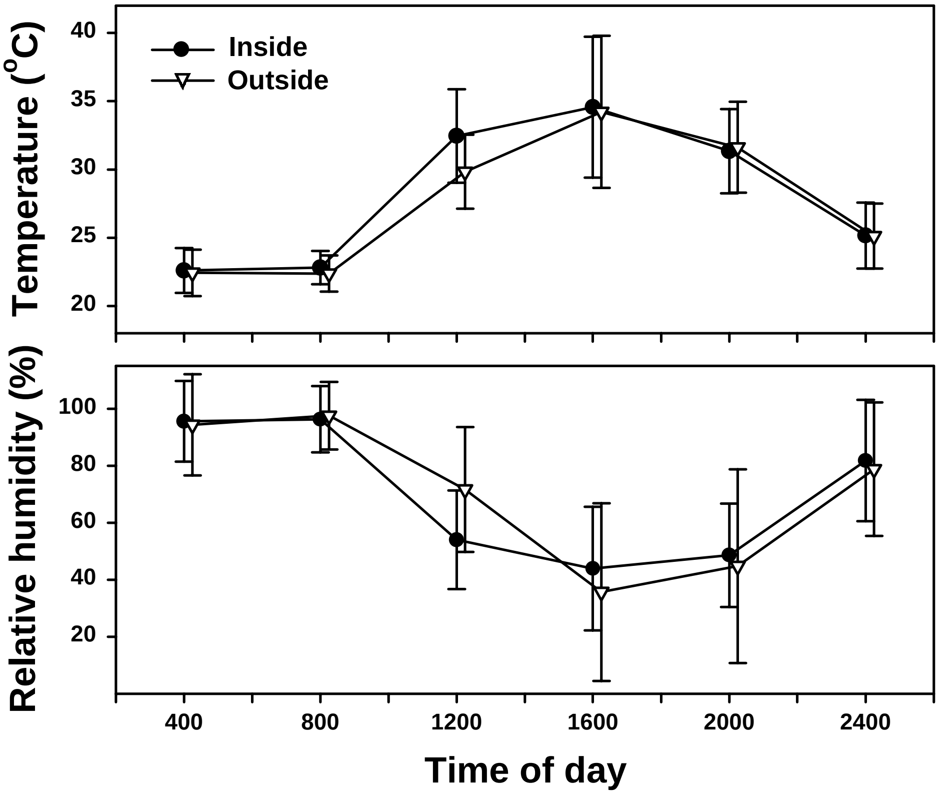

Fig. 4. Daily temperature (°C) and relative humidity (%) profiles inside and outside field cages during 2002. Values are presented as means (± SD) at 4 h intervals over the duration of the experiment (*n* = 30 days).

Table 3: ANOVA results for putative causes of predator movement, 2001-2002

Year	Factor	df	*F*	*P*
2001	Model (overall *F*-test)	17	2.65	0.003
	Phenology	2	13.96	<0.001
	Aphid treatment	3	1.03	0.387
	Release location	1	1.60	0.212
	Phenology × aphid treatment	6	0.95	0.467
	Phenology × release location	2	1.17	0.318
	Aphid treatment × release location	3	1.44	0.241
2002	Model (overall *F*-test)	17	7.04	<0.001
	Phenology	2	36.01	<0.001
	Aphid treatment	3	2.89	0.044
	Release location	1	25.01	<0.001
	Phenology × aphid treatment	6	1.08	0.388
	Phenology × release location	2	1.71	0.190
	Aphid treatment × release location	3	1.35	0.267

hard dough and maturity stages. The presence of a release location effect (F = 25.01; df = 1,54 ; $P < 0.001$) indicated that more beetles were recovered from cotton when they were initially released onto cotton. Finally, the effect of aphid density manipulations to cotton and sorghum plants was suggested by the ANOVA (F = 2.89; df = 3,54 ; $P = 0.044$) and examined by post-ANOVA analysis of the aphid treatments. Results showed a greater proportion of *H. convergens* was found on cotton when cotton aphids were present (with or without greenbugs present) than when no aphids were present in the cages. Recovery of *H. convergens* was also greater with cotton aphids only than with no aphids or greenbugs only (Fig. 5). Again, none of the two-way interactions tested were shown to be significant model components (Table 3).

Discussion

Results from predator marking experiments in 2001 showed that a greater number of predators moved into cotton than into sorghum while suggesting that movement of predators between the crops was unaffected by changes in grain sorghum phenology. These results agree with previous studies that showed enhanced predator levels in cotton adjacent to or intercropped with grain sorghum. Data revealed a gain of 2.7 predators immigrating into cotton for each predator leaving for adjacent grain sorghum. This is surprisingly close the estimate of Prasifka et al. (1999), which noted a predator gain-to-loss ratio in cotton of 2.0 with a sample size of marked predators roughly 1/20th of the current study. Subsequent analysis of smaller predator groups indicated that the coccinellids *Hippodamia convergens* and *Scymnus loewii* moved disproportionately from grain sorghum into cotton. Because these two species represented 60%

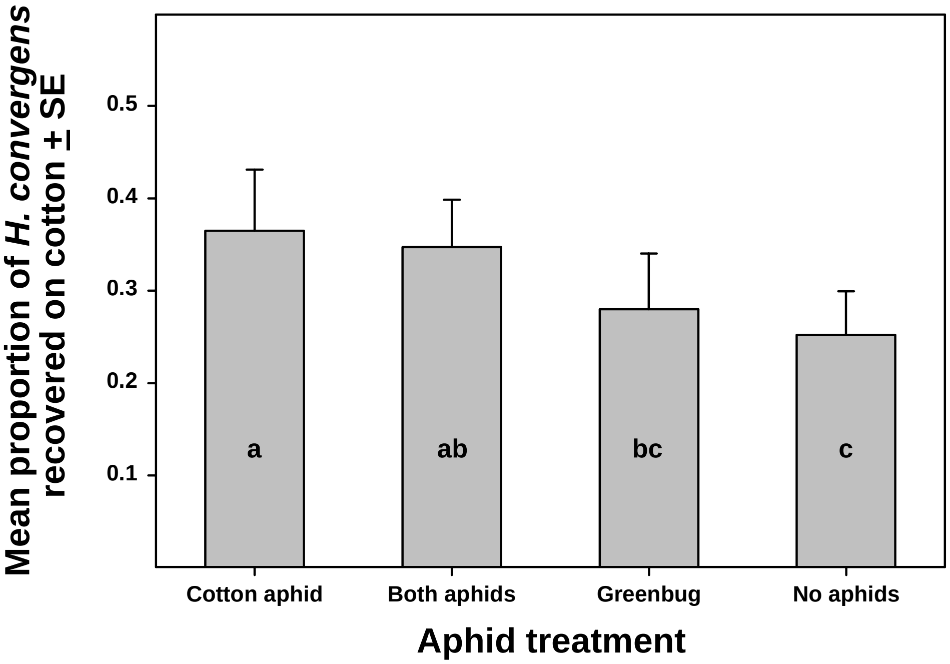

Fig. 5. Mean proportion of *Hippodamia convergens* collected on caged cotton plants, 2002. Aphid treatments containing the same letter do not differ. Data are presented as back-transformed means for ease of interpretation.

(1397 / 2331) of all predators collected in cotton and 66% (293 / 443) of all marked predators moving into cotton from adjacent grain sorghum fields, it seems likely that coccinellids were responsible for the overall pattern of predator movement into cotton during 2001.

Though no differences in 2001 predator movement were found over the three stages of phenology, this may be attributable to experimental design; replicates were located at relatively distant sites with crop planting and management under the control of cooperating growers. This arrangement was chosen in an effort to have results best reflect the conditions of crop management in the region, but may have resulted in greater variance in predator movement data. Previous studies suggesting the role of sorghum phenology have had more standardized conditions with experiments unreplicated or pseudoreplicated at a single location (Fye 1971, Fye and Carranza 1972).

Data on the rate at which predators move from cotton into grain sorghum indicated mean dispersal rates from 16 – 20 m/d for all predator groups and no differences between taxa were found. The indicated dispersal rates are likely underestimates because of difficulties associated with sampling; a predator collected four days after rubidium application had its estimated movement divided by four to estimate a daily rate, but the individual may have arrived at its position two days earlier. However, the mobility indicated by the dispersal rates suggests that the use of grain sorghum as a source of predators for cotton need not be confined to the small alternating strips of cotton and sorghum previously proposed (Robinson et al. 1972a, 1972b, Burleigh et al. 1973, Parajulee et al. 1997, Parajulee and Slosser 1999).

The lower number of marked predators recaptured during 2002 is not completely explained by the number of total predators collected. The percentage of marked predators as a fraction of all predators collected was markedly lower in 2002 (5.9%) than in 2001 (16.4%). It seems possible that precipitation on the day of the final rubidium sprays may have interfered with the efficacy of our predator marking technique if rubidium chloride was washed off plants before absorption could occur. This hypothesis is supported by the experimental results showing that foliar-applied rubidium may require 8 – 12 h for maximal absorption into plant tissues (Reickenberg and Pritts 1996).

Cage studies designed to test the hypotheses that aphid levels and phenology may motivate movement of *H. convergens* between crops showed an effect of phenology during both 2001 and 2002. Overall, a greater proportion of beetles was collected on cotton during the hard dough and maturity stages of sorghum. Because both crops matured over the study period, it is not immediately clear whether the growth of cotton rendered it more desirable as a habitat or if the gradual senescence of sorghum repelled *H. convergens*. However, since this effect was consistent across years whether predators were released onto cotton or sorghum (with no interactions), both of the above statements are probably true. In 2002 the combinations of aphid treatments to sorghum and cotton also influenced the proportion of beetles collected on cotton. Treatments with aphids on cotton had more *H. convergens* collected on cotton compared to when no aphids were present on either crop.

Based on the results from both years, it appears that aphid levels and crop phenology both cause *H. convergens* to move between cotton and sorghum. Several species of Coccinellidae are known to respond via aggregration to high levels of aphid prey (Kareiva 1982, Ives et al. 1993), and recent evidence suggests that *Hippodamia convergens* accomplishes this response to prey levels by utilizing olfactory cues from the aphids (Hamilton et al. 1999, Acar et al. 2001). However, results here suggest that *H. convergens* responds to relatively low levels of aphids on cotton and grain sorghum.

Though previous studies have suggested that an association of cotton and grain sorghum may have potential for improving cotton pest management, currently no purposeful use of grain sorghum is made with regard to arthropod pest management. This study confirms and quantifies the relationship of sorghum to cotton as a source of colonizing predators and indicates that both phenology and prey densities may motivate predator colonization of cotton. Because predators of all classes are competent dispersers, the use of grain sorghum as a predator source is not limited to the small-scale strategy of strip-cropping cotton and grain sorghum. A mosaic of cotton and grain sorghum fields over an agricultural landscape should be useful to improve early-season populations of predators in cotton and may also produce benefits as a source of predator recolonization if early-season pesticide applications to cotton are necessary. Grain sorghum will probably remain part of many cotton production systems as a rotation crop because of its tolerance to insect pests and drought, but in order to realize the full potential of improved pest management that may be provided in this system, further research on the impacts of predator movement on pest levels and cotton yields is needed.

CHAPTER III

RELATIONSHIPS OF LANDSCAPE, PREY AND AGRONOMIC VARIABLES TO THE ABUNDANCE OF GENERALIST PREDATORS IN COTTON

Changes in crop production over the last several decades have transformed modern agriculture from a mosaic of small family farms to relatively large tracts of monoculture, resulting in a greatly simplified agricultural landscape (Nickel 1973, Hietala-Koivu 2002). This trend towards large monocultures represents a loss in plant diversity and has predictably altered the composition and stability of arthropod populations in agriculture. Problems arising from this trend include an increased severity of pest outbreaks (Root 1973, Andow 1991a) as well as a decrease in the number and effectiveness of natural enemies, particularly indigenous generalist predators (Rabb et al. 1976, Altieri and Letourneau 1982).

One way to address these problems is to increase plant diversity within agricultural fields. The use of polycultures (i.e. planting two or more crops on the same parcel of land) and the planting or growth of non-crop vegetation (e.g. weeds, flowering plants, and hedgerows) are tactics aimed at attracting, retaining, or otherwise improving the performance of predators and parasitoids. Though frequently successful in research trials, creating functional, economically feasible programs of diversification in modern agriculture is challenging; polycultures can reduce yields via plant competition (Andow 1991b), while planting non-crop vegetation requires removing agricultural land from production (Landis et al. 2000). Required changes to agronomic practices including irrigation, planting, and weed or pest control may also reduce the feasibility of both strategies (Beets 1982). As a result, a recent review of habitat management in agriculture (Landis et al. 2000) notes that worldwide, only six such programs are widely adopted by growers in commercial agricultural systems.

Varied vegetation across a landscape may be more important to predators and parasitoids than diversity within agricultural fields (Elliott et al. 1999, Thies and Tscharntke 1999, Elliott et al. 2002a). Therefore a more practical strategy may be working with the diversity already present in agricultural landscapes to optimize pest control by existing natural enemies. The arrangement of crops across a landscape may be largely arbitrary, but crops of higher value or pest vulnerability could be planted nearer to sources of natural enemy colonization or refugia (Fig. 6). Such an arrangement reduces the distance natural enemies must move to arrive at higher value crops in an agricultural system, likely resulting in earlier or greater overall colonization by predators and parasitoids. Though perhaps more complex logistically, this strategy requires no modification of within-field management and no loss of available agricultural land. To implement such a strategy requires, at minimum, knowing (1) the habitat or plant types that are beneficial to the crop of interest, and (2) the scale at which benefits may be realized.

Cotton production in the Southern Rolling Plains region of Texas provides a relatively simple model system for exploring the effects of existing habitat diversity on natural enemies at the landscape scale. In this area, land used for crop production is divided among winter wheat, cotton and grain sorghum. Remaining agricultural land is devoted to rangeland and forage production, but uncultivated areas with natural

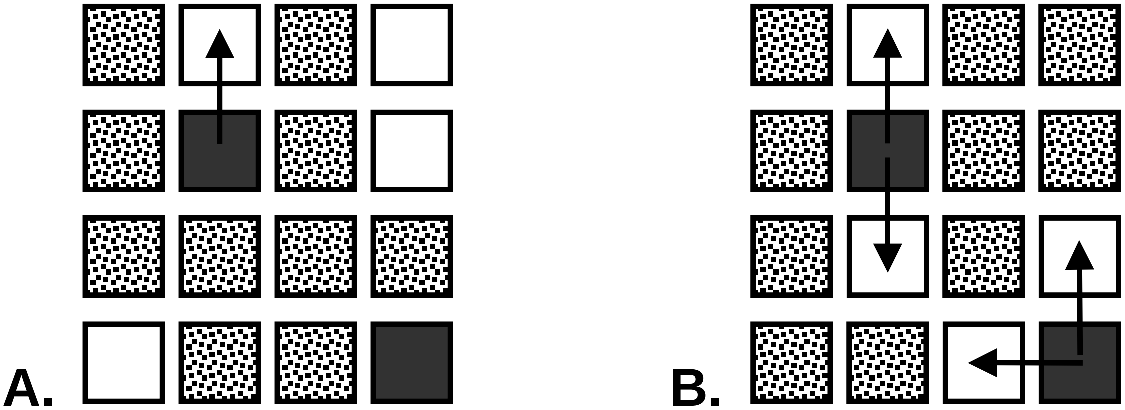

Fig. 6. Representation of arbitrary (A.) and strategic (B.) placement of high value crops (white plots) relative to natural enemy sources (black plots). Arrows indicate movement of natural enemies into the crop of interest. A strategic placement of high value crops near sources of natural enemies should promote earlier or greater colonization by predators and parasitoids.

vegetation are also a large component of the landscape. Previous research in Texas and elsewhere suggests that grain sorghum is a source for predatory arthropods in adjacent cotton plots (Fye and Carranza 1972, Lopez and Teetes 1976) and is supported by research in the Southern Rolling Plains (Prasifka et al. 1999, 2003a). Preliminary evidence also indicates uncultivated areas may increase predator numbers in nearby cotton fields (Heinz, unpublished data). Though grain sorghum and uncultivated areas appear to contribute to the predator fauna in cotton, the scale of any beneficial effects is currently unknown. Field studies conducted during 2001 and 2002 were designed to determine (1) if grain sorghum and uncultivated areas influence predator abundance in cotton on a landscape scale, and (2) how these effects, if detected, compare to biological and agronomic variables in determining predator abundance.

Materials and Methods

Manipulation of landscape, biological and agronomic variables on a large scale was not technically feasible, so a large number of cotton fields were selected and used in what is sometimes referred to as a “natural experiment” (Pianka 1994); the variation among fields was used as a substitute for experimentally manipulated treatments. Totals of 70 (2001) and 63 (2002) commercial cotton fields over a three-county area were used with the permission of cooperating growers. These locations encompassed wide ranges of field areas, planting dates, cultivars grown, and crop management practices.

Predator and Pest Sampling. Approximately three weeks after planting, each field was sampled to determine pest and predator levels. Cotton plants at 13 arbitrarily selected locations were visually inspected within fields, though all sampling was conducted at least 60 m from the nearest field border. A total of 100 plants per field was searched in the earliest stages of cotton growth, but sampling was reduced to 40 plants per field after six unfurled leaves were present on each cotton plant. Pest numbers on each plant were counted, and included bollworms (*Helicoverpa zea* [Boddie]), tobacco budworms (*Heliothis virescens* [Fabricius]), cotton aphids (*Aphis gossypii* Glover), cotton fleahoppers, (*Pseudatomoscelis seriatus* [Reuter]), and thrips (*Thrips* spp. and *Frankliniella* spp.). Because of their similar appearance, bollworms and tobacco budworms were pooled into one pest category referred to as heliothines. Further, numbers of eggs and larvae (heliothines) or nymphs and adults (cotton fleahoppers) were distinguished as separate pest categories. The same plants were inspected for predators including ladybeetles, (*Hippodamia convergens* Guérin-Méneville and *Scymnus loweii* Mulsant), minute pirate bugs (*Orius insidiosus* [Say] and *Orius tristicolor* [White]), damsel bugs (*Nabis* spp.), big-eyed bugs (*Geocoris punctipes* [Say] and *Geocoris pallens* Stål) and spiders (Araneae). All predators sampled were only counted as adults except spiders, which were counted at all life stages. Sampling was conducted once weekly for nine weeks, unless inclement weather or recent pesticide use prohibited entry into fields.

Landscape and Agronomic Variables. In addition to predator and pest sampling, data on agronomic and landscape variables also were collected. Agronomic variables were classified as those factors potentially under control of a single grower and included the planting date and field shape (perimeter-to-area ratio) of selected cotton fields. The planting date of the nearest grain sorghum field also was included because sorghum maturity has been implicated as a cause of predator movement from grain sorghum to cotton (Fye 1972). Although pesticide use is certainly another important agronomic factor, reliable pesticide application data for all of the selected fields could not be obtained, so the inclusion of this parameter as an agronomic variable was prevented.

Area maps provided by the Texas Boll Weevil Eradication Foundation were used as a framework for obtaining landscape data. These maps indicated which agricultural fields in the area were used for cotton production each year. The information on these maps was verified and the location of grain sorghum and uncultivated areas was added (MapInfo Corporation 2000). Image analysis software (Jandel Scientific 1995) was then used to measure the following variables for each field: total lengths of field perimeter shared with grain sorghum and uncultivated land; total areas of grain sorghum and uncultivated land area within 1.6 km; the total areas of grain sorghum and uncultivated land between 1.6 and 3.2 km distant (Fig. 7). These parameters were chosen to represent plant diversity at local (field perimeter), intermediate (0 – 1.6 km) and area (1.6 – 3.2 km) scales. Because the cotton fields selected varied widely in size (12 – 206 ha), landscape variables were scaled relative to cotton field size. For example, the amount of cotton perimeter shared with grain sorghum was expressed as a percentage of total cotton field perimeter. Accordingly, estimated of uncultivated land between 0 – 1.6 km from a specific cotton field were calculated as the total area of uncultivated land within 1.6 km divided by the cotton field's area.

Analytical Methodology and Statistical Analyses. Stepwise regression analysis was used to determine the relationships of biological, agronomic and landscape variables to

Fig. 7. Sample image for analysis of landscape variables. Grain sorghum fields are shown in black and uncultivated land in white. Cotton, harvested wheat and fields recently left fallow are indicated in gray, with studied cotton fields indicated by numbers. Dashed-line circles indicate radii 1.6 and 3.2 km from centroid of cotton field number 32.

predator abundance. This approach differs from analyses focused on constructing the best model as judged by the amount of variation explained (i.e. maximum R^2, minimum SSE). The intent was to obtain regression models whose interpretation was as simple and straightforward as possible, thus increasing confidence that all model components represented meaningful effects. Given the additional complexity or 'noise' introduced by uncontrolled variables not used as potential predictors (e.g. local weather, pesticide use, cotton variety) and the high number of fields sampled, the inclusion of a given predictor in a regression is unlikely to be a spurious result.

Preliminary data analysis was conducted on independent variables to determine if landscape and agronomic conditions differed between years; if the ranges of conditions differed from one year to the next, the relationships of predator levels to independent variables might also be expected to vary. Most independent variables were not normally distributed, so the non-parametric Mann-Whitney test was used to compare independent variables between years. Suspected correlations between landscape variables were also examined. Extremely high correlations among these variables could cause a variable with no direct relationship to predator abundance to be accidentally included as a model predictor or hinder overall interpretation of results. Spearman's rank correlation procedure was used to test for bivariate correlations among landscape variables. These and all other analyses were conducted using SPSS software (SPSS Inc. 2000).

In the stepwise regression analysis the dependent variable, predator density, consisted of the sum of all five predator categories sampled for each field on a given sampling date, giving an estimate of the number of predators per 100 cotton plants. Data from pest densities, landscape variables and agronomic practices were all used as independent variables. Scatter plots of predator abundance versus all independent variables were used to search for outliers before regressions were performed. Data were censored to remove (1) extreme values of independent variables, (2) instances of apparent sampling error, and (3) cases where pesticide applications were suspected (decreases $\geq$ 50% in predator numbers for at least two weeks). In no case were more than two observations censored in a regression. Stepwise regressions (entry $\alpha = 0.05$, removal $\alpha = 0.10$) were then conducted for three sample dates per year at times corresponding to the half-bloom, hard dough and maturity stages of grain sorghum phenology (Vanderlip 1993). Multiple sample dates were analyzed separately because factors influencing arthropod populations in agriculture may vary during the growing season (Brazzle et al. 1997), while the specific periods selected were timed to closely coincide with previous mark-recapture studies of predator movement in the Southern Rolling Plains.

Results

Trends in Predator and Pest Populations. Mean predator levels increased steadily throughout the period of observation in both 2001 and 2002 (Fig. 8). Among the five predator groups included in the analysis, ladybeetles and spiders were most common (38% each), with minute pirate bugs (13%), damsel bugs (9%), and big-eyed bugs (2%) found in lower numbers. Both the occurrence and peak abundances of various pest groups were segregated temporally (Figs. 9-10). Thrips were found only in early sampling periods, whereas fleahoppers and heliothines reached their maximum densities

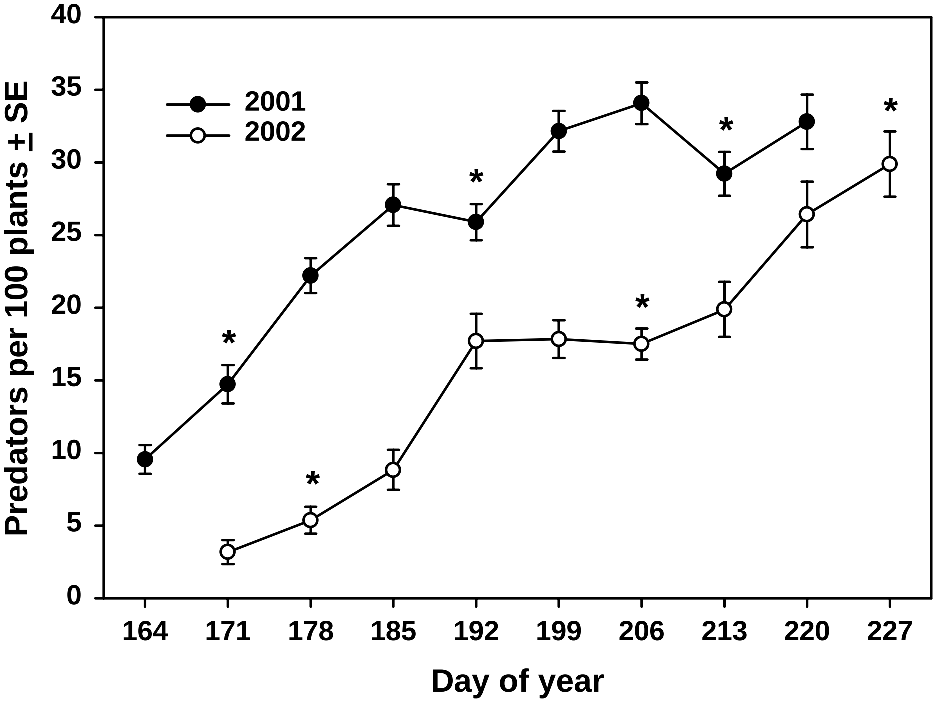

Fig. 8. Number of generalist predators per 100 plants in sampled cotton fields during 2001 (filled circles) and 2002 (empty circles). Asterisks indicate dates for which stepwise regressions on predator levels were conducted.

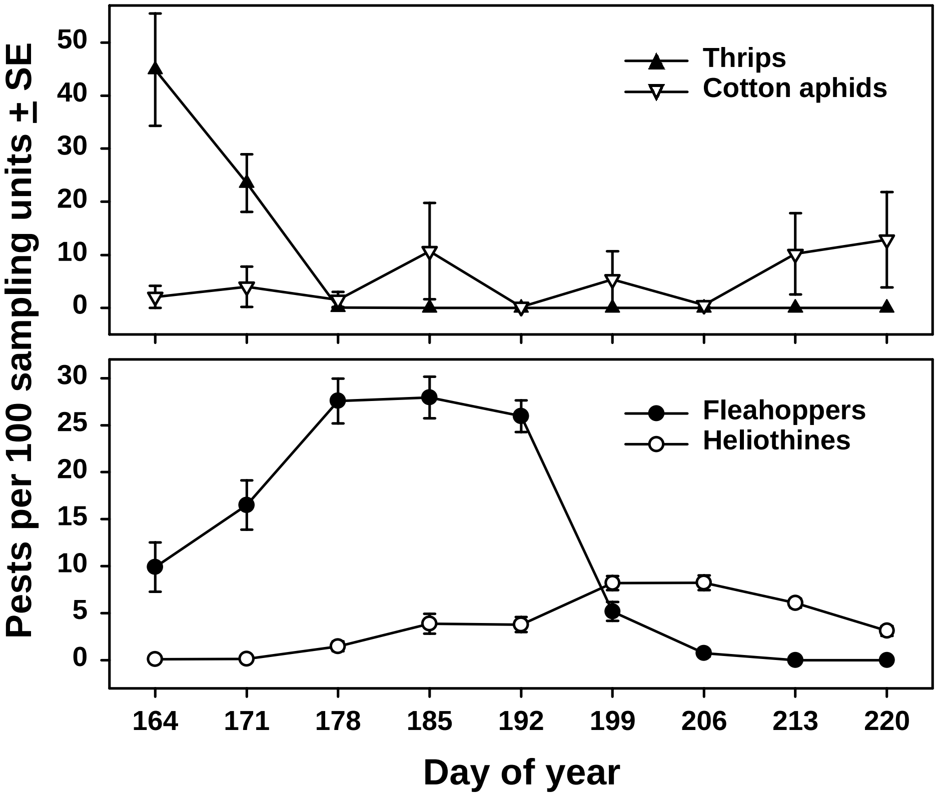

Fig. 9. Mean number (± standard error) of pests per sampling unit versus time, 2001. Pest levels expressed as number per 100 plants, except for aphids (per 100 leaves) and thrips (per 100 terminals). Data for distinct life stages of heliothines and fleahoppers are pooled for presentation.

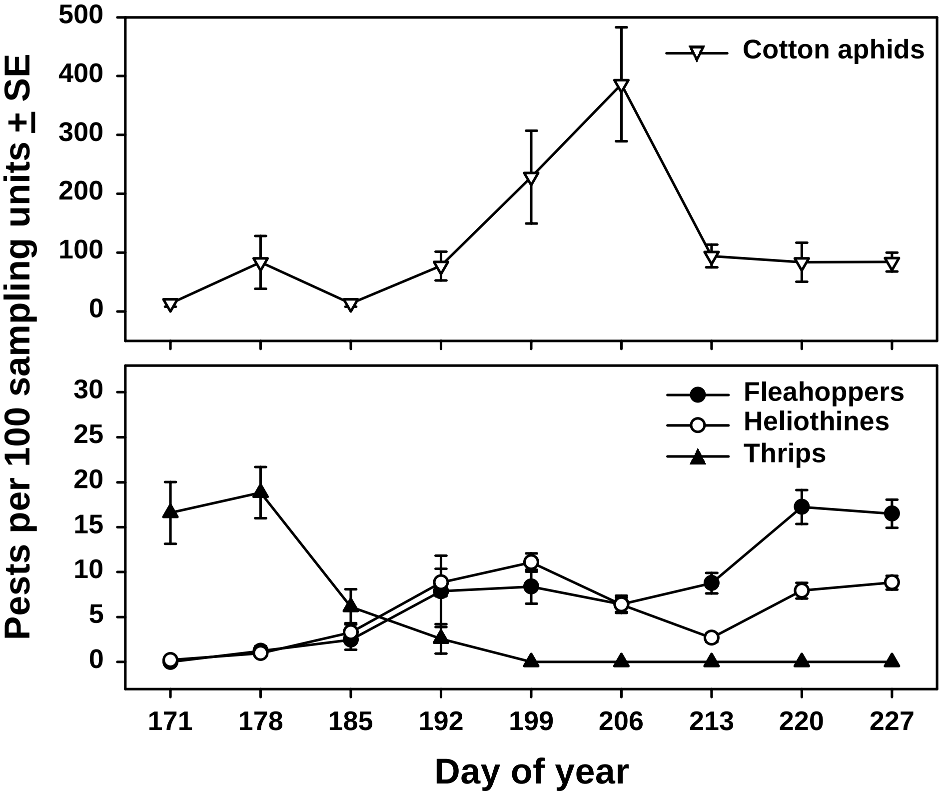

Fig. 10. Mean number (± standard error) of pests per sampling unit versus time, 2002. Pest levels expressed as number per 100 plants, except for aphids (per 100 leaves) and thrips (per 100 terminals). Data for distinct life stages of heliothines and fleahoppers were pooled for presentation.

around the middle and late sampling dates. Peak mean abundance of cotton aphids also increased 30-fold between 2001 and 2002.

Comparisons and Correlations of Landscape and Agronomic Variables. Wide ranges of values for agronomic and landscape variables were apparent over both years (Table 4). Mann-Whitney test results showed differences in two agronomic variables between 2001 and 2002. First, the median cotton planting date was delayed 13 days in 2002, a result of unseasonable May rains over much of the study area. Also, cotton fields sampled in 2002 also tended to have greater perimeter-to-area ratios than in 2001. Among the landscape variables, greater relative areas of grain sorghum and uncultivated land were found within 1.6 km of selected cotton fields during 2002. Several significant Spearman's rank correlations ($\alpha = 0.05$) between landscape variables were found (Table 5). The strongest relationships were found between the relative amount of uncultivated areas at the intermediate (0 – 1.6 km) and area (1.6 – 3.2 km) scales in 2001 and 2002.

Regression Analyses of Predator Abundance. Stepwise regressions explained up to 36% of the variation in predator levels among the study fields in 2001, though the strength of the regressions and the significant predictors of predator density differed among sampling periods (Table 6). Data collected in the early sampling period, which corresponded with the half-bloom stage of grain sorghum maturity, best explained the abundance of predators during 2001 ($R^2 = 0.36$; $F_{2,49} = 13.95$; $P < 0.001$). During this period, fields planted earlier tended to have greater numbers of predators, while those with greater numbers of fleahopper adults also showed higher predator abundance. At the hard-dough stage, only fleahopper adults entered the stepwise regression model,

Table 4: Agronomic and landscape variables used in stepwise regressions of predator abundance, 2001-2002

Variable	Median (range)		*T*	*P*
	2001	2002		
Cotton planting date (d)	143 (121 – 161)	156 (125 – 165)	3426.5	< 0.01
Cotton perimeter-to-area ratio ([km/ha ×] 100)	6.6 (3.2 – 12.6)	8.0 (4.0 – 14.0)	4092.5	< 0.01
Planting date of nearest grain sorghum field (d)	100 (87 – 109)	99 (71 – 118)	4666.0	0.91
Grain sorghum perimeter (%)	8.3 (0 – 79.6)	11.0 (0 – 62.0)	4676.5	0.95
Uncultivated perimeter (%)	8.2 (0 – 63.0)	10.2 (0 – 100.0)	4636.5	0.80
Grain sorghum area within 1.6 km	0.7 (0 –15.2)	1.2 (0 – 15.8)	4191.5	0.02
Grain sorghum area between 1.6–3.2 km	2.8 (0 – 17.3)	3.6 (0 – 28.2)	4421.5	0.23
Uncultivated area within 1.6 km	2.0 (0 – 23.9)	3.4 (0 – 29.4)	4138.5	0.01
Uncultivated area between 1.6–3.2 km	12.8 (0.4 –132.1)	17.1 (0.5 –92.5)	4337.5	0.11

T = test statistic for Mann-Whitney test (*n* = 70, *m* = 63). Areas expressed as ratios relative to cotton field area.

Table 5: Spearman's rank correlation coefficients (r_s) among landscape variables, 2001 and 2002

Variable	Year	Uncultivated perimeter (%)	Grain sorghum % within 1.6 km	Grain sorghum % between 1.6–3.2 km	Uncultivated % within 1.6 km	Uncultivated % between 1.6–3.2 km
Grain sorghum perimeter (%)	2001	–0.310*[1]	0.629*	0.172	–0.039	–0.080
	2002	–0.242	0.617*	0.236	–0.127	–0.044
Uncultivated perimeter (%)	2001		–0.217	–0.299*	0.587*	0.413*
	2002		–0.308*	–0.369*	0.550*	0.480*
Grain sorghum area within 1.6 km	2001			0.574*	–0.048	–0.134
	2002			0.687*	–0.067	–0.127
Grain sorghum area between 1.6–3.2 km	2001				–0.164	–0.250*
	2002				–0.145	–0.156
Uncultivated area within 1.6 km	2001					0.890*
	2002					0.920*

Asterisks indicate significant ($\alpha < 0.05$) correlations between variables.

Table 6: Predictors of cotton predator abundance as indicated by stepwise regression analysis, 2001

Sampling period	Variable	Partial correlation coefficient	*t*	*P*
Half-bloom	Cotton planting date	–0.441	–3.44	0.001
	Fleahopper adults	0.304	2.23	0.030
Hard-dough	Fleahopper adults	0.405	3.52	0.001
Maturity	Uncultivated area between 1.6–3.2 km	0.315	2.67	0.009
	Heliothine eggs	0.300	2.54	0.014
	Grain sorghum perimeter (%)	0.254	2.12	0.038

Table 7: Predictors of cotton predator abundance as indicated by stepwise regression analysis, 2002

Sampling period	Variable	Partial correlation coefficient	*t*	*P*
Half-bloom	Cotton planting date	–0.470	–3.80	< 0.001
	Grain sorghum area within 1.6 km	0.349	2.66	0.011
Hard-dough	Uncultivated area within 1.6 km	0.271	2.11	0.040
Maturity	Cotton planting date	–0.414	–3.37	0.001
	Cotton aphids	–0.308	–2.40	0.020
	Fleahopper adults	0.284	2.19	0.032

explaining little of the overall variation in predator abundance ($R^2 = 0.16$; $F_{1,63} = 12.35$; $P < 0.001$). As grain sorghum fields reached maturity, predator levels in cotton were positively related to the amount of uncultivated area from 1.6 to 3.2 km distant, the abundance of heliothine eggs, and the proportion of cotton field perimeter shared with grain sorghum ($R^2 = 0.30$; $F_{3,65} = 9.46$; $P < 0.001$). This is the first period in which landscape variables were significant model components.

Results from 2002 data showed similarities to the previous year (Table 7). During the half-bloom period, cotton planting date was again negatively related to predator abundance, while cotton predator levels increased with the amount of grain sorghum between 1.6 and 3.2 km distant ($R^2 = 0.35$; $F_{2,51} = 13.51$; $P < 0.001$). As in 2001, the model R^2 value was lowest during hard-dough, when only a positive effect of uncultivated land within 1.6 km entered the regression model ($R^2 = 0.07$; $F_{1,56} = 4.43$; $P = 0.040$). At grain sorghum maturity, cotton planting date, fleahopper adult abundance, and cotton aphid levels were significant model components ($R^2 = 0.35$; $F_{3,55} = 9.83$; $P < 0.001$). As in previous models, predator abundance was related negatively to cotton planting date and positively with fleahopper adult abundance, but a negative relationship between cotton aphids and predators was also indicated for this period.

Discussion

Effects of Grain Sorghum and Uncultivated Areas on Predator Abundance. The first goal of this study was to determine if landscape variables influenced cotton predator abundance. Although correlations cannot be used to define causality, the results convincingly suggest positive influences of the measured landscape variables on the abundance of predatory arthropods in cotton. Significant relationships between predator abundance and diversity across the agricultural landscape appear in both years and in all three sampling periods. At grain sorghum maturity during 2001, cotton fields with increasing uncultivated areas beyond 1.6 km or shared perimeters with grain sorghum had greater numbers of generalist predators than those without these landscape components. At grain sorghum's half-bloom period the following year, greater numbers of predators were associated with increasing amounts of grain sorghum within 1.6 km of cotton fields; the same relationship was found in the hard-dough period with respect to the extent of uncultivated land.

Potential problems with the regression results include the inconsistent nature of results between years and the pair-wise correlations between landscape variables. The fact that the precise identity and timing of landscape variables in regression models differ between years is not a concern for at least three reasons. First, the distributions of four independent variables differed between years (Table 4), three of which entered at least one regression model. Changes in the independent variables between years suggest that predators may have experienced slightly different conditions (or combinations of conditions) in 2001 and 2002. Consequently, the expectation of consistent regression results between years is unrealistic. Second, landscape variables were always positively correlated with predator abundance. The fact that grain sorghum and uncultivated land always showed positive relationships with natural enemy abundance in cotton suggests that the general nature of any effects of landscape diversity was consistent. Finally, other variables in the regression models were also inconsistent between years (e.g. prey levels, Figs. 9-10). As one exception, cotton planting date appeared as a model component in the half-bloom sampling period both years, though this is probably an artifact of experimental design; at this time, 10 to 50 days after planting of cotton fields, the most mature fields will almost certainly harbor greater predator numbers than plants at the cotyledon stage of growth.

Correlation among landscape variables was a concern for interpretation of results. Stepwise regression may prevent highly correlated variables from remaining in the same regression model, but does not ensure that the parameter entering the model is most appropriate. All pair-wise comparisons indicate several significant correlations (Table 5), but few are strong enough to present serious problems ($|r_s| \geq 0.70$). However, strong correlations between the intermediate and area scales of uncultivated land (r_s = 0.890 [2001], r_s = 0.920 [2002]) indicate that the two variables are too similar to be effectively distinguished. An inspection of area maps shows that uncultivated land often occurs as a few large, continuous patches (Fig. 7). Therefore, the rarity of discrete units prohibits distinction between these two scales of uncultivated land. Even with this limitation, the results suggest that the effects of landscape at intermediate and area scales are more important than adjacent habitats as predictors of predator abundance.

Magnitude of Landscape Effects. A second goal of the analysis was to estimate how the importance of the landscape composition compared with that of prey levels and crop management. Partial correlations represent the influence of one independent variable on predator abundance while taking into account the effects of other independent variables, and therefore represent the unique contribution of an independent variable to the overall

R^2. In the three regression models that used landscape variables in the final stepwise models, the influence of landscape variables appeared considerable. In two cases (maturity, 2001; hard-dough, 2002) landscape variables were the most important model components based on partial correlations (Tables 3-4). In the third instance (half-bloom, 2002) the relationship between grain sorghum and predators was secondary only to cotton planting date. Because the selected fields differed phenologically by up to 40 days, cotton planting date was the single most important predictor over the duration of the study. To examine the importance of landscape variables in another way, squared partial correlations the contributions of each group of variables can be assessed as a fraction of the total R^2 from all models together. Using this comparison, agronomic variables and prey levels each accounted for 38% of the total predictive power of the regression models, and landscape variables accounted for the remaining 24%.

Landscapes and Pest Management. While the idea that agricultural fields are not isolated, non-interacting units is not new (Levins 1969), an increasing number of recent publications have examined the effects of diverse vegetation on predators or parasitoids at a landscape scale (Elliott et al. 1999, Menalled et al. 1999, Thies and Tscharntke 1999, Östman et al. 2001a, 2001b, Elliott et al. 2002a, 2002b). Results of this study suggest that positive effects of grain sorghum and uncultivated land on cotton predator abundance may come from relatively distant areas, and that the influence of landscape composition can be of equal or greater importance than other types of variables. The corollary of such research is that increased natural enemy abundance and diversity will result in improved control of agricultural pests, though not all studies explicitly address the issue of pest management (Menalled et al. 1999, Thies and Tscharntke 1999, Östman et al. 2001a). Further observational studies are planned to more explicitly examine the movement arthropods among cotton, grain sorghum and uncultivated areas, while manipulative studies will focus on establishing the direct impacts of grain sorghum and uncultivated areas on cotton pest management. These studies will be necessary in showing quantifiable benefits to agricultural production by managing agricultural systems on a landscape scale.

CHAPTER IV

CROP COLONIZATION, FEEDING AND REPRODUCTION BY THE PREDATORY BEETLE, *HIPPODAMIA CONVERGENS*, AS INDICATED BY STABLE CARBON ISOTOPE ANALYSIS

Prominent differences between natural and cultivated habitats include artificially reduced plant diversity and persistence, and an increased frequency of disturbance from pesticide use (Levins and Wilson 1980, Hobbs and Huenneke 1996). These contrasts produce an overall reduction in the diversity and abundance of arthropod predators and parasitoids that help to control herbivorous crop pests (Russell 1989). Consequently, outbreaks of pest populations are more frequent in agriculture than in natural systems. One ecologically based strategy to address pest problems is to promote earlier or greater colonization of natural enemies through specific habitat management techniques (Landis et al. 2000). Several such strategies have been proposed, but little research has been directed at the explicit process of natural enemy colonization and the behavior of predators or parasitoids after entering a new habitat.

Carbon isotope analysis can be used to elucidate both the process of natural enemy colonization and the behavior of predators and parasitoids after entering a new environment. To use this method, the stable carbon isotope ratios ($^{13}C:^{12}C$) of plants acting as a source of natural enemies and the habitat being colonized must be distinct, as is the case with plants using exclusively C_3 or C_4 photosynthetic pathways to fix inorganic carbon. The mean ratios of the two non-radioactive isotopes of carbon (expressed as $\delta^{13}C$, a parts per thousand [‰] difference relative to a reference material) of C_3 and C_4 plant species are –28‰ and –14‰, respectively (O'Leary 1988). These values are transferred with little distortion to herbivores and to the predators or parasitoids that consume these plant-feeding pests (De Niro and Epstein 1978, Petelle at al. 1979, Ostrom et al. 1997, Oelbermann and Scheu 2002). This process effectively marks all herbivorous insects and their natural enemies, but any change from a C_3 to a C_4-based diet (or vice versa) causes a shift in carbon isotope ratio approaching the $\delta^{13}C$ value of the new diet (Ostrom et al. 1997, Markow et al. 2000, Oelbermann and Scheu 2002).

In this study, stable isotope analysis was used to examine the process of crop colonization and subsequent feeding and reproduction by the predatory lady beetle *Hippodamia convergens* Guérin-Méneville in an agroecosystem including the isotopically distinct crops cotton (*Gossypium hirsutum* L.) and grain sorghum (*Sorghum bicolor* [L.] Moench). This native coccinellid is widely distributed in North America and is the most abundant predator species in some agroecosystems (Gordon 1985, Prasifka et al 1999, Mohamed et al. 2000, Wright and DeVries 2000). Although it consumes prey from several insect orders**,** the convergent lady beetle is most closely associated with aphids (Homoptera: Aphididae), consuming 300 or more as larvae and continuing to feed throughout adulthood (Michels and Behle 1991). *H. convergens* adults move within and between habitats, with adults often aggregating at areas of high aphid density where females generally deposit their eggs (Elliott and Kieckhefer 2000, Hodek and Honěk 1996). To address the hypothesis that *H. convergens* from grain sorghum colonize nearby cotton fields (Fye 1971, Lopez and Teetes, 1976, Prasifka et al. 1999) and to explore the behavior of colonizing beetles, study objectives were to determine: (1) how rapidly lady beetle carbon isotope ratios change after a dietary shift between C_3 and C_4 resources, (2) over what period *H. convergens* adults in grain sorghum colonize nearby cotton, (3) the extent of adult feeding after colonization of cotton, and (4) if prey resources from grain sorghum directly contribute to egg production by *H. convergens* in cotton.

Materials and Methods

Laboratory Diet Experiment. Two food sources with distinct $\delta^{13}C$ values were given to adult *H. convergens* to examine how quickly carbon isotope ratios changed after a shift in the isotopic composition of the beetles' diet. Lady beetles obtained from a commercial insectary (Rincon-Vitova Insectaries Inc., Ventura, CA) were separated into groups of five adults with at least one female per group and placed into petri dishes inside an environmental chamber. Lighting in the chamber was set to a 16L:8D photoperiod, while temperature and relative humidity were monitored for the duration of the diet experiment with a HOBO® H8 Pro Series data logger (Onset Computer Corporation, Bourne, MA) recording at 1 h intervals (daily means ± SD; 26.7 ± 0.8 °C, 57.0 ± 11.3 % RH; $n = 38$ days). Water was provided using dental wicks saturated with reverse-osmosis filtered water. These beetles were fed, *ad libitum*, a diet of greenbug, *Schizaphis graminum* (Rodani) reared on greenhouse-grown grain sorghum plants. To produce a group of *H. convergens* with uniform isotope ratios, 35 individual eggs laid by the insectary-supplied beetles (from at least six different females) were separated into new petri dishes and provided the same diet of *S. graminum* and water until pupation.

Upon emergence, a sample of adult beetles (n = 5) was removed, labeled and placed into a freezer for preservation as control samples. Remaining beetles were fed on *S. graminum* for another three days, at which point a second group of control samples (n = 4) was collected. The diet provided to *H. convergens* adults was then switched to cotton aphid, *Aphis gossypii* Glover, which was reared on potted cotton plants grown in a greenhouse. Samples of four to five of the remaining beetles were removed 1, 3, 5, 7 and 14 d after the diet was changed. Four beetles that died before their scheduled removal were discarded. To establish the carbon isotope ratios of plants and aphids in the diet experiment, aphid and plant samples were also collected. Plant samples were cut from upper leaves of cotton and sorghum plants with care taken to avoid main leaf veins. Aphids were collected in groups of 10 or more by disturbing aphid colonies and collecting fallen or walking aphids with fine point forceps. As with the lady beetle samples, aphid and plant material was preserved by freezing before sample preparation and analysis.

Field Collections of *H. convergens* Eggs and Adults. In 2001 and 2002, four sites were selected near Ballinger, TX (Runnels County). Each site was comprised of a pair of commercially-managed cotton and grain sorghum fields that shared one lengthwise border and were oriented with parallel rows. In each cotton field, a plot 100 × 40 m (l × w) was marked with landscaping flags, with plots located at least 100 m from the field borders not shared with grain sorghum (Fig. 11). These plots were then divided into

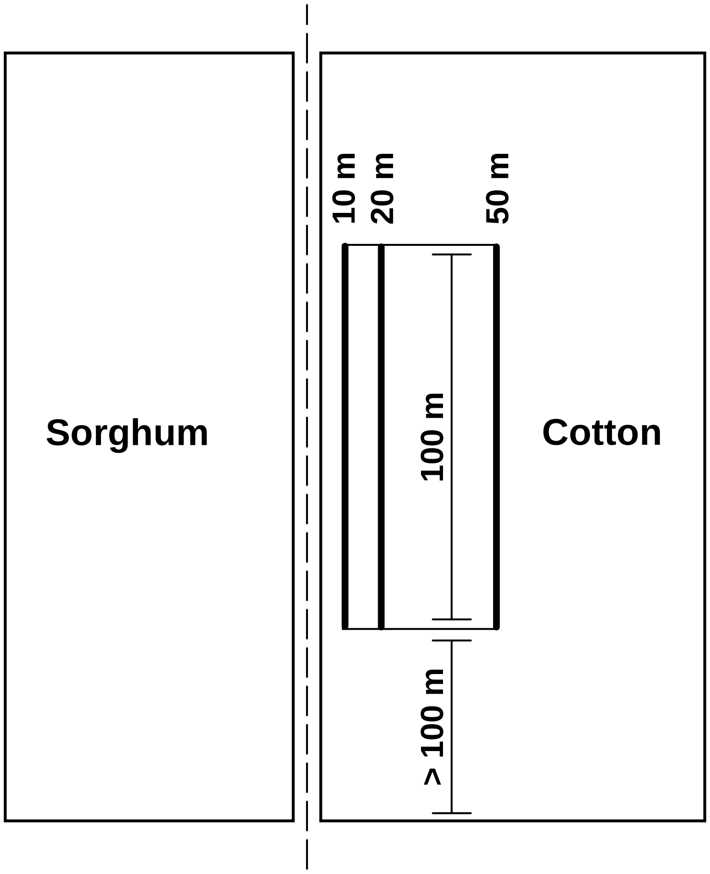

Fig. 11. Diagram of field sites, plots and subplots for collection of *Hippodamia convergens* eggs and adults in cotton, 2001 – 2002. Dashed line indicates boundary between cotton fields. Diagram is not to scale.

subplots positioned 10, 20 and 50 m from the interface of the cotton and grain sorghum fields.

Sampling of *H. convergens* adults and egg masses in cotton began three weeks after cotton emergence, when adjacent grain sorghum fields reached the soft-dough stage of development (Vanderlip 1993). At each site, cotton plants in all subplots were sampled for *H. convergens* eggs and adults by visual inspection with 40 person-minutes of effort expended per subplot. Adults found in a single subplot were collected into a double-chambered aspirator whose removable inner chamber (a 2-dram screw cap vial) was used for storage of samples. Egg masses were collected by removing the portion of plant tissue on which they were found (usually the lower leaf surface) and placing them into 2-dram vials. Collections of eggs and adults continued for six to seven weeks, until the grain sorghum at each site reached physiological maturity and senesced. For reference, samples of green leaf tissue from cotton and sorghum plants at each site were also collected as in the laboratory experiment. All plant and insect material collected was preserved on dry ice until it could be returned to the laboratory for storage in a freezer (≈ -16°C).

In addition to insect and plant materials collected, the levels of both convergent lady beetle (adults) and cotton aphids were monitored in each cotton field as part of a separate study. The numbers of lady beetles per 100 plants and cotton aphids per 100 leaves were determined by visually inspecting 40 plants per field spread among 13 arbitrarily selected locations. However, sampling was not conducted in the plots from which *H. convergens* eggs and adults were collected, but from areas at least 60 m from all field borders in an effort to represent an overall aphid level for each cotton field.

Sample Preparation and Analysis. All collected material from laboratory and field experiments was washed twice in reverse-osmosis filtered water. Accurate isotope analysis often requires homogenization by grinding solids into a fine powder and subsampling, but this was not always necessary because of the small sample masses. For analysis, *H. convergens* adults were sliced halved along the anterior-posterior axis with a surgical scalpel. Egg masses were treated as whole clusters after using a scalpel to separate eggs from plant material. Aphids were used in groups of about 10 individuals. These samples were then dried for 72 h at 65 °C before being massed to an accuracy of ± 1μg and packaged into tin sample capsules (Costech Analytical Technologies, Valencia, CA). Plant samples were large enough to require homogenization. After drying, leaf tissues were pulverized to a powder with a Wig-L-Bug mill (Spex Certiprep, Metuchen, NJ) before enclosing a subsample of desired mass (2-3 mg) into a sample capsule.

Sample carbon isotope ratios were determined at the University of Georgia's Stable Isotope Laboratory via a combustion – gas chromatography – mass spectrometry process. In this process the gases produced by flash combustion of samples are sent to a gas chromatograph where carbon dioxide (CO_2) is separated out and sent to a mass spectrometer. The mass spectrometer separates CO_2 molecules based on their charge-to-mass ratio, producing a ratio of ^{13}C:^{12}C for each sample. These isotope ratios are expressed as $\delta^{13}C$, where:

$$\delta^{13}C = [R_{sample} - R_{standard}] \times 1000$$

and the R_{sample} and $R_{standard}$ are the ratios of ^{13}C:^{12}C for an individual sample and the analytical standard (Pee Dee Belemnite). This expresses isotope composition on a relative scale, but the use of an analytical standard allows for conversion to absolute values.

Statistical Analysis. All statistical analyses were conducted using SAS software (SAS Institute Inc. 1999). For the laboratory diet experiment, mean carbon isotope ratios ($\delta^{13}C$ ± standard deviation) and shifts between trophic levels ($\Delta\delta^{13}C$) were calculated for each sample type. The changes in beetle isotope ratios over time were presented graphically but not analyzed statistically. For field studies, a separate but identical analysis was conducted for each sample type (adults and eggs) in each year, with each site representing one replicate or *H. convergens* population. To determine whether the carbon isotope ratios differed between sampling dates, a repeated-measures analysis of variance (repeated-measures ANOVA, PROC MIXED) was used, with date treated as a repeated measure and the square root of the number of samples analyzed (per field-date combination) used as a weighting factor. When variation in isotope ratios was shown by the repeated-measures analysis, pairwise comparisons of adjusted means (produced using the LSMEANS option) were made using the Tukey-Kramer test to control the experiment-wise error rate.

Results

Changes in Isotope Ratio Following a Dietary Shift. Cotton and grain sorghum plants grown for the diet-switching experiment showed distinct isotope ratios that were transferred to the respective aphid species reared on each crop, and both groups of *H.*

Table 8: Carbon isotope ratios (mean $\delta^{13}C$ ± standard deviation) and isotope ratio shifts ($\Delta\delta^{13}C$) between trophic levels from diet-switching experiment

Sampled organisms	*n*	$\delta^{13}C \pm SD$	$\Delta\delta^{13}C$
Cotton	4	-27.2 ± 0.4	
Cotton aphids	4	-28.4 ± 1.0	-1.3
Grain sorghum	4	-12.7 ± 0.1	
Greenbugs	4	-11.6 ± 0.3	1.1
Convergent lady beetles	9	-10.4 ± 0.3	1.1

Control beetles collected at adult emergence and three days after adult emergence pooled for convenience.

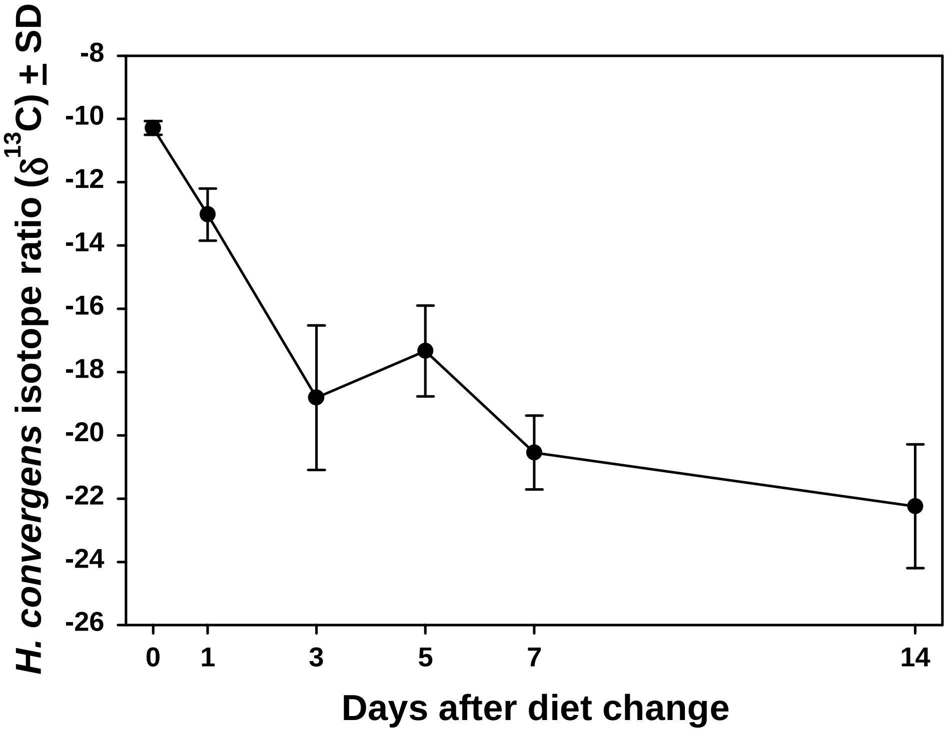

Fig. 12. Carbon isotope ratios (mean $\delta^{13}C$ ± SD) of laboratory-reared *Hippodamia convergens* adults at and after the initiation of a change in diet from a C_4-based resource (greenbugs reared on grain sorghum) to one based on C_3 plants (cotton aphids reared on cotton).

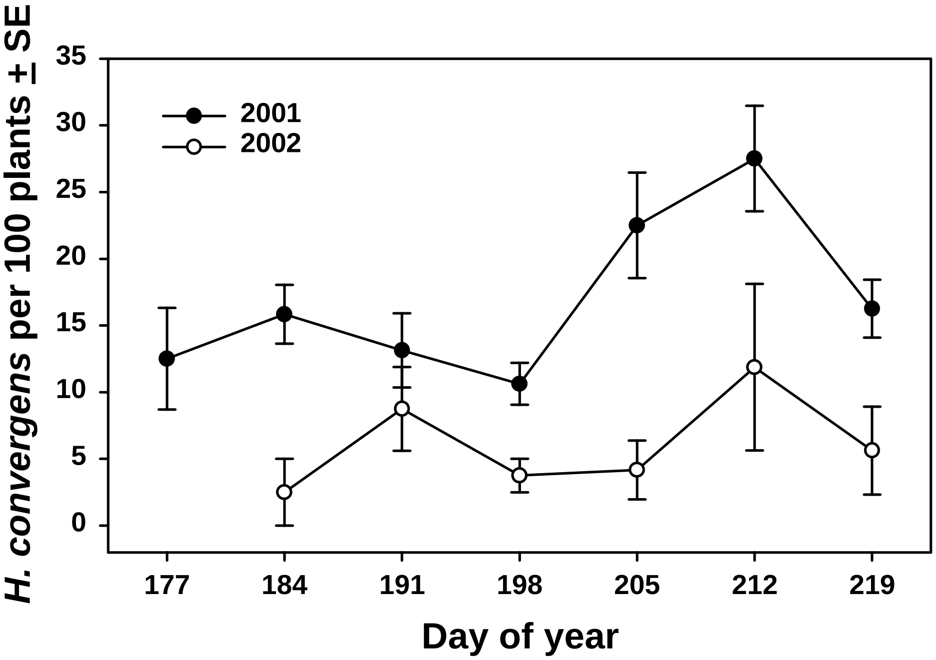

Fig. 13. Convergent lady beetle populations at field sites in 2001 and 2002. Data presented as beetles per 100 cotton plants (mean ± SE) with separate field sites used as replicates.

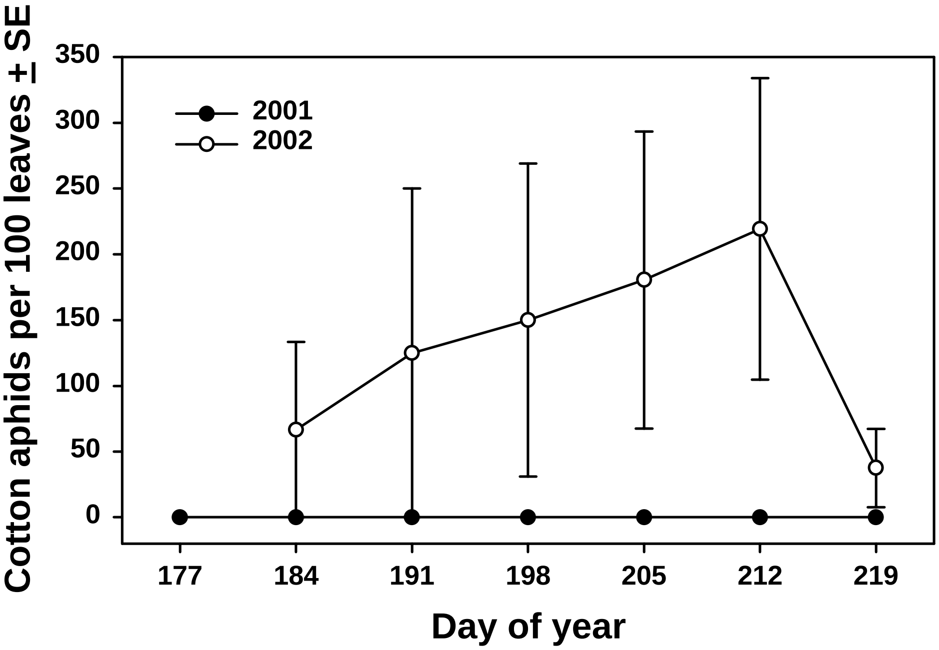

Fig. 14. Cotton aphid populations at field sites in 2001 and 2002. Data presented as aphids per 100 cotton leaves (mean ± SE) with separate field sites used as replicates.

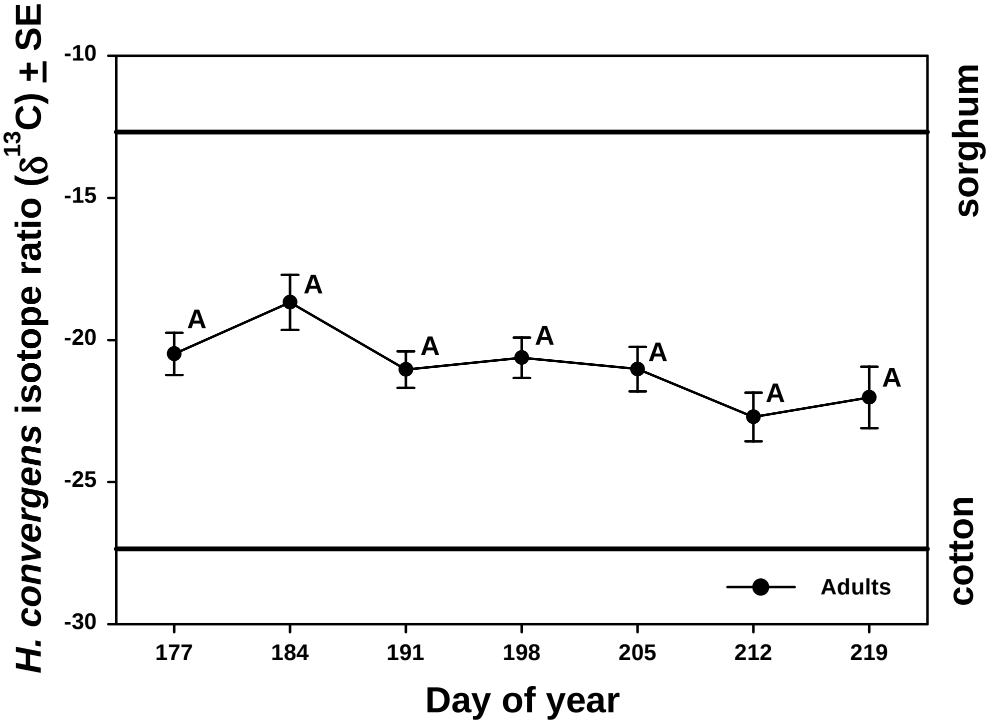

Fig. 15. Carbon isotope ratios (mean $\delta^{13}C$ ± SE) of field-collected *Hippodamia convergens* adults, 2001. Separate field sites used as replicates, with means shown as least-squares estimates from repeated-measures ANOVA. Differences in capital letters indicate differences between paired means (Tukey-Kramer test, $\alpha = 0.05$). Horizontal lines represent isotope ratios of field-collected cotton and sorghum plants for comparison.

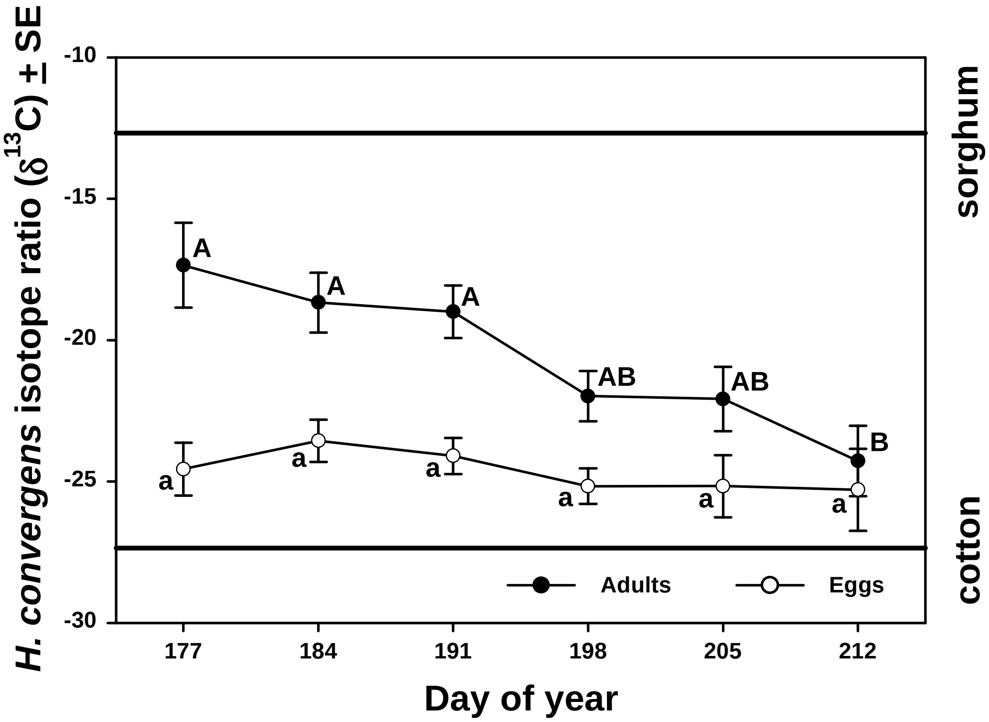

Fig. 16. Carbon isotope ratios (mean $\delta^{13}C$ ± SE) of field-collected *Hippodamia convergens* adults and eggs masses, 2002. Separate field sites used as replicates, with means shown as least-squares estimates from repeated-measures ANOVA. Differences in capital or lowercase letters indicate differences between paired means (Tukey-Kramer test, $\alpha = 0.05$). Horizontal lines represent isotope ratios of field-collected cotton and sorghum plants for comparison.

convergens control samples reflected the δ^{13}C values of the greenbug diet on which they were reared (Table 8). Mean differences, or isotopic shifts ($\Delta\delta^{13}$C) between trophic levels ranged from +1.1‰ (grain sorghum to greenbugs, greenbugs to *H. convergens*) to –1.3‰ (cotton to cotton aphids). The δ^{13}C values of *H. convergens* changed greatly after the original C_4-based diet (greenbugs) was changed to a C_3-based resource (cotton aphids), moving from –10.4 ± 0.3 to –18.8 ± 2.3 (mean ± SD) in three days (Fig. 12). After 14 d of feeding on only cotton aphids, *H. convergens* δ^{13}C values reached –22.2 ± 2.0 but were still enriched in ^{13}C relative to their cotton aphid prey (–28.4 ± 1.0).

Field Collections: General Results. The carbon resource bases for field-collected samples appeared to be similar to those used in the laboratory experiment, with mean δ^{13}C values of field-collected cotton (–27.4) and grain sorghum (–12.7) plants within 0.2‰ of those grown in greenhouse conditions. Population trends for *H. convergens* adults generally increased during the six to seven week sampling interval in both years, but appeared to be higher overall during 2001 (Fig. 13). Population trends of cotton aphids showed a distinct difference between years; *A. gossypii* were undetectable in the four study fields during 2001, but were present on all sample dates in 2002 (Fig. 14).

Carbon Isotope Ratios of Field-collected *H. convergens* Adults and Eggs. Carbon isotope ratios for *H. convergens* adults in 2001 began with estimated population means intermediate between cotton and grain sorghum, (Fig. 15), but a repeated-measures ANOVA suggests mean δ^{13}C values did not vary significantly over time (F = 2.17; df = 5, 15; P = 0.10). Isotope ratios from early collections of *H. convergens* in 2002 appeared slightly higher (less negative) than in 2001 (Fig. 16), but significantly increased during the sampling period (*F* = 5.25; df = 5, 13; *P* < 0.01). Tukey-Kramer means separation shows δ^{13}C values higher from days 177 to 191 compared to day 212, with carbon isotope ratios on other dates similar to both early and late sample periods.

Only one egg mass was collected during 2001 (δ^{13}C = −25.1‰), prohibiting any generalizations regarding the resources used for *H. convergens* egg production that year. However, 64 egg masses were collected in 2002, including eggs collected during all six sample dates. Analysis indicated no differences in the isotope ratios of eggs over time (*F* = 1.48; df = 5, 5; *P* = 0.34), and mean isotope ratios (least-squares estimates) ranged from −23.6 to −25.3‰ (Fig. 16).

Discussion

Changes in Isotope Ratio Following a Dietary Shift. The rapid change in *H. convergens* carbon isotope ratios suggests that individual beetles moving from grain sorghum to cotton should start to reflect the isotope ratio of their new C_3 habitat within two weeks if adequate food is available. Though the mean isotope ratio of *H. convergens* moved toward that of its cotton aphid diet, after two weeks it remained approximately 6.2‰ richer in ^{13}C than the aphid diet. Similar results were obtained in a diet-switching experiment on the related coccinellid *Hippodamia variegata* [Goeze], which showed a distinct transition towards the δ^{13}C value of its new synthetic diet two to six days after the isotopic composition of its diet was changed (Ostrom et al. 1997). At four weeks after the diet switch, adult *H. variegata* isotope ratios remained about 3‰ higher than its artificial diet. It has been shown that specific tissues assimilate ingested carbon at different rates (Tieszen et al. 1983), and this phenomenon likely explains the pattern of a period of relatively rapid carbon isotope transition followed by a slower progression towards the isotope ratio of the new diet (Fig. 12). For example, the hardened forewings (elytra) of beetles may reflect both larval and adult dietary history, as thin layers of carbon are periodically added to the adult exoskeleton (Hepburn 1985, Tallamy and Pesek 1996).

Carbon Isotope Ratios of Field-collected *H. convergens* Adults and Eggs. Because selected fields were kept weed-free through regular cultivation, mean isotope ratios intermediate to cotton and grain sorghum values indicate recent immigration from nearby grain sorghum by a portion of the *H. convergens* population in cotton. In both years isotope ratios suggested that colonization of cotton by adult beetles started before sampling began, when cotton plants were rather small (two to four true leaves unfurled). Further, beetles with relatively high ($< -16.0‰$) isotope ratios were collected from cotton in all sample dates in both years, and populations reached their highest levels during the penultimate sample date. Combined, these observations suggest that adult movement of *H. convergens* from grain sorghum continued for the duration of sample collection. These conclusions are supported by results from a concurrent mark-capture movement study that included two of the four fields used in isotope collections (Prasifka et al. 2003a).

Using $\delta^{13}C$ values to examine adult feeding in cotton yielded unexpected results. Adult beetles showed relatively constant $\delta^{13}C$ values over time in 2001, but feeding by adult beetles in cotton should decrease isotope ratios over time. Two simple, nonexclusive hypotheses may explain this result. First, evidence suggests that adult *H.*

convergens continually colonized cotton from grain sorghum throughout the study period. This constant addition of individuals with high (C_4) isotope ratios could partially offset the expected changes towards more negative (C_3) carbon isotope values that would result from *H. convergens* feeding in cotton. Second, because the expected change in isotope ratios is based on dietary intake of carbon, the constancy of isotope ratios could indicate that lady beetles in cotton were eating very little. The absence of detectable cotton aphid populations in 2001 (Fig. 14), supports the hypothesis that lady beetle feeding was greatly reduced in 2001. However, potential alternate prey (nymph and adult populations of the cotton fleahopper, *Pseudatomoscelis seriatus* [Reuter]) was abundant in cotton throughout the area in 2001 (Prasifka et al. 2003b).

Isotope ratios for adult *H. convergens* in 2002 allowed for a more straightforward interpretation, decreasing throughout the sample dates, indicating active feeding on prey in cotton. Most likely this is a result of feeding on cotton aphids, which were present throughout the duration of the study that year (Fig. 14). Even with their favored prey (aphids) available, mean isotope ratios of lady beetle populations changed slowly relative to the results of the diet-switching experiment. It is unknown whether the slow overall change in $\delta^{13}C$ values is a result of continued immigration from grain sorghum or aphid consumption at a much lower rate compared to *ad libitum* feeding in the laboratory.

Because *H. convergens* egg masses are produced from prey recently consumed by adult females, any egg masses with high, C_4 ($< -16.0‰$) isotope ratios are interpreted as eggs produced from resources consumed chiefly in grain sorghum. In 2001, egg masses were extremely rare in studied cotton fields. The absence of detectable cotton aphid populations (Fig. 15) and the constancy of adult *H. convergens* carbon isotope ratios over time suggest that insufficient prey resources may have been available for egg production in cotton. In 2002, lady beetle egg production in cotton was greatly increased, but mean isotope ratios were consistently within the range of C_3 plants. Two egg masses collected had isotope ratios in the C_4 range, but this represented a very small fraction (3%) of all samples collected. In general, results from both years suggest that the direct contribution of prey resources in grain sorghum to egg production of *H. convergens* in cotton was negligible.

Summary and Conclusions. This study uses stable carbon isotopes to study movement and reproduction in a predatory insect, and the results agree with those of a concurrent study using more traditional mark-recapture techniques (Prasifka et al. 2003a). In both study years, movement of *H. convergens* adults from grain sorghum into nearby cotton began at the earliest stages of cotton growth, and appeared to continue at a lower level for several weeks. During 2001 *H. convergens* adults remained in cotton fields but fed very little, possibly due to the absence of their preferred cotton aphid prey. In 2002, aphids were more abundant and feeding by *H. convergens* adults resulted in a slow shift of population carbon isotope ratios towards C_3 values. Egg production by lady beetles in cotton appeared to be almost entirely based on resources consumed in cotton.

Compared to crop colonization by pests, the establishment of predator and parasitoid populations in agriculture tends to be late (Price 1976). This may be attributed to simple differences between herbivores and their natural enemies; fields of young crops represent an abundant and homogenous food supply for herbivores, but natural enemies are dependant on populations of prey (or hosts) that are both spatially and temporally variable (Price 1976, O'Neil and Wiedenmann 1987). However, natural enemies may still be attracted to crop habitats when prey are absent (Price 1986). In such cases, the challenge then becomes maintaining an adequate number of natural enemies in the crop in spite of low prey availability. The retention and continuous colonization by *H. convergens* in 2001 suggests that this is possible. If *H. convergens* adults have experienced poor foraging success prior to moving into cotton, the apparently low quality habitat in cotton may still be above the marginal value necessary to retain them (Krebs 1978). Retention of adult beetles in cotton could also reflect the convergent lady beetle habit of subsisting on nectar and pollen when aphid prey are scarce (Hagen 1962). This type of diet breadth is suggested to be particularly desirable for natural enemies in ephemeral environments (Gilstrap 1997), but how frequently other natural enemy species show similar habitat fidelity under adverse food conditions is unknown.

CHAPTER V

GENERAL CONCLUSIONS

The results of the preceding chapters build upon previous research (Fye 1971, Fye and Carranza 1972, Robinson et al. 1972a, 1972b, Lopez and Teetes 1976, Prasifka et al. 1999) and further explore the potential role of grain sorghum as a source of predatory arthropods in cotton agroecosystems. The first objective focused on quantifying the movement of predators between these two crops. By using an elemental marker applied directly in the field, the sample size of recovered insects compared to previous mark-recapture studies (Lopez and Teetes 1976, Prasifka et al. 1999) improved by an order of magnitude. The results of the rubidium marking confirmed that an association of adjacent cotton and grain sorghum fields results in a net gain of predatory arthropods for the cotton crop. Approximately 2.7 predators moved from grain sorghum into cotton for every one lost to adjacent grain sorghum. This value is relatively close to the gain-to-loss ratio (2.0) calculated by Prasifka et al (1999) using a much smaller number of samples.

One difference between the results of this marking study and those of Prasifka et al. (1999) is that no pattern of movement relative to time (phenology) was detected in the rubidium marking study. That is, a relatively large number of predators appeared to move from grain sorghum into cotton during all three sampling periods. This may be a result of using replicates (fields) that were relatively distant from one another and under independent management of individual cotton and sorghum growers; earlier studies suggesting a relationship between phenology and predator movement took place under much more homogenous conditions (Fye 1971, Fye and Carranza 1972) where between-site variation could not interfere with detection of main effects. Examination of separate predator taxa indicated that the abundant coccinellids *Hippodamia convergens* and *Scymnus loweii* moved preferentially into cotton and were likely responsible for the overall pattern of predator movement between crops. Surprisingly, estimated rates of dispersal (15.8 – 19.9 m/d) were found to be similar among all taxa moving into cotton, including spiders, which are the only predator group studied that is unable to fly as an adult. Collectively, the mark-recapture results support the premise that grain sorghum may be a useful source of predators during cotton's early growth stages, but also suggest that grain sorghum may continue to contribute to natural enemy populations during later stages of cotton growth.

The second objective examined possible causes of movement between these crops for the predator *Hippodamia convergens*, which was chosen as a subject largely because of its abundance in many agroecosystems (Gordon 1985, Prasifka et al 1999, Mohamed et al. 2000, Wright and DeVries 2000) including cotton and sorghum grown in the study area. Cage experiments testing plant phenology and aphid density as putative causes of lady beetle movement gave positive results. During both years, more *H. convergens* adults were found moving onto caged cotton plants later in the season. During the second year, lady beetles also appeared to respond to relatively low levels of aphid prey that were created artificially for this study; in treatments where 15 *Aphis gossypii* (cotton aphids) were placed onto cotton plants, the number of beetles collected on cotton were higher, regardless of whether *Schizaphis graminum* (greenbugs) were placed onto nearby sorghum plants at an equal per-plant density. It is known that some lady beetle species, including *H. convergens*, aggregate in areas of high aphid density (Elliott and Kieckhefer 2000, Hodek and Honěk 1996), possibly as result of their olfactory response to aphids (Hamilton et al. 1999, Acar et al. 2001). However, the results of the cage study suggest that *H. convergens* may respond to relatively low levels of aphids on cotton and grain sorghum.

The next research component also focused on the role of *H. convergens* in the cotton – grain sorghum system. For the third research objective, the distinct stable carbon isotope values of cotton and grain sorghum provided an innovative tool to explore the feeding and reproductive behavior of *H. convergens* colonizing cotton. A laboratory study indicated that *H. convergens* carbon isotope ratios, $\delta^{13}C$, changed during two weeks after its food supply was shifted from a C_4 to a C_3-based diet, agreeing with the results of Ostrom et al. (1997) on a related species. This result suggests that feeding by beetles moving from sorghum into cotton should result in changes in isotope ratios over a relatively short period of time. In a field study, *H. convergens* adult isotope ratios suggested that nearby grain sorghum was a continuous source for lady beetles until many area sorghum fields matured and senesced. When populations of cotton aphid prey were absent, carbon isotope ratios of adult beetle populations did not change over time and virtually no egg production by *H. convergens* adults was detected. This indicates beetles were not feeding on resources originating in cotton, but were still retained in the crop. When cotton aphids were present, lady beetle isotope ratios gradually decreased towards the isotope ratio of the cotton crop, indicating feeding by adult beetles in their new habitat. As a result, egg masses produced had carbon isotope ratios in the C_3 range of values. Results suggest that *H. convergens* may be retained in cotton without large prey populations present, a quality that may be essential in controlling crop pests in agricultural systems.

The final research objective focused on testing for and quantifying the possible area-wide effects of landscape composition on cotton production. Stepwise regressions revealed the relationships of landscape, agronomic and prey variables to the levels of generalist predators in cotton fields. Significant relationships between predator abundance and agricultural landscape composition appear in three of six periods analyzed over two years, but the specific relationships of landscape variables to cotton predator levels differed between and within years. At grain sorghum maturity during the first year, predator levels rose with increases in the amount of uncultivated land from 1.6 to 3.2 km distant and the perimeter shared with grain sorghum. In the second year, the area of grain sorghum (at sorghum's half-bloom) and uncultivated land (at hard-dough) within 1.6 km of cotton fields were both positively related to predator numbers. Cotton planting dates and the abundance of cotton fleahoppers (*Pseudatomoscelis seriatus*) were also strongly linked to predator numbers during both years. Results suggest that the total amount of grain sorghum or uncultivated land in an area is more important than the simple presence of these habitats adjacent to cotton fields, and that landscape composition may sometimes be the most important factor in determining predator abundance.

Considering results from all research components collectively, the tactic of using grain sorghum as a source of predators in cotton agroecosystems is supported. One important difference between the research presented here and that explored by earlier publications is the greater spatial scale of the present research. The use of alternating small to medium size strips of cotton and grain sorghum may not be practical for a number of reasons, but multiple avenues of evidence presented here suggest that arrangements of whole fields of cotton and sorghum may be a compatible predator conservation strategy. Additionally, the research results point to an intuitive but unresolved relationship of non-agricultural habitats to the natural enemy fauna in area cotton fields. Though perhaps compelling, the results represent an intermediate step to developing a predator conservation technique that cotton producers can implement. To bring such a technique closer to fruition, future studies will need to focus more directly on the direct impacts of grain sorghum on pest levels and the overall profitability of cotton production.

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