Spillover of agriculturally subsidized arthropods to adjacent natural arid habitats: effects on community structure

**Thesis submitted in partial fulfillment
of the requirements for the degree of
"DOCTOR OF PHILOSOPHY"**

by

Valeria Hochman Adler

**Submitted to the Senate of
Ben-Gurion University of the Negev**

September 2012

Beer-Sheva

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Research-Student's Affidavit when Submitting the Doctoral Thesis for Judgment

I,__Valeria Hochman Adler, whose signature appears below, hereby declare that (please mark the appropriate statements):

_x__ I have written this Thesis by myself, except for the help and guidance offered by my Thesis Advisors.

_x__ The scientific materials included in this Thesis are products of my own research, culled from the period during which I was a research student.

__This Thesis incorporates research materials produced in cooperation with others, excluding the technical help commonly received during experimental work. Therefore, I am attaching another affidavit stating the contributions made by myself and the other participants in this research, which has been approved by them and submitted with their approval.

Date: ___19- Sept-2012_____   Student's name: _____Valeria Hochman Adler_____

Signature: _____

For my bear and my little wolf

Abstract

Spillover of arthropods from agricultural areas may affect the dynamics of food webs in adjacent natural habitats. I studied the occurrence of pest spillover from agricultural fields into surrounding non-crop habitat, its timing with respect to the cropping season, the degree of spillover at increasing distance from the crop, and its effects on the desert arthropod community in the hyper-arid Arava Valley, Israel. My working hypotheses were that pests will move from ephemeral high productivity habitats into low productivity habitats, and that spillover of pests will alter the structure of the recipient desert arthropod community. The Arava Valley provides a unique opportunity for studying pest spillover effects, as the arable land is surrounded by desert habitat, forming productive "islands" in a desert matrix. Particularly, I was interested in four main questions: 1) Is there pest spillover from crops into adjacent desert habitat, and does it decrease along a gradient of increasing distance from agricultural fields? 2) If spillover occurs, can pests survive and reproduce in desert habitats? This is relevant as pests may subsidize desert predators, scavengers, or both. 3) Are pests consumed by desert predators, and do they influence predator intraguild interactions? and 4) Are there changes in species composition in the desert arthropod community as a consequence of pest spillover? I investigated these questions by studying the abundance and dispersal of crop pests from agricultural areas into adjacent desert habitats, and their interactions with natural-habitat species. First, I monitored pest occurrence over the crop cycle in desert habitats and in home gardens in villages near agricultural areas. Second, I tested pest persistence and reproduction on desert plants. Third, I conducted lab experiments to investigate interactions between pests and desert predators, and to test some of the pathways by which spillover of pests might influence the desert arthropod community. Finally, I sampled the desert arthropod communities along a gradient of increasing distance from agricultural fields. This study attempted to improve our understanding of the effects of agricultural pests on natural ecosystem biodiversity in an extreme desert environment. I showed that pests spill over into adjacent natural habitats, and survive on some desert plant species within these habitats. In addition, these pests are consumed by common desert predator species under lab conditions, suggesting that they could subsidize desert communities. Results showed differences in composition between the communities nearest the crop area and those at the greatest distance, but the changes were not related to distance from the crop area. Predator abundance decreased with distance from the crop area, suggesting that predators may respond to the pest subsidy. Few other studies have shown such weak impact of subsidies of agricultural herbivores on natural habitats. In this study, prey spillover effects were noticeable on one group of predators (spiders), but not on the desert

arthropod community overall. More studies over a longer time period and with greater temporal resolution should be conducted to examine the ecological consequences of both prey and predator spillover effects from agricultural areas to adjacent natural habitats.

<u>Acknowledgments</u>

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Chapter I: General introduction

Introduction: defining spillover

The movement of resources and organisms across different habitats, and the consequences for population dynamics, community structure and biodiversity, constitute a central theme of landscape ecology (Holt, 1996; Polis *et al.*, 1997; Huxel *et al.*, 2004). Movement of organisms creates connectivity between different landscape components such that the dynamics of each component are not independent (Huxel *et al.*, 2004). A dramatic example of connectivity is the mass movement of organisms or resources into an adjacent habitat, which subsidizes consumers in the recipient habitat and can have far-reaching consequences for the entire food web.

Spatial subsidies are donor-controlled resources that originate in one habitat but move into another habitat, and alter the dynamics of recipient populations and communities. In some cases, spatial subsidies arrive continuously, and in other cases, subsidies may arrive in pulses (Anderson *et al.*, 2008). Pulsed resources include episodes of increased resource availability that combine low frequency (rarity), large magnitude (intensity), and short duration (see Yang *et al.*, 2008 for a review). Pulsed resources may originate *in situ* or arrive from allochthonous sources (outside the habitat). When the subsidies are pulsed and allochthonous, they are referred to as spillover (Fig. 1.1).
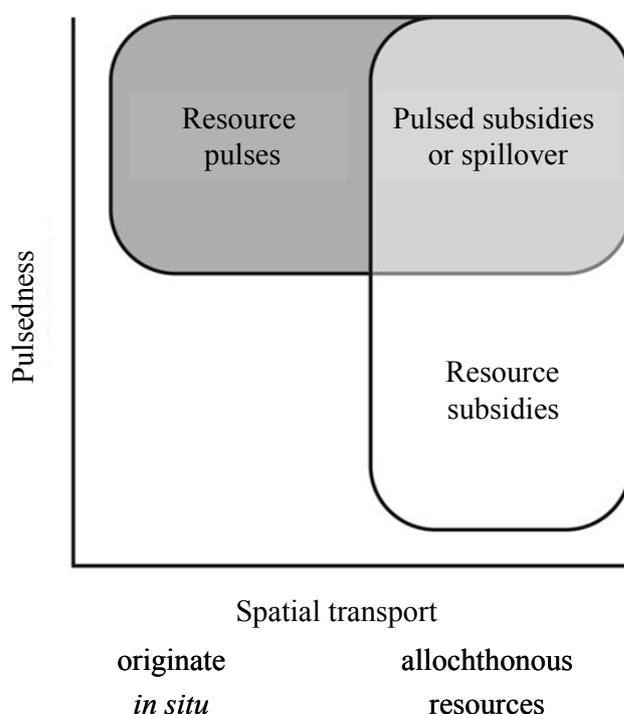
Fig. 1.1: Schematic diagram showing the relationship among resource pulses, spatial subsidies, and pulsed subsidies (spillover); after Yang *et al.*, 2008.

Allochthonous inputs can influence the energy and nutrient budget of the recipient habitats. From the perspective of local consumers in the recipient habitat, spillover can deliver ephemeral resource pulses that exceed rates of local productivity. Recipient organisms may utilize spillover resources and thereby increase their populations above the level that could be maintained by resources from the focal habitat alone (Polis *et al.*, 1997; Holt and Hochberg, 2001). These external subsidies to consumer populations can affect other trophic levels, particularly at the boundary of the two habitats (reviewed in Ries *et al.*, 2004). For instance, detrital and prey inputs produce numerical responses in their consumers (Polis *et al,.* 1997). The imported food permits consumers to overexploit the resident prey. Thus, spillover can alter the consumer-resource dynamics in the recipient habitat (Polis *et al.,* 1997; Huxel et *al.*, 2002). The effect of this spillover will depend on the food web configuration, and on the trophic roles of the mobile "donor" organisms and their recipients. These effects are generally asymmetric. It is suggested that the direction of subsidized consumer effects is from high productivity areas to low productivity habitats (Polis *et al.*, 1997).

A quick decline in the suitability of one habitat type can result in the spillover of individuals (Rand *et al.,* 2006). Resource subsidies enhance predators in the recipient habitat, and thus predators increase in abundance. Afterwards, when the subsidy is no longer available, they overexploit their natural prey. A low-productivity recipient habitat is more prone to collapse of prey than a high- productivity recipient habitat, because natural prey is not abundant (Polis *et al.*, 1997).

Spillover and agroecosystems

Agroecosystems consist of a mosaic of cropland and unmanaged habitats. The agricultural landscapes have at least three components: the agricultural field, any native or weedy vegetation that may be at the field borders, and the vegetation occurring in native or uncultivated habitat in the surrounding areas. The composition of the agricultural landscape determines the existence of alternative sites when crops are unavailable, and therefore the ability of crop herbivores to find suitable habitats and food resources (Corbett and Rosenheim, 1996).

Agroecosystems are characterized by individuals moving between crop and non-crop areas, and thus may function as a source for arthropods that spill over from agricultural to natural or semi-natural areas. The high productivity of arable fields during the season increases the density of arthropod populations, which may spill over into the surrounding landscape (Tscharntke *et al.*, 2005). The spillover of insects from agricultural to natural

habitats might be a common event, as many herbivorous agricultural arthropods are polyphagous (Symondson *et al.*, 2002).

Spillovers are likely to have important effects on the dynamics of food webs in natural habitat patches adjacent to agricultural areas. Predators may spill over from crop habitats to natural habitats, especially when they exploit prey resources in both habitats. Spillover, as a source of alternative prey, may also change interactions among predators in the natural habitats (e.g., intraguild predation; Anderson *et al.*, 2008). Crop to non-crop spillover also occurs in herbivorous insects. However, there are only a few studies where this situation has been explored (Blitzer *et al.*, 2012 for a review). Theory predicts that the direction of spillovers is from high to low productivity habitats (Holt and Hochberg, 2001). Sufficiently high predator numerical response in recipient habitats could destabilize the food web, as resident prey in low-productivity habitats could be eliminated. However, the few examples studying herbivore crop-non-crop spillover were not from hyper-arid systems, as in the case of the present study.

Spillover is a spatial process, and therefore its effects are expected to be stronger along patch edges and to diminish as distance from the agriculture edge increases. Distance from habitat edges seems to be an important factor affecting patterns of predator abundance and their impact on the natural habitats (Rand and Louda, 2006; Rand *et al.*, 2006). An increase in predator abundance near the edge could increase its impact in adjacent natural habitats as well as in agriculture systems. However, habitat edges can reduce animal movement, and therefore the spillover effects could be attenuated (Rand *et al.*, 2006). For several taxa, edge permeability is often asymmetric: immigrants cross into patches, but are less likely to leave the new patch (Fagan *et al.*, 1999). This might result in a unidirectional edge filtering and such unidirectional movement was suggested to be the pattern for several agricultural pests (Wissinger, 1997).

The spillover effects are also influenced by the temporal dynamics of resource availability. Many crop systems are ephemeral, providing resources during part of the season. Disturbances in the crops may force insects to look for refuge in neighboring natural or semi-natural areas (Tscharntke *et al.*, 2005). For instance, habitat structure of annual crop systems is remarkably ephemeral. During harvest, the habitat structure breaks down and the conditions in the crop area become unfavorable to agrobiont arthropods (Gavish-Regev *et al.*, 2008). However, this breakdown of habitat structure in annual crop systems is more predictable than disturbances in natural systems (Wissinger, 1997). In agricultural fields, herbivorous pest populations tend to reach high densities during the crop season. Pest arthropods then spill

over into nearby, unmanaged habitats. Non-crop habitats associated with agricultural fields may provide resources for arthropods when resources are no longer available in the crop habitat (Dyer and Landis, 1997).

Spillover and desert agroecosystems

Productivity and abiotic conditions of cropland and natural habitats contrast more strongly in arid than in temperate agroecosystems (Lubin, 2006; Gavish-Regev *et al*., 2008). For instance, agricultural areas are irrigated, while surrounding desert areas show water deficiency. Desert areas contain annual vegetation that is available only for a short period, and perennial plants are patchily distributed.

Desert agroecosystems provide an opportunity to study spillover between highly productive agricultural fields and extremely poor desert habitats. When the recipient habitat has low productivity, then the contrast with the high productivity habitat is large, and this influences the way the subsidies affect the recipient habitat. Cropland herbivorous arthropod subsidies are expected to have an impact on desert predators by serving as prey (Fig. 1.2). At the population level, spillover of large numbers of arthropod prey may subsidize natural enemies in the desert community, leading to a short-term decrease in predation on desert species. This is similar to apparent competition between herbivores with shared natural enemies (Holt, 1984; Rand *et al*., 2006). In the long run, however, prey subsidy may lead to a positive numerical response by desert predator populations. This, in turn, would result in greater suppression of desert prey populations, and possibly even local extinctions. At the community level, the spillover of prey may lead to the local replacement of desert species with agricultural ones, which may exhibit higher growth rates and better dispersal abilities (Snyder and Evans, 2006). Thus, community composition and diversity could change in habitats adjacent to agricultural fields, and as the latter expand in area, the fauna of natural desert habitat fragments may be altered permanently.

Desert predators

Desert scavengers   ◄ ·· — ·· —   Desert herbivores

Crop predators   ◄———   *Crop herbivores*   allochthonous inputs ▌ spillover)
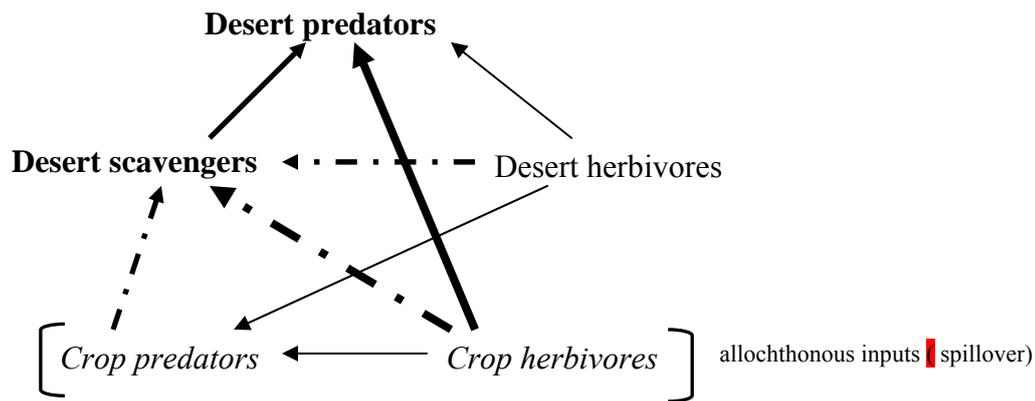
Fig 1.2: Schematic diagram of a hypothesized food web in a natural desert habitat, influenced by spillover (italics) of crop prey and predators. Solid arrows indicate pathways involving live prey; dashed arrows indicate feeding on dead prey. Arrow thickness indicates relative energy flow in the web, and bold facing is indicative of relative biomass of the guild.

The nature of the spillover impact on natural communities depends on whether agriculturally-subsidized herbivores are able to persist in desert habitats. Polyphagous crop herbivores may survive and reproduce in desert refugia after the destruction of crop habitats, and thus subsidize predators that might increase above a threshold sustainable by the local prey (Holt and Lawton, 1994; Polis *et al.*, 1997). As a consequence of the predator population buildup, intraguild interactions between the different predators in the recipient habitat might be affected. Alternatively, harsh climatic conditions could hamper the persistence of agricultural herbivores in desert habitats. Agricultural herbivore species might not be able to persist for long periods outside the crop field, subsidizing scavengers. An increase in scavenger activity could affect herbivores and predators, by preying on them or by consuming their eggs or larvae. Nonetheless, even short-term changes in prey and predator abundance may have a long lasting effect due to perturbation of predator-prey dynamics in the natural areas. How these two different scenarios influence the effect of crop arthropods on dynamics of the native habitat community depends on the spatial and temporal patterns of spillover, and on the structure of arthropod communities in the desert habitat.

Objectives and significance of this study

In this study, I investigated the occurrence of prey spillover from agricultural fields into surrounding desert habitats, and its impact on the desert arthropod community. Specifically, I looked at the spillover of crop herbivores, namely insect pests. My working hypotheses were:

1) Crop pests will move from high productivity crop fields into low productivity desert habitats; and 2) spillover of pests will affect the recipient desert community.

Specifically, the questions I wanted to answer were:

1. Is there pest spillover from crops into adjacent desert habitat? *If so,* does it decrease along a gradient of increasing distance from agricultural fields?

2. Assuming that there is spillover, can pests reproduce and survive in desert habitats? This is relevant, as pests can subsidize either predators if they survive and reproduce, or scavengers if they do not (Fig. 1.2).

3. Are pests consumed by desert predators, and do they influence predator intraguild interactions?

4. Are there changes in species composition of the desert arthropod community as a consequence of pest spillover, and does these effects change with distance from the agricultural area?

Agroecosystems, one of the dominant managed habitats in many landscapes, are generally more productive than the surrounding matrix because of high human inputs (fertilization, irrigation, etc), but tend to be unstable due to routine disruptions associated with cultivation. Accumulating evidence indicates that an increase in the area used for crop production is associated with reduced landscape heterogeneity and species diversity (reviewed in Benton *et al.* 2003). However, the effects of agricultural habitats on processes occurring in natural areas are poorly understood. There is little empirical evidence of the potential impact of the agricultural prey spillover on natural communities, and none on the effect of spillover in hyper -arid landscapes. This is despite abundant studies on the movement of arthropods in the opposite direction (Rand and Louda, 2006; Rand *et al.*, 2006; Blitzer *et al.*, 2012). This study provides a direct measurement of the impact of agriculture on the desert arthropod community.

General description of the research

I tested my working hypothesis by studying the abundance and distribution of arthropods from agricultural areas into adjacent desert habitats and their interactions with natural-habitat species. First, I monitored pest occurrence in desert habitats at increasing distances from agricultural areas and ornamental plants in villages near agricultural areas over the crop cycle.

Second, I tested pest ability to persist and reproduce on desert plants. Third, I conducted lab experiments to investigate interactions between pests and desert predators, and to investigate some of the pathways by which spillover of pests might influence the desert

arthropod community. Finally, I sampled the desert arthropod communities along a gradient of increasing distance from agricultural fields.

General description of materials and methods

A. The study area: the Arava agroecosystem

The study took place in the hyper-arid Arava Valley, a relatively isolated region in southern Israel, characterized by hot summers with temperatures reaching more than 40 $^{\rm o}$C, and a relative humidity of less than 20%. During this study, temperatures were higher than 40$^{\rm o}$C on an average of 40 days each year. The maximum registered air temperature was 45.7$^{\rm o}$C, and maximal ground level temperature was 56.7 $^{\rm o}$C. In winter (January and February), the average daily temperature was 12–14$^{\rm o}$C. Average annual rainfall in the area is 25 mm, all during winter.

Moderate winter temperatures combined with intense solar radiation render the region ideal for the production of winter vegetables, herbs and cut flowers mostly for export. Yet, the intensive farming occupies only about 3% of the total hectares of the Central and Northern Arava region (Central-and Northern-Arava Research and Development Center). Crops are planted in screen houses, high tunnels open at both ends, under shade nets (without walls), or in open fields. The arable land in the study area is surrounded by desert habitat, forming productive "islands" in a desert matrix.

Crop plants are grown under conditions of intense irrigation and fertilization. As a result, the agricultural land is extremely productive, sustaining vegetative biomass thousands of times greater than that in the adjacent desert habitat. The growing season extends from August to early June, and at this point all plant material is removed from cultivated fields. Thus, a mandatory crop-free "sanitation" period is imposed in the Arava from mid-June to the beginning of August, in order to reduce buildup of pest populations. This practice mandates ending the growing season in June and cleaning the crop fields by removing all the vegetation, leaving the fields clean of any plant material before planting again in August (Hilje *et al.,* 2001).

Based on crop phenology, the annual crop cycle can be divided into four periods (hereafter, agricultural phenological stages). The first agricultural phenological stage is the planting period, from the beginning of August until mid-September. During this stage, the plants are transplanted and the first flowers appear. The second stage, the growing stage, takes place from mid-September until the end of April. The third agricultural phenological stage, the pre-sanitation stage, extends from the beginning of May until mid-June. During this

period, farmers reduce care of the agricultural fields, and the crop biomass is removed. This stage is followed by the sanitation period previously described.

During this study, the mean area occupied by crops was about 2,400 hectares per season (Central and Northern Arava Research and Development Center). Sweet pepper *Capsicum annuum* occupied 1560 ha (65%), melon *Cucumis melo* took 321 ha (13.5%), 155 ha were planted with watermelon *Citrullus lanatus*, while cherry tomato and other tomatoes, *Solanum lycopersicum*, took 63.6 ha and 97 ha respectively (2.7% and 4%, respectively). The rest of the cultivated land (187 ha, 9 %) was planted with other crops.

The most numerous herbivores on crop plants in the study area are thrips, whiteflies, aphids, and tetranychid and tarsonemid mites. *Frankliniella occidentalis* (western flower thrips) is the most abundant thrips species (95% of the thrips species), occurring on 19 out of 22 monitored crops (Chyzik and Ucko, 2002). Western flower thrips can be found on plants throughout the growing season, but dispersal activity has been detected primarily in late spring (late April and May) and fall (September) (Chyzik and Ucko, 2002), corresponding to plant senescence and planting times, respectively. They can travel long distances on wind currents (Mound, 1983).

Bemisia tabaci is the dominant whitefly species on many crops in the area, including melon, basil (*Ocimum basilicum*) (Ucko *et al.,* 1998), eggplant (*Solanum melongena),* sweet pepper*,* cucumber (*Cucumis sativus*) and tomatoes*.* Even though whiteflies are poor flyers (Byrne and Bellows 1991), they have been captured in the northern Arava 20 km away from the nearest agricultural fields (Ucko *et al.,* 1998).

Except for a few unpublished observations, no systematic sampling of arthropod predators (e.g., spiders) has been conducted in desert areas near agricultural fields in the Arava.

B. Materials and methods
B.1. Monitoring the pests

To study the distribution and abundance of pests away from the crops as the agricultural season progressed, sticky traps were placed in three different habitat types: (a) near desert: desert habitat 50 m away from greenhouse areas; (b) agricultural blocks: in the middle of greenhouse areas (but outside the greenhouses); and (c) villages: in the center of villages adjacent to the agricultural fields. Also, in order to compare the abundance of pests in desert habitats close to agricultural areas and in desert habitats distant from agricultural areas as the agricultural season progressed, sticky traps were placed in four desert habitats 3000 to 7000 m (average distance 5500 m) from the nearest greenhouse.

B.2. Testing persistence and reproduction of pests on desert plants

Persistence and reproduction of agricultural herbivores on desert plants were determined by caging adult insects on desert plant species and recording the ability of the adults to survive, deposit eggs and produce viable offspring. The host plants used for the experiment were selected based on an earlier arthropod sampling in the study area. I chose host plants in which whiteflies or thrips were found during this sampling (see below, *B.4*). Twenty one plants of each of these test species, located in natural desert area, were caged with whitefly- and thrips-proof tested mesh screen. The plants were seeded with lab-reared whiteflies or thrips. On three different dates, seven monitored plants of each species were taken to the lab in their sealed cages and inspected thoroughly for the presence of all life stages of the seeded pest, as well as other arthropods.

B.3. Investigating interactions between pests and desert predators

Short-term laboratory experiments in enclosures were used in order to (i) test whether desert predators would consume agricultural pests, (ii) investigate the resulting intraguild interactions between desert predators when offered agricultural pests, and (iii) record changes in feeding behavior in the presence of a competitor. The desert predators chosen for this experiment were two spider species: *Thanatus* sp. and *Phlegra amitai* (Fam. Philodromidae and Salticidae respectively). These two spider species were chosen based on their abundance in the earlier arthropod sampling in the study area. The two predators were offered lab -reared whiteflies, thrips and fruit flies in different scenarios: one predator was put alone in the enclosure and offered one prey type or both prey simultaneously, or both predators were placed together and offered one prey type. The enclosures were observed between one to two and a half hours, and the number of prey consumed and the intraguild interactions were recorded. Predators were weighed at the beginning and again at the end of the experiment.

B.4. Sampling desert arthropod communities at increasing distances from the agricultural areas

Patches of desert vegetation were sampled for the presence of desert and agricultural arthropods, at increasing distances from the greenhouses. Arthropods were collected on and under desert plants by visual searching, and using a hand-held suction device. A total of 42 desert perennial and annual plants (when available) were sampled every two months between March 2008 and July 2009, totaling 9 sampling events. I sampled along four transects set in three different agricultural areas. Two of these four transects were upwind of the crop fields,

and two of them were downwind. The sampling was done at 0, 5, 50, 100, 300 and 700 m from the field edges. Four additional sampling points were set between 3000 and 7000 m from the crop (average 5500 m).

Chapter II: Spillover of agricultural pests into adjacent desert habitats

Introduction

Movement of organisms creates connectivity between different landscape components such that the dynamics of each component are not independent of one another (Huxel *et al.*, 2004). Resources that originate in one habitat and move into another habitat may alter the dynamics of recipient populations and communities (Polis *et al.*, 1997). These allochthonous resources can arrive continuously or in pulses, and may subsidize consumers in the recipient habitat (Anderson *et al.,* 2008). One example of resource pulses is that of population outbreaks. Outbreaks may create resource pulses for consumers, affecting their response at the individual level, at the population level, or indirectly at the community level (Yang *et al.*, 2008). For instance, the increase in insect abundance could result in spillover of the super-abundant insects.

Spillover of insects from agricultural to natural habitats might be a common event, as many herbivorous agricultural arthropods are polyphagous (Symondson *et al.*, 2002). Modern agricultural landscapes are highly productive, fertilized, and irrigated areas, where pest outbreaks represent abundant, but ephemeral, resources for predators (Rand and Louda, 2006). The high productivity of arable fields during the season increases the density of insect pest populations, and might result in the export of organisms to the surrounding landscape (Tscharntke *et al.*, 2005). When the difference in productivity between agricultural and natural habitats is large, the natural habitat becomes a sink for the influx of arthropods coming from the agricultural fields (Duelli *et al.,* 1990).

Many cropping systems are ephemeral, providing abundant resources during part of the season. Disturbances may force insects to seek refuge in nearby natural or semi-natural areas (Tscharntke *et al.,* 2005, Rand and Louda, 2006; Rand *et al.,* 2006,). After harvesting, crop habitats are no longer available, and thus non-crop habitats associated with agricultural fields may provide resources for arthropods (Dyer and Landis, 1997). Pest arthropods and their enemies then spill over into nearby, unmanaged habitats. Some pest populations could persist and even increase in numbers in non-crop habitats, when suitable crops are unavailable (Kennedy and Storer, 2000).

Productivity and abiotic conditions of agricultural fields and natural habitats contrast more strongly in arid than in temperate agroecosystems (Lubin, 2006; Gavish-Regev *et al.,* 2008). Arable land in desert agroecosystems forms productive "islands" in a desert matrix: agricultural areas are irrigated while surrounding desert areas are water deficient, and the contrast between agricultural areas and adjacent desert habitats becomes larger as the crop grows (Gavish-Regev *et al.,* 2008). The contrast between agricultural fields and desert

habitats may increase pest abundance in agricultural fields, as well as the intensity of spillover of the pests to the surrounding desert habitat.

This study took place in the Arava agroecosystem in the southeastern part of Israel, where crops are grown over 10 months of the year, and there is a mandatory 'sanitation period' between crop seasons, when no crops are grown. During this study, more than 60% of the agricultural fields were planted with pepper plants (Central and Northern Arava Research and Development Center). All pepper plants were planted in screen-houses. This plant is a suitable host for several pest species, primarily thrips and whiteflies. Both pests are known to occur in the Arava pepper fields, and could potentially spill over into the desert habitat and other surrounding non-crop areas, where they may find refuge until the next crop season. In the present study, I investigated whether the two crop pests spill over from agricultural areas into the adjacent desert habitat and into other non-crop habitats, by measuring abundances of pest species in non-crop habitats over the agricultural season.

I predicted that i) spillover of pests from high-productivity habitat to low-productivity habitat will occur when crop plants senesce, i.e. during the presanitation agricultural stage; ii) highest pest abundances will be found in habitats closer to the agricultural areas, and numbers will decrease with distance from the crop; and iii) pests will be found in non-crop habitats throughout the non-crop (sanitation) stage.

Materials and methods

Study Area

The study took place in the hyper-arid Arava Valley in southern Israel (see detailed description in chapter I).

Sampling methods

Yellow sticky traps were used to monitor two agricultural pest herbivores, whitefly *Bemisia tabaci* (hereafter whiteflies) and the western flower thrips *Frankliniella occidentalis* (hereafter thrips). The traps were constructed of PVC pipes (50 cm tall and 10 cm diameter), with a 15 cm-wide yellow painted strip at the upper end. During each trapping period, the PVC pipes were set vertically into the ground and the yellow section of the trap was covered with a transparent sheet (modifications after Ben-Yakir *et al.,* 2006) that was coated with Rimifoot glue (Rimi Chemicals Co. Ltd, Petach Tikva, Israel). The sticky sheets were collected and brought to the lab, where trapped insects were identified and counted with the aid of a dissecting microscope. Monitoring the insects over the agricultural season provided information on the distribution and abundance of the pests in different habitat types. From this information, I inferred movement of the pests from agricultural areas into surrounding habitats.

A. Distribution and abundance of pests

Traps were placed in three different habitat types: (a) near desert: desert habitat 50 m away from greenhouse areas; (b) agricultural fields: in alleyways between the greenhouses; and (c) villages: in the center of villages adjacent to the agricultural fields. Ornamental plants in villages are known to be hosts for the two pest species (Ucko *et al.* 1998, Chyzik *et al.,* 1999), and may thus be refuges for the pests when crops are not available during the sanitation period.

Sticky traps were set for three consecutive days every two weeks, and more frequently at the end of the agricultural season to capture transient dispersal events, totaling 59 trapping sessions in the three habitat types between July 2006 and November 2008. Three additional sampling sessions took place between May and June 2009. During each sampling session, eighteen traps were placed between greenhouses in three different agricultural areas (9 in each), twenty in their adjacent natural habitats (10 in each), and twelve sticky traps in three villages (4 in each), totaling 50 traps set simultaneously in the three habitat types.

B. Pest abundance in desert habitats

B.1. Pests in desert sites near and distant from agricultural fields

I compared the abundance of the pests in desert habitats close to agricultural areas and in desert habitats distant from agricultural areas as the agricultural season progressed. At the same time twenty traps were placed 50 m from the nearest greenhouse (as described in section *A*), sixteen traps were placed in four desert habitats between 3000 to 7000 m from the nearest greenhouse (hereafter "far desert" habitat). Trapping sessions were conducted as described above (section *A*). A total of 44 sampling sessions took place between March 2007 and November 2008. Three additional sampling sessions were added during May and June 2009.

B.2. Pest abundance along a distance gradient from agriculture

The effect of the trap position with respect to wind direction, and the effect of increasing distance from the agricultural fields on the abundance of the two pests were tested by setting sticky traps at six increasing distances from agricultural fields into the nearby desert. Four line transects were established from the three different agricultural areas. Two of these transects were upwind of the crop fields in two agricultural areas, and two were downwind in the third area (prevailing winds in the region are from the NW). These three agricultural areas were separated from each other between 8.5 to 12.5 km. On each transect, the traps were set at 0, 5, 50, 100, 300 and 700 m from the field edge. Sticky traps were set for three consecutive days every two weeks, and more frequently at the end of the agricultural season to capture transient dispersal events. A total of 18 sampling sessions took place

between February 2008 and November 2008. Three additional sampling sessions were added during May and June 2009.

Statistical analysis

For the analysis, the sampling sessions were grouped into the four agricultural phenological stages described in chapter I (planting, growing, pre-sanitation and sanitation). The effect of habitat type (agricultural area in between greenhouses, near desert, and villages) and agricultural phenological stage on the abundance of each herbivorous pest was tested using multivariate analysis of variance (MANOVA). Repeated-measures ANOVA could not be used, as Mauchly's test indicated that the assumption of sphericity (equality of the variances of the differences between all combinations of related groups (levels) was not met (Lehman *et al.,* 2005, Appendix 2.1.A). Data were not normally distributed, even after applying standard data transformation techniques (Zar, 1999). The data were calculated as mean per trap per day across all samples in each agricultural phenological stage. Pest abundance in each of the four agricultural phenological stages was the response variable. The same procedure was used to compare the abundance of whiteflies and thrips in desert habitats near and far from agricultural fields (Appendix 2.1.B). Far desert counts of whiteflies and thrips were compared to the counts trapped at near desert habitats (using the near desert data from section *A*).

To test whether spillover of the two pests occurs over a short time scale, when crop plants senesce during the pre-sanitation stage, I constructed a correlation matrix of pest abundance per trap between the screen houses, the near desert habitat, and in villages for this stage. Pest abundance was log transformed as $X'= log (X+1)$ to meet analysis requirements (Zar, 1999).

The effect of trap position with respect to direction of prevailing winds on the abundance of each of the pest species was tested using a two–way ANOVA (wind direction and agricultural phenological stage). The effect of wind was expected to be more pronounced near the crop, where the number of trapped insects is high; therefore, only those traps set at 50 m from agricultural edges were considered for this analysis. All abundance data were calculated as mean per trap per day across all samples in each agricultural phenological stage. Data were log transformed as $X'= log (X+1)$ to meet analysis requirements (Zar, 1999).

To test the effect of increasing distance from the agricultural fields and agricultural phenological stage on the abundance of each of the pests, a two–way ANOVA (distance and agricultural phenological stage) was used. All abundance data were calculated as mean per trap per day across all samples in each agricultural phenological stage. Data were log transformed as $X'= log (X+1)$ to meet analysis requirements (Zar, 1999) In order to

determine whether the relationship between increasing distance from the agricultural fields and pest abundance was monotonically decreasing, or if the relationship was nonlinear, a quadratic term was included in the regression model. Afterwards, I examined the improvement in fit using a quadratic term with Akaike's Information Criterion corrected for small sample size (AICc).

Results

A. Distribution and abundance of pests

Habitat and agricultural phenological stage interacted significantly in their effects on the number of trapped insects of both species (Table 2.1).

The population dynamics differed for the two pest species (Fig.2.1). Whitefly populations peaked during the pre-sanitation stage in all three habitats. During the planting stage, whiteflies were significantly more abundant in the agricultural areas than in the desert or village habitats, which did not differ statistically. A similar pattern was detected during the pre-sanitation stage (Fig 2.1A). During the growing stage, more whiteflies were found in the agricultural areas than in other habitats. During the pre-sanitation stage, there was a significant pair-wise correlation between whitefly abundance in agricultural areas and near desert ($r= 0.423$; $p= 0.005$), but no correlation between the agricultural areas and villages ($r= -0.239$; $p= 0.198$).

Overall, the number of thrips trapped in sticky traps was low. Their populations peaked in the agricultural fields during the growing stage. During the sanitation stage, they were significantly more abundant in the villages than in the desert habitat. There was no difference in thrips abundance during the pre-sanitation and planting periods in the three habitats types (Fig. 2.1B). During the sanitation stage, there were no significant pair-wise correlations between thrips abundance in near desert and agricultural areas, nor between villages and agricultural areas ($r= -0.061$; $p=0.554$ and $r= -0.041$; $p=0.708$, respectively).

Table 2.1: Multivariate analysis of variance (MANOVA) for (A) whitefly and (B) thrips abundance, monitored over four agricultural phenological stages in three different habitat types. An exact F is calculated for each factor, and an approximate F is given for the interaction term. Significant differences are shown in bold ($p< 0.05$).

(A) Whitefly

Source of variation	df	Test	F	p
Habitat type	2,44	F	**6.48**	**0.003**
Agricultural stage	3,42	F	**3.4**	**0.026**
Agricultural stage* habitat type	6,84	Wilk's Lamda	**3.26**	**0.006**

(B) Thrips

Source of variation	df	Test	F	p
Habitat type	2,44	F	**4.9**	**0.012**
Agricultural stage	3,42	F	**18.74**	**<0.001**
Agricultural stage* habitat type	6,84	Wilk's Lamda	**4.3**	**<0.001**
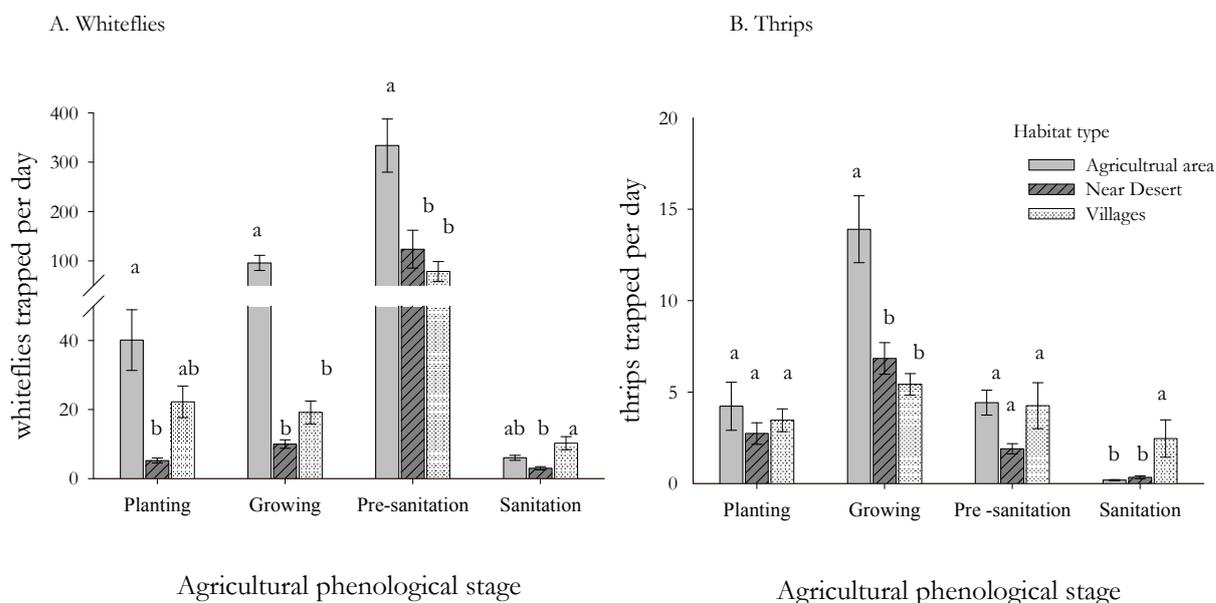
Fig. 2.1: Effect of habitat type and agricultural phenological stage on trapped whiteflies (A) and thrips (B) (Mean ±SE). Bars with same letters do not differ significantly (Tukey-Kramer multiple comparisons of means within each agricultural phenological stage).

B. Pest abundance in desert habitats

B.1. Pests in desert sites near and distant from agricultural fields

There was a significant interaction between distance of desert habitat and agricultural phenological stage for both whitefly and thrips populations. In the desert sites, the effect of distance from agricultural fields on whitefly populations increased as the agricultural season progressed (Fig. 2.2A; Table 2.2A). In all phenological stages, however, significantly more

whiteflies were found in the near desert habitat than in the far desert habitat. Thrips were significantly more abundant near the agricultural fields than at the distant sites only during the growing stage (Fig. 2.2B; Table 2.2B). During the planting, pre-sanitation, and sanitation stages, there was no statistically significant difference in the number of thrips found in the desert habitats near or far from the crop areas. This may be due to the low numbers of trapped thrips.

Table 2.2: Multivariate analysis of variance (MANOVA) for (A) whitefly and (B) thrips abundance, monitored over four agricultural phenological stages in desert habitats near and far from greenhouses. An exact F is calculated for each factor. Significant differences are shown in bold (p< 0.05).

(A) Whitefly

Source of variation	df	Test	Value	F	p
Habitat type	2,44	F	0.147	**6.04**	**0.018**
Agricultural stage	3,42	F	3.212	**41.78**	**<0.001**
Agricultural stage* habitat type	6,84	F	0.4966	**6.45**	**0.001**

(B) Thrips

Source of variation	df	Test	Value	F	p
Habitat type	2,44	F	0.076	31. 46	0.084
Agricultural stage	3,42	F	2.678	**34.82**	**<0.001**
Agricultural stage* habitat type	6,84	F	0.155	**2.02**	**0.013**
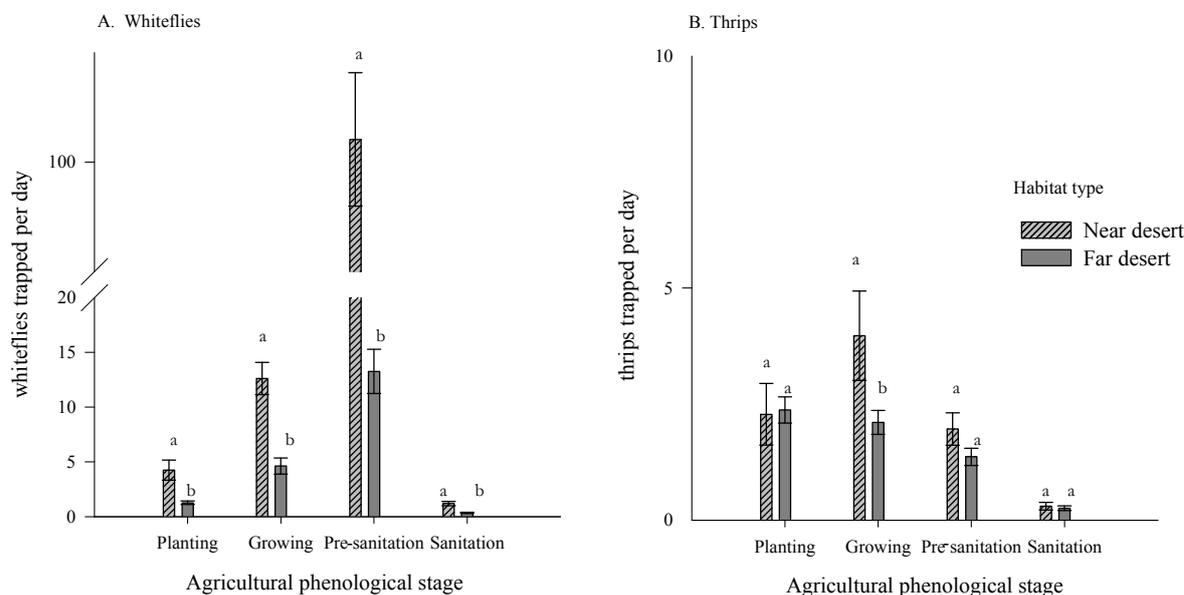
Fig 2.2: Effect of distance from desert habitat to greenhouses and agricultural phenological

stages on the abundance of whiteflies (A) and thrips (B) (Mean ±SE). Bars with same letters do not differ significantly (t- test comparisons of means within each agricultural stage).

B.2. Pest abundance along a distance gradient from agriculture

Trap position with respect to the prevailing winds did not influence whiteflies or thrips trapped 50 m from agricultural fields, and there was no significant interaction with phenological stage (Table 2.3).

Table 2.3: Two- way analyses of variance to test the effects of the trap position with respect to the prevailing winds and phenological stages on the log-transformed abundance of whiteflies (A) and thrips (B) 50 m from the agricultural fields. Significant differences are shown in bold (p< 0.05).

(A) Whitefly

Source of variation	df	Sum of Squares	F	p
Trap position	1	0.068	0.312	0.578
Agricultural stage	3	22.77	**34.95**	**<0.001**
Agricultural stage*trap position	3	0.891	1.367	0.259

(B) Thrips

Source of variation	df	Sum of Squares	F	p
Trap position	1	0.006	0.061	0.804
Agricultural stage	3	1.765	**6.263**	**<0.001**
Agricultural stage*trap position	3	0.386	1.367	0.259

Adding a quadratic term improved the fit of the relationship between whitefly abundance and distance from the agricultural fields (Table 2.4) for all agricultural phenological stages. Distance had a significant effect on whitefly abundance during all four agricultural phenological stages (for planting stage, r^2=0.19; p = 0.008; for growing stage, r^2=0.13; p < 0.001; for pre-sanitation stage, r^2=0.22; p = 0.016 and for sanitation stage, r^2=0.19; p <0.001). Whitefly numbers decreased with distance, but showed a significant slight increase at the most distant traps (Fig. 2.3, Table 2.5A). There was no significant interaction between the distance of traps in the desert habitat and the agricultural phenological stage (Table 2.5A).

Adding a quadratic term to analyze thrips abundance improved the fit of the model during the planting and sanitation stages (Table 2.4). There is a significant increase in thrips abundance with increasing distance from the fields (Table 2.5B). However, distance had a significant effect on thrips abundance only during the sanitation stage (r^2= 0.13; p<0.001; Fig. 2.4)**.**

Table 2.4: AICc values of linear and quadratic models to study the effect of increasing distance from the agricultural fields on the log-transformed abundance of pests. I examined the improvement in fit using a quadratic term with Akaike's Information Criterion (AICc). The better model is the one with the lower AICc value.

Agricultural phenological stage	Whiteflies AICc		Thrips AICc	
	linear	quadratic	linear	quadratic
Planting	132.919	128.593	37.123	35.647
Growing	352.366	341.768	202.849	203.581
Pre-sanitation	227.4	219.357	109.77	111.871
Sanitation	5.459	2.555	-16.078	-13.909

Table 2.5: Two- way analysis of variance to test the effects of increasing distance from the greenhouses and phenological stages on the log-transformed abundance of whiteflies (A) and thrips (B). Significant differences are shown in bold (p< 0.05).

(A) Whitefly

Source of variation	df	Sum of Squares	F	P
Distance	1	35.003	**10.652**	**0.001**
Agricultural stage	3	580.581	**58.896**	**<0.001**
Agricultural stage* distance	3	8.163	0.828	0.481

(B) Thrips

Source of variation	df	Sum of Squares	F	P
Distance	1	0.117	0.967	0.326
Agricultural stage	3	9.57	**26.38**	**<0.001**
Agricultural stage* distance	3	0.758	2.091	0.107
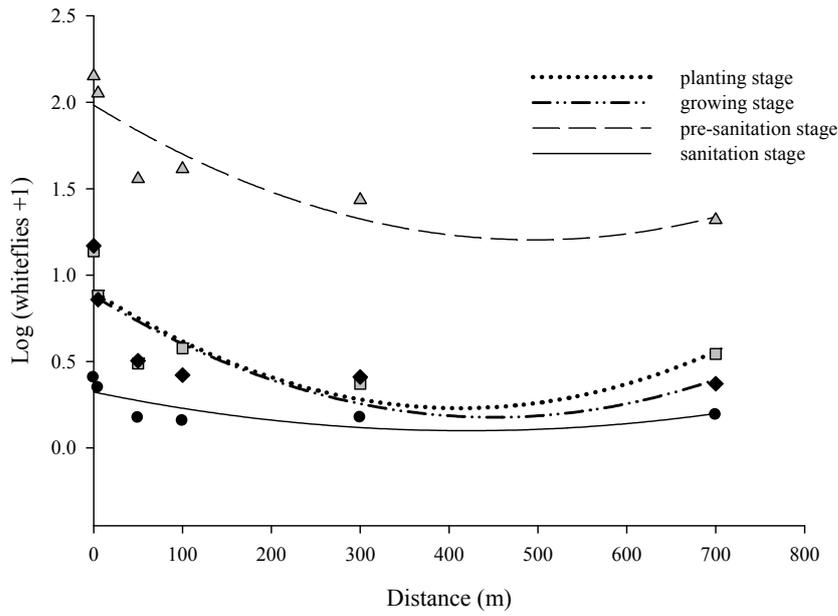
Fig 2.3: Regression of log-transformed abundance of whiteflies in desert habitat (non-linear model) over increasing distance from agricultural fields, at four agricultural phenological stages:

☐ planting   ◆ growing   △ pre-sanitation   ● sanitation
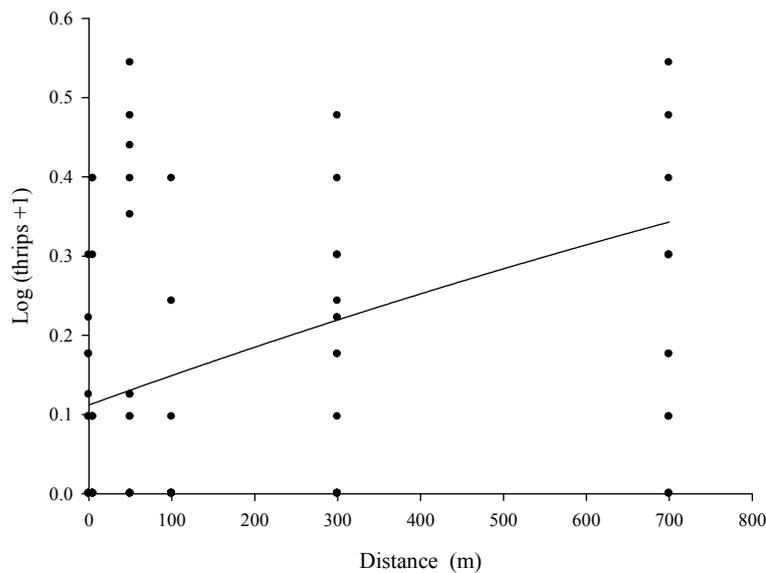
Fig 2.4: Regression of log-transformed abundance of thrips in desert habitat (non-linear model) over increasing distance from agricultural fields, at the sanitation phenological stage.

Discussion

The abundance of both pest species was affected by the habitat type and by the agricultural phenological stage. However, the population dynamics of the two pest species showed different patterns.

Whitefly populations peaked during the pre-sanitation stage. During this period, the mean number of whiteflies trapped in the near desert habitat was 10 times greater than during the growing stage, while in the far desert habitat, the increase was only 3 times greater than in the growing stage. This increase in whitefly abundance suggests that whiteflies move from agricultural fields, reaching mainly desert habitats relatively close to agricultural fields. The mean number of whiteflies trapped insides villages was 4.5 times greater during the pre-sanitation stage compared to the growing stage. This correlative evidence suggests that whiteflies were spilling over into the adjacent desert habitat as well as into villages located approximately 3000 m from the agricultural areas. The correlation between whitefly abundance in agricultural areas and near desert habitats during the stage when crop plants begin to senesce also supports the hypothesis that this pest spills over from the crop into the nearby desert.

During the sanitation stage, few whiteflies were trapped in all habitat types, suggesting that whiteflies cannot survive as adults in the hot and dry summer of the region. Studies of whitefly physiology have shown that they have several means of protection from heat damage in extreme environments: feeding on the abaxial part of the leaves, employing heat-shock proteins, and raising the level of sorbitol in their hemolymph (Gerling *et al.,* 2001). Under laboratory conditions, Cui *et al.* (2008) found that less than 30% of whitefly offspring developed into adults at temperatures of 43°C and 45°C, and that a source of food supply and an acclimation period are required for the whiteflies to adjust to these extreme conditions. During the course of the present study, the average maximum air temperature was 40 ºC, and no crops were available during the sanitation stage. During this period, only ornamental plants in the villages and patches of weed plants among the greenhouses could act as hosts for whiteflies. Ucko *et al.* (2002) suggested that the presence of whitefly populations in the region during summer could be a source of crop re-infestation.

Whiteflies reproduce continuously, and maintain populations by moving between crop and non-crop host plants during the year in climatically distinct areas (Naranjo *et al.*, 2007, Naveed *et al.*, 2007). Since whiteflies do not diapause, they are always associated with their host plants. Thus, when their preferred habitat (i.e. crop fields) is no longer available, whiteflies spill over into adjacent habitats, searching for suitable plant hosts. In the next chapter, I will present the results of field experiments showing that whiteflies could persist

and reproduced on some of the desert plants in the study area. In addition, weed patches close to agricultural areas may be attractive to whiteflies.

Wind direction did not have an effect on the number of whiteflies trapped. Yet whitefly abundance decreased with increasing distance from agricultural fields, and this decline in abundance was seen in all agricultural phenological stages. Whiteflies are capable of horizontally oriented flight as a response to an attractive visual stimulus (Isaacs *et al.*, 1999). For instance, whiteflies may be attracted to weed plants. In this study, weed plants were found close to the greenhouses (personal observation). The small, but statistically significant increase in whitefly activity at the greatest distance is difficult to explain.

Thrips were trapped in low numbers during all agricultural stages. Their populations peaked only during the growing stage of the crop, and more thrips were found in desert habitats near the crop areas than far from them. This increase in thrips abundance suggests the existence of spillover from agricultural fields into adjacent desert. During the remaining agricultural phenological stages, the number of thrips trapped in natural desert habitats near and far from crop areas did not differ statistically.

The peak in thrips abundance during the growing stage was not reflected in increased thrips abundance in the villages. Their abundance in non-agricultural areas seems to be independent of their population dynamics close to agricultural areas, in contrast to whitefly dynamics. This is consistent with the lack of any positive correlation between abundance of thrips in agricultural areas and in the adjacent non-crop habitats during the pre-sanitation stage.

Thrips abundance was not affected by trap distance to agricultural areas or by wind direction. These results may be explained by the dispersal pattern of thrips. They can travel long distances on wind currents (Mound, 1983), and their spread is further enhanced by the fact that they are polyphagous and can feed on numerous plant species. As in the case of the whiteflies, thrips could persist and reproduce on some desert plants. The thrips' ability to persist on some desert plants will be discussed in the next chapter. Thrips seem to be present and able to persist in all habitat types in the study area. There are numerous reports of decline in thrips abundance as weather conditions become hotter. For instance, Contreras *et al.* (1998*)* and Kitamura *et al.* (1999) suggested that 40°C is the limit for thrips development. However, they may be able to overcome the harsh summer conditions during the sanitation period by inhabiting plants in the villages. Even though they are found in low numbers, their life history characteristics may allow them to rapidly rebuild new populations from small founder colonies. Thrips might also be estivating in crop land, or they may arrive quickly from outside the crops (Chyzik and Ucko, 2002). However, it is important to note that the low trapping

levels of thrips probably did not provide high enough statistical power to detect treatment effects.

A few studies have shown herbivorous crop to non-crop spillover (Blitzer *et al.*, 2012 for a review). These few examples however, were not from arid agroecosystems, as in the case of the present study. In this chapter, I showed that both pest species spill over from agricultural areas into surrounding non-crop areas. While their distribution patterns differ, both species are moving into the desert habitats and into villages close to the agricultural areas. These two habitats are likely to play a role in the pests' persistence, especially during the mandatory sanitation period, by providing alternative plant hosts.

Appendix 2.1:

A. Mauchly's test of sphericity for the effect of habitat type (alleyways between greenhouses, desert, and villages) and agricultural phenological stages (planting, growing, pre-sanitation, and sanitation) on the abundance of whitefly and thrips pests. Results indicate that the assumption of sphericity has not been met for either whiteflies or thrips.

	Whiteflies	Thrips
Mauchly Criterion	0.004	0.085
χ^2	235.551	105.424
p	<0.001	<0.001

B. Mauchly's test of sphericity for the effect of habitat type (near and far desert) and agricultural phenological stages (planting, growing, pre-sanitation, and sanition) on the abundance of whitefly and thrips pests. Results indicate that the assumption of sphericity was not met for either whiteflies or thrips.

	Whiteflies	Thrips
Mauchly Criterion	$6.95E^6$	0.16
χ^2	388.614	59.19
p	<0.001	<0.001

Chapter III: Testing pest persistence and reproduction on desert plants

Introduction

Agroecosystems may be a source of arthropods that spill over to natural or semi-natural areas. The high productivity of arable fields during the cropping season increases the density of populations, and might result in an export of organisms into the surrounding landscape (Tscharntke *et al.,* 2005). This spillover phenomenon is likely to have important effects on the dynamics of food webs in natural habitat patches.

Cropland arthropod subsidies are expected to have an impact on desert predators by providing prey. The impact of agricultural herbivore spillover on natural desert communities depends in part on whether these herbivores are able to persist in desert habitats, or fail to persist and then are scavenged. Polyphagous crop arthropods may survive and reproduce in desert refugia after the destruction of crop habitats. The persistence of an agricultural pest may have negative or positive consequences for native herbivores. Input of persistent prey could increase the abundance and reproductive output of desert predators. These predators might increase above a threshold sustainable by the local prey, and may overexploit it and even cause local extinction (Holt and Lawton, 1994; Polis *et al*., 1997). Alternatively, the presence of alternative prey can release the native species from predation ("dilution effect") (Holt and Hochberg, 2001). Harsh climatic conditions could hamper the persistence of agricultural arthropods in desert habitats. Agricultural pests might not be able to survive for long periods outside the crop habitat. Nonetheless, even short-term changes in prey abundance may have a long-lasting effect due to perturbation of predator-prey dynamics in the natural areas. Also, non-persisting prey will subsidize scavenger species. An increase in scavenger activity could affect herbivores, by preying on their eggs or larvae, and predators that feed on these scavengers.

In the previous chapter, I showed that pest species can be found in habitats adjacent to agricultural fields. These habitats may provide alternative plant hosts when the agricultural habitat is destroyed. I therefore tested whether whitefly and thrips subsidies from crop fields can establish themselves on local desert plants.

Materials and methods

Study area

This experiment took place in the Arava agroecosystem, (see description in Chapter I). The ability of agricultural herbivores to persist and reproduce on desert plants was determined in the spring, when most colonization of desert plants occurs.

Pest species

The pest species used for this experiment were *Bemisia tabaci* (whitefly) and *Frankliniella occidentalis* (thrips). Both species were reared at the Dead Sea and Arava Science Center, Central Arava Branch. The whitefly colony was obtained from Dr. Shai Morin's lab (The Hebrew University of Jerusalem, Rehovot campus, Israel). Whiteflies were reared on cotton plants (*Gossypium hirsutum*) in an insect-proof cage. Insects were maintained at 22 °C under natural light.

The thrips colony was started from individuals supplied by Dr. David Ben-Yakir's laboratory (Agricultural Research Organization, Volcani Center, Ministry of Agriculture and Rural Development, Israel). Thrips were reared on green bean (*Phaseolus vulgaris*) pods in a incubator (FOC 225I VELP Scientifica) at 25 °C, photoperiod of L:D 12:12 (modifications after Steiner *et al.* 1998). A flat container with 1000 cc of water was placed in the incubator to keep humidity constant.

Host plants

The plants used for the experiment were selected based on earlier sampling of arthropods in the study area. This sampling took place from February 2008 to December 2008, on 36 desert plant species (Appendix 3.1). Whiteflies were found on six plant species, while thrips were found in 19. From these plants, I selected two annual and two perennial species to be tested as host plants. Annual plants are available only during a short period, thus during the rest of year only perennial plants could be hosts of the spillover pests. *Malva parviflora* (Malvaceae), *Diplotaxis acris* (Brassicaceae), *Zygophyllum dumosum* (Zygophyllaceae) and *Ochradenus baccatus* (Resedaceae) were chosen as potential hosts for the whiteflies. During the sampling, whiteflies were found on 20% of *M. parviflora*, 24% of *D. acris*, 16% of *Z. dumosum* and 15% of *O. baccatus* sampled individuals.

M. parviflora, Chenopodium murale (Amaranthaceae), *Z. dumosum* and *Haloxylon persicum* (Amaranthaceae) were chosen as potential hosts for the thrips. During the sampling, 40% of the *M. parvilofra* sampled individuals had thrips, while 23%, 17% and 26 % of *C. murale, Z .dumosum,* and *H. persicum* respectively had thrips.

Persistence experiment

Persistence of agricultural herbivores on desert plants was determined by caging adult insects on desert plant species, and monitoring adult survival, egg deposition and offspring production. Twenty one plants of each of the test species were located in natural desert areas at two sites in the Arava valley (30.804017 N, 35.302162 E and 30.75122 N, 35.27151 E).

Between the 11th and 19th of February 2009, the plants were cleaned of all herbivores and predators by visual searching and by using a hand-held suction device (STIHL, SH 55, diameter of the sampling tube is 0.15 m), and then caged in whitefly- and thrips-proof mesh screen. The plants were cleaned of all arthropods two more times at three-day intervals, before being seeded with 45 adult whiteflies or 40 adult thrips per caged plant. The fate of the adults and the appearance of offspring on each plant were determined three times after seeding the herbivores: 8, 20, and 42 days after release for the whiteflies, and after 7, 16, and 27 days for the thrips. On each date, seven monitored plants of each species were randomly selected, taken to the lab in their sealed mesh cages, and inspected thoroughly for the presence of all life stages of the pest, as well as for presence of other arthropods. The duration of the experiment was set to exceed the generation time and estimated adult longevity of each pest species: 12 and 15 days, respectively, for the thrips, for a total of 27 days (Zhang *et al.*, 2007); and 20 and 22 days, respectively, for the whiteflies, for a total of 42 days (Coudriet *et al.*, 1985; Wagner, 1995).

The inspected plants were weighed using an analytical balance (Mettler Toledo AB204-S), and arthropod counts were expressed as density per g of plant fresh weight. The life stages recorded for whiteflies were: eggs, four nymphal states, and adults. The nymphal states are referred to as crawlers (first instars), nymph 2, nymph 3, and red-eye nymph. For thrips, the recorded life stages were eggs, larva 1, larva 2, and adults. Because thrips eggs are deposited inside leaf tissue, their presence was inferred by the presence of characteristic puncture spots.

Cage effect

To test for possible effects of the cage on the temperature experienced by the insects, I compared the temperature inside and outside four cages in the field, using temperature data loggers (i-Button, DS1921G model). Temperatures were measured every half hour for 43 days. Four data loggers were placed individually inside four cages and four other loggers were set outside each of these cages, all at 10 cm above ground.

Results

No evidence was found for cage effect: the daily maximum temperature did not differ significantly inside and outside the cages (matched pair t-test; $t_{(42)} = -1.1836$, $p = 0.2432$). The average daily maximum temperature was 36 ºC.

Whitefly nymphs were found on *D. acris* 8 and 42 days after seeding (Fig 3.1A). Three different nymphal stages and adults were found on *M. parvilofra* 8 days after adult

seeding. Third instars and adults were found on day 20, and three different nymphal stages and adults were found on the last inspection date on this host plant (Fig. 3.1B). No whitefly eggs, nymphs, or adults were found on *Z. dumosum* and *O. baccatu*s.

Different developmental stages of thrips were found on caged *M. parviflora* (Fig. 3.2A). Seven days after seeding, four stages were recorded on this plant: eggs, larvae 1 and 2, and adults. At the second and third monitoring dates (after 16 and 27 days, respectively), larvae 1 and 2 and adults were observed. Eggs and adult thrips were recorded on *C. murale* after 7 days; eggs, larvae 1, and adults were recorded on day 16; and larvae 1 and 2 and adults were found after 27 days (Fig. 3.2B).

Larvae 2 and adult thrips were recorded on *Z. dumosum* after 7 and 16 days, but only one adult was found on this plant at the end of the experiment (after 27 days; Fig. 3.2C). Only a single adult was found on *H. persicum* on the first inspection date (7 days).
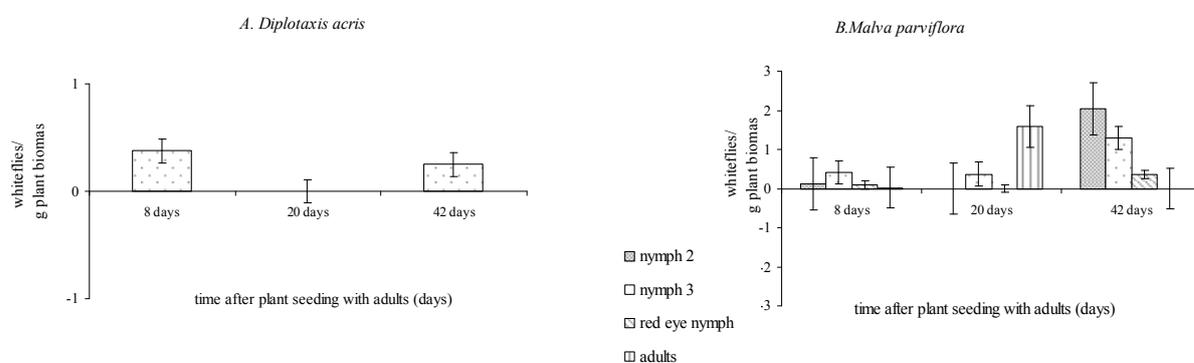
Fig. 3.1: Density (Mean ± SE) of whitefly nymphs and adults per unit plant biomass (g) on two desert plants, (A) *D. acris* and (B) *M. parviflora*. Seven plants were removed and examined destructively at each census.
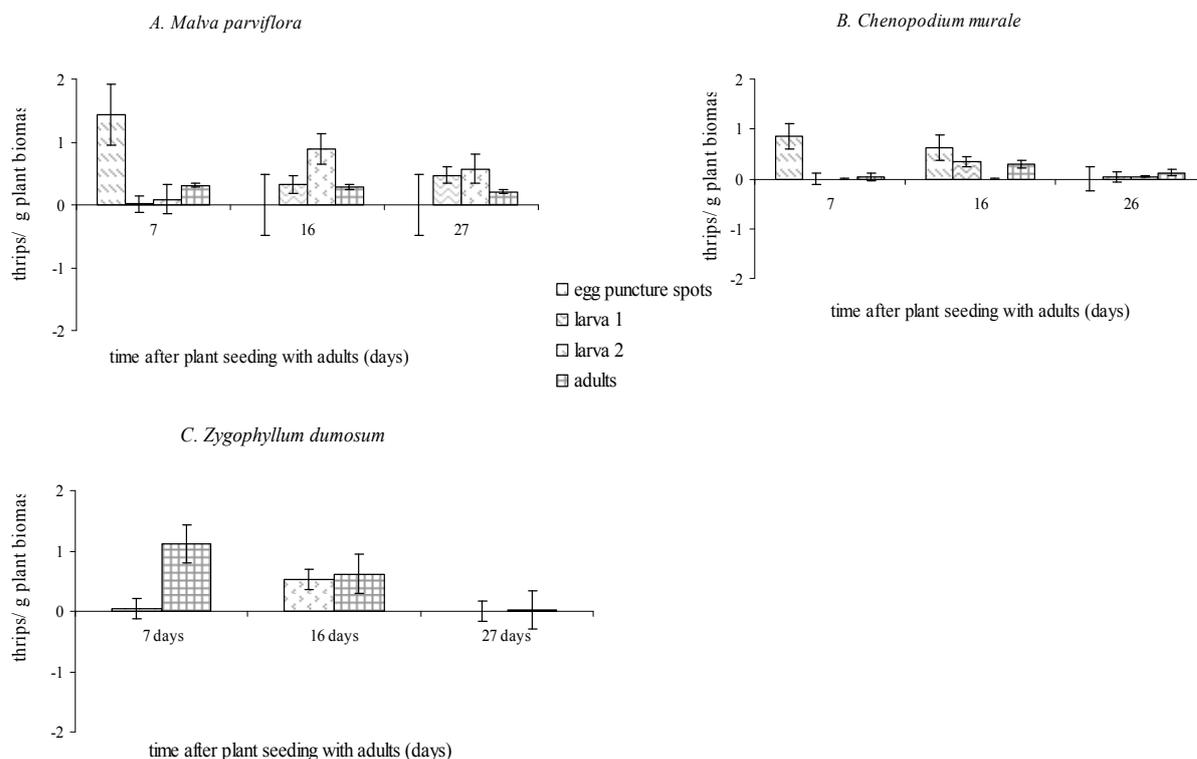
Fig. 3.2: Density (Mean ± SE) of trhips larva and adults per unit fresh plant biomass (g) on three desert plants, (A) *M. parviflora,* (B) *C. murale* and (C) *Z. dumosum.* Seven plants were removed and examined destructively at each census.

Discussion

I found that different life cycle stages of whiteflies and thrips were found on some of the tested host desert plants after seeding them with the pests. The results suggest that the whitefly is able to survive and reproduce on *D. acris* and *M. parvilofra*, while thrips survive and reproduce on *M. parviflora*, *D. acris* and *Z. dumosum*. A recent study in desert habitats showed that several thrips species are found on desert plants, but that they showed low fidelity to these host plants (Logarzo *et al.*, 2012). This study took place in the Chihuahuan desert, New Mexico, U.S.A., and thrips were sampled in 13 plant species. Logarzo *et al.* found that *Frankliniella occidentalis*, the same thrips species as in my study, was present on all 13 species. In the Imperial Valley, Californa, U.S.A, several desert plants were found to be hosts of *Bemisia tabaci* and several other whitefly species (Hoelmer and Goolsby 2003, Hoelemer *et al.*, 2008). These studies showed that weedy native plants and other plant species in unmanaged habitats act as whitefly hosts. These results support the findings of my experiment.

Because whiteflies and thrips are able to survive and reproduce in desert habitats, they represent a potential allochthonous food source for desert predators. Predators could show a

numerical response to prey subsidies, and thus desert food webs could be altered by the arrival of such subsidies. Yet it appears that the two pest species are not able to maintain large enough populations on desert plants. Even so, they could still have a short-term effect on desert food webs; serving as prey, they may temporarily release other desert herbivores from predation. In the longer run, non-persisting prey may subsidize scavengers, who in turn would increase in numbers and prey on eggs and immature stages of various desert arthropods. This is expected, then, to negatively affect prey availability for desert predator populations.

It is also possible that whitefly and thrips spillover does not subsidize either predators or scavengers. Theory predicts that subsidized communities, in comparison to non-subsidized communities, would exhibit stronger population fluctuations and lower species diversity (Anderson *et al*., 2008). In subsidized communities, recipient organisms could exhibit a strong numerical response to the subsidy, and competitively exclude other species under the subsidized conditions. Work described in chapter IV tested the effects of prey spillover on community structure, species richness, arthropod abundance and species composition in desert habitats.

To effectively subsidize desert predator populations, it is not enough that whiteflies and thrips sustain themselves in desert habitats; they must be consumed by predators in the recipient desert habitat. In the next chapter, I present evidence from laboratory experiments that strongly suggest that desert spiders readily consume spillover whitefly and thrips prey.

Appendix 3.1: Desert plant species that were monitored for the presence of arthropods between February and December 2008. Listed are only the species on which the collected individuals could be identified to the species or genus levels.

Plant species	Arthropod species
Acacia raddiana (Fabales: Fabaceae)	*Casana innotata* (Lepidoptera: Lymantriidae)
	Haplothrips sp. (Thysanoptera: Phlaeothripidae)
	Philodromus sp. (Araneae: Philodromidae)
Acacia tortilis (Fabales: Fabaceae)	*Bemisia tabaci* (Hemiptera: Aleyrodidae)
	Frankliniella occidentalis (Thysanoptera: Thripidae)
	Galeatus scrophicus (Hemiptera: Tingidae)
	Gibbaranea bituberculata (Araneae: Araneidae)

	Leptothrips sp. (Thysanoptera: Phlaeothripidae)
	Philodromus latrophagus (Araneae: Philodromidae)
	Philodromus sp. (Araneae: Philodromidae)
	Physatocheila sp. (Hemiptera: Tingidae)
	Thanatus sp. (Araneae: Philodromidae)
	Tmarus sp. (Araneae: Thomisidae)
Aerva persica (Caryophyllales: Amaranthaceae)	*Frankliniella occidentalis* (Thysanoptera: Thripidae)
	Haplothrips sp. (Thysanoptera: Phlaeothripidae)
	Heliophanus decoratus (Araneae: Salticidae)
	Heliophanus sp. (Araneae: Salticidae)
	Neoscona sp. (Araneae: Araneidae)
	Piocoris erythrocephalus (Hemiptera: Lygaeidae)
	Thanatus sp. (Araneae: Philodromidae)
	Uloborus sp. (Araneae: Uloboridae)
	Yllenus sp. (Araneae: Salticidae)
Anabasis articulata (Caryophyllales: Amaranthaceae)	*Aelurillus* sp. (Araneae: Salticidae)
	Bemisia tabaci (Hemiptera: Aleyrodidae)
	Blepharopsis mendica (Dictyoptera: Mantidae)
	Cheiracanthium sp. (Araneae: Miturgidae)
	Chrysolina sp. (Coleoptera: Chrysomelidae)
	Creontiades pallidus (Hemiptera: Miridae)
	Cyrtophora sp. (Araneae: Araneidae)
	Frankliniella occidentalis (Thysanoptera: Thripidae)
	Haplothrips sp. (Thysanoptera: Phlaeothripidae)
	Heliophanus sp. (Araneae: Salticidae)
	Latrophagus sp. (Araneae: Philodromidae)
	Leptothrips sp. (Thysanoptera: Phlaeothripidae)
	Liorhyssus hyalinus (Hemiptera: Rhopalidae)
	Mogrus sp. (Araneae: Salticidae)
	Neoscona sp. (Araneae: Araneidae)
	Nomisia sp. (Araneae: Gnaphosidae)
	Orius albidipennis (Hemiptera: Anthocoridae)
	Orius sp. (Hemiptera: Anthocoridae)
	Oxyopes sp. (Araneae: Oxyopidae)

	Philodromus sp. (Araneae: Philodromidae)
	Phylloforma laciniata (Hemiptera: Coreidae)
	Pimelia sp. (Coleoptera: Tenebrionidae)
	Pseudicius wadis (Araneae: Salticidae)
	Thanatus sp. (Araneae: Philodromidae)
	Thanatus setigerus (Araneae: Philodromidae)
	Theridion negebense (Araneae: Theridiidae)
	Theridion sp. (Araneae: Theridiidae)
Asteriscus graveolens (Asterales: Asteraceae)	*Micaria coarcata* (Araneae: Gnaphosidae)
Atriplex halimus (Caryophyllales: Amaranthaceae)	*Philodromus* sp. (Araneae: Philodromidae)
	Thanatus sp. (Araneae: Philodromidae)
Atriplex spongiosa (Caryophyllales: Amaranthaceae)	*Araniella* sp. (Araneae: Araneidae)
	Coccinella septempunctata (Coleoptera: Coccinellidae)
	Coccinella undecemountate(Coleoptera: Coccinellidae)
	Haplothrips sp. (Thysanoptera: Phlaeothripidae)
	Heliophanus decoratus (Araneae: Salticidae)
	Nomisia sp. (Araneae: Gnaphosidae)
	Pimelia sp. (Coleoptera: Tenebrionidae)
	Spathulina sicula (Dipterta: Tephritidae)
	Thanatus sp. (Araneae: Philodromidae)
	Theridion dromedarius (Araneae: Theridiidae)
Centaurea ammocyanus (Asterales: Asteraceae)	*Cheiracanthium* sp. (Araneae: Miturgidae)
	Frankliniella occidentalis (Thysanoptera: Thripidae)
	Thrips tabaci (Thysanoptera: Thripidae)
Centaurea cineraria (Asterales: Asteraceae)	*Phlegra amitai* (Araneae: Salticidae)
Chenopodium murale (Caryophyllales: Amaranthaceae)	*Enoplognatha* sp. (Araneae: Theridiidae)
	Frankliniella occidentalis (Thysanoptera: Thripidae)
	Orius laevigatus (Hemiptera: Anthocoridae)
	Orius sp. (Hemiptera: Anthocoridae)
	Spathulina sicula (Dipterta: Tephritidae)
	Spilostethus pandurus (Hemiptera: Lygaeidae)
	Thanatus sp. (Araneae: Philodromidae)

Diplotaxis acris (Brassicales: Brassicaceae)	*Bemisia tabaci* (Hemiptera: Aleyrodidae) *Frankliniella occidentalis* (Thysanoptera: Thripidae)
Diplotaxis hara (Brassicales: Brassicaceae)	*Frankliniella occidentalis* (Thysanoptera: Thripidae) *Haplothrips* sp. (Thysanoptera: Phlaeothripidae) *Leptothrips* sp. (Thysanoptera: Phlaeothripidae) *Orius albidipennis* (Hemiptera: Anthocoridae) *Orius* sp. (Hemiptera: Anthocoridae)
Eucaria boveana (Brassicales: Cruciferae)	*Frankliniella occidentalis* (Thysanoptera: Thripidae) *Liorhyssus hyalinus* (Hemiptera: Rhopalidae) *Pimelia* sp. (Coleoptera: Tenebrionidae)
Fagonia bruguierei (Zygophyllales: Zygophyllaceae)	*Acanthaclisis* sp. (Neuroptera: Myrmeleontidae) *Haplothrips* sp. (Thysanoptera: Phlaeothripidae) *Nomisia* sp. (Araneae: Gnaphosidae) *Pimelia* sp. (Coleoptera: Tenebrionidae) *Tmarus* sp. (Araneae: Thomisidae)
Haloxylon persicum (Caryophyllales: Amaranthaceae)	*Acanthaclisis* sp. (Neuroptera: Myrmeleontidae) *Enoplognatha* sp. (Araneae: Theridiidae) *Frankliniella occidentalis* (Thysanoptera: Thripidae) *Latrophagus* sp. (Araneae: Philodromidae) *Philodromus latrophagus* (Araneae: Philodromidae) *Philodromus* sp. (Araneae: Philodromidae) *Speiacolor* sp. (Araneae: Theridiidae) *Thanatus* sp. (Araneae: Philodromidae) *Tmarus* sp. (Araneae: Thomisidae) *Yllenus* sp. (Araneae: Salticidae)
Kochia indica (Caryophyllales: Amaranthaceae)	*Frankliniella occidentalis* (Thysanoptera: Thripidae) *Haplothrips* sp. (Thysanoptera: Phlaeothripidae) *Oxyopes* sp. (Araneae: Oxyopidae) *Phlegra amitai* (Araneae: Salticidae) *Pholcus* sp. (Araneae: Pholcidae) *Pimelia* sp. (Coleoptera: Tenebrionidae) *Thanatus* sp. (Araneae: Philodromidae)
Launaea mucronata (Asterales: Asteraceae)	*Frankliniella occidentalis* (Thysanoptera: Thripidae)

Lycium shawii (Solanales: Solanaceae)	*Arenivaga hebraica* (Dictyoptera: Polyphagidae)
	Cheiracanthium sp. (Araneae: Miturgidae)
	Creontiades pallidus (Hemiptera: Miridae)
	Evarcha sp. (Araneae: Salticidae)
	Frankliniella occidentalis (Thysanoptera: Thripidae)
	Haplothrips sp. (Thysanoptera: Phlaeothripidae)
	Heliophanus sp. (Araneae: Salticidae)
	Leptothrips sp. (Thysanoptera: Phlaeothripidae)
	Neoscona sp. (Araneae: Araneidae)
	Nomisia sp. (Araneae: Gnaphosidae)
	Pimelia sp. (Coleoptera: Tenebrionidae)
	Thanatus sp. (Araneae: Philodromidae)
Malva parviflora (Malvales*:* Malvaceae*)*	*Bemisia tabaci* (Hemiptera: Aleyrodidae)
	Berlandina plumalis (Araneae: Gnaphosidae)
	Berlandina sp. (Araneae: Gnaphosidae)
	Chrysoperla carnea (Neuroptera: Chrysopidae)
	Erodius sp. (Coleoptera: Tenebrionidae)
	Frankliniella occidentalis (Thysanoptera: Thripidae)
	Haplothrips sp. (Thysanoptera: Phlaeothripidae)
	Leptothrips sp. (Thysanoptera: Phlaeothripidae)
	Orius laevigatus (Hemiptera: Anthocoridae)
	Orius sp. (Hemiptera: Anthocoridae)
	Pyrrhocoris apterus (Hemiptera:Pyrrhocoridae)
	Scymnus levaillanti (Coleoptera: Coccinellidae)
	Spathulina sicula (Dipterta: Tephritidae)
	Thanatus sp. (Araneae: Philodromidae)
	Thanatus setigerus (Araneae: Philodromidae)
	Thomisus sp. (Araneae: Thomisidae)
Melilotus indicus (Fabales: Fabaceae*)*	*Adesmia* sp. (Coleoptera: Tenebrionidae)
	Thanatus sp. (Araneae: Philodromidae)
Nitraria retusa (Sapindales: Nitrariaceae)	*Bemisia tabaci* (Hemiptera: Aleyrodidae)
	Haplothrips sp. (Thysanoptera: Phlaeothripidae)
	Nomisia sp. (Araneae: Gnaphosidae)
	Thanatus sp. (Araneae: Philodromidae)

	Thanatus fornicatus (Araneae: Philodromidae)
	Theridion dromedarius (Araneae: Theridiidae)
	Thomisus sp. (Araneae: Thomisidae)
Ochradenus baccatus (Brassicales: Resedaceae)	*Araniella* sp. (Araneae: Araneidae)
	Bemisia tabaci (Hemiptera: Aleyrodidae)
	Haplothrips sp. (Thysanoptera: Phlaeothripidae)
	Leptothrips sp. (Thysanoptera: Phlaeothripidae)
	Nomisia sp. (Araneae: Gnaphosidae)
	Pimelia sp. (Coleoptera: Tenebrionidae)
	Thrips tabaci (Thysanoptera: Thripidae)
Plantago cylindrical (Lamiales: Plantaginaceae)	*Arenivaga hebraica* (Dictyoptera: Polyphagidae)
	Frankliniella occidentalis (Thysanoptera: Thripidae)
	Galeatus scrophicus (Hemiptera: Tingidae)
	Haplothrips sp. (Thysanoptera: Phlaeothripidae)
	Orius sp. (Hemiptera: Anthocoridae)
	Spilostethus pandurus (Hemiptera: Lygaeidae)
	Thanatus sp. (Araneae: Philodromidae)
	Thomisus onustus (Araneae: Thomisidae)
Salsola sp. (Caryophyllales: Amaranthaceae)	*Chrysolina* sp. (Coleoptera: Chrysomelidae)
	Frankliniella occidentalis (Thysanoptera: Thripidae)
	Heliophanus decoratus (Araneae: Salticidae)
	Heliophanus sp. (Araneae: Salticidae)
	Liorhyssus hyalinus (Hemiptera: Rhopalidae)
	Orius sp. (Hemiptera: Anthocoridae)
	Oxyopes sp. (Araneae: Oxyopidae)
	Thanatus sp. (Araneae: Philodromidae)
Sonchus oleraceus (Asterales: Asteraceae)	*Berlandina* sp. (Araneae: Gnaphosidae)
	Frankliniella occidentalis (Thysanoptera: Thripidae)
	Leptothrips sp. (Thysanoptera: Phlaeothripidae)
Tamarix nilotica (Caryophyllales: Tamaricaceae)	*Chrysolina* sp. (Coleoptera: Chrysomelidae)
	Creontiades pallidus (Hemiptera: Miridae)
	Thomisus onustus (Araneae: Thomisidae)
Zilla spinosa (Brassicales: Brassicaceae)	*Cheiracanthium* sp. (Araneae: Miturgidae)
	Mogrus sp. (Araneae: Salticidae)

	Philodromus latrophagus (Araneae: Philodromidae)
	Philodromus sp. (Araneae: Philodromidae)
	Pimelia sp. (Coleoptera: Tenebrionidae)
	Thomisus sp. (Araneae: Thomisidae)
	Acanthaclisis synclis baetica (Neuroptera: Myrmeleontidae)
	Aelurillus sp. (Araneae: Salticidae)
	Bemisia tabaci (Hemiptera: Aleyrodidae)
	Chrysolina sp. (Coleoptera: Chrysomelidae)
Zygophyllum dumosum (Zygophyllales: Zygophyllaceae)	*Frankliniella occidentalis* (Thysanoptera: Thripidae)
	Orius sp. (Hemiptera: Anthocoridae)
	Pimelia sp. (Coleoptera: Tenebrionidae)
	Thanatus sp. (Araneae: Philodromidae)
	Thanatus setigerus (Araneae: Philodromidae)
	Thomisus sp. (Araneae: Thomisidae)
	Thomisus onustus (Araneae: Thomisidae)

Chapter IV: Interaction between desert predators and agricultural prey

Introduction

The rapid population buildup of agricultural pests and the ephemerality of their managed habitat could lead to massive spillovers into adjacent natural habitats. The degree to which agricultural herbivores act to subsidize native predators depends in part on their acceptance and suitability as prey by predator species in the recipient habitat. As I have shown in chapters II and III, whiteflies and thrips move from agricultural fields into adjacent desert areas, and are able to reproduce on some of the wild plants there. In this chapter, I investigate the short-term responses of selected desert predators to whiteflies and thrips.

Spillovers are expected to influence desert predators not only through the increase in prey availability, but also by relaxing antagonistic interactions among predators. Interactions among predators may help regulate the size of predator populations, and thus either enhance or reduce their effect on the prey (Snyder and Wise, 1999). Predator interactions could be antagonistic: through intraguild predation, or by disrupting the foraging of another predator, and thus diminish their impact on shared prey (Rosenheim *et al.,* 1995; Finke and Denno, 2002). Thus, the net predator impact could be either reduced, increased, or unchanged by the presence of other predators in the guild (Polis and Holt, 1992; Sih *et al.* 1998; Casula *et al.,* 2006). Therefore, I was interested in studying the interactions between the different predators in the desert habitat. I expected to find that (i) desert predators consume agricultural herbivores, and (ii) presence of agricultural prey alters intraguild interactions among desert predators.

Upon first encounter with prey subsidy in the desert habitat, a predator may alter its foraging behavior to feed preferentially on the new and more abundant prey. I therefore focused my enquiry first on (1) predator attack and consumption of agricultural pests on the first and second encounters with prey; (2) differences in time spent feeding on the first and second encounter; (3) change in predator body mass after consuming the prey; and (4) preference of desert predators for agricultural prey.

Since prey availability has been shown to reduce antagonistic interaction among predators, I also asked: (1) does the number of intraguild interactions change when the predators are offered different prey types? and (2) do predators catch less prey and spend less time feeding in the presence of a competitor?

Materials and methods

A. Agricultural herbivore consumption by desert predators: experimental design and statistical analysis

       Short-term laboratory experiments in enclosures were used to test whether desert predators consume the agricultural pests *Bemisia tabaci*, whitefly, and *Frankliniella occidentalis*, thrips. The desert predators chosen for this experiment were two spider species: *Thanatus* sp. (Philodromidae) and *Phlegra amitai* (Salticidae). These two species were chosen based on results of arthropod sampling in the study area (see Appendix 3.1). Philodromids and salticids together represented 56% of all collected spiders, and *Thanatus* sp. and *P. amitai* were the most abundant taxa in each family. The two species are of similar body size: the total body length of *Thanatus* sp. is 5-6 mm, while that of *P. amitai* is 6-7 mm. However, the two spiders exhibit different hunting strategies: *Thanatus* sp. is a 'run and wait' hunter, while *Phlegra amitai* is an active stalker (V. Hochman-Adler and Y. Lubin, unpublished observations).

       Field-collected juvenile spiders were fed fruit flies (*Drosophila melanogaster*) in the lab, and used in the experiment when they reached the subadult age (one molt before adulthood). Prior to their use in the experiment, the spiders were starved for 10 days. They were weighed before the start of the experiment to an accuracy of 0.0001 g, and then put in the test enclosures individually for one hour, for acclimation. Each spider was placed individually in a transparent enclosure (diameter at the base 2.7 cm, diameter at the top 3.6 cm, height 4.2 cm) with a substrate of plaster of Paris. Each spider was offered ten whiteflies, ten thrips, or two fruit flies, amounts that constitute similar prey wet mass. In addition, ten spiders were not fed. The whiteflies and thrips used for the experiment were reared in the lab as described in Chapter III, and used in the experiment at the adult state.

       Each spider was tested on two consecutive days, in order to observe any behavioral effect of the predator's experience with a prey. Each day, ten *Thanatus* sp. individuals were fed with whiteflies, ten with thrips, ten with fruit flies and ten were not fed, totaling forty individuals per day. When *P. amitai* spiders were observed, five individuals were fed with whiteflies, five with thrips, five with fruit flies and five were not fed, totaling twenty individuals per day. Afterwards, the experiment was repeated for another two consecutive days using a different set of spiders. In total, eighty *Thanatus* sp. individuals and forty *P. amitai* individuals were used in this experiment.

       I observed the spider individuals using the simultaneous scanning technique for 1 hour, and recorded the following events: catching the prey, dropping the prey after consuming it, and failing to catch it. The time of each event was recorded, and thus the time predators spent feeding was calculated.

Predator body size and body mass were measured immediately at the end of the observations. Body size was determined by the combined length of the cephalothorax and the abdomen as measured with an electronic caliper, with an accuracy of 0.1mm. Body mass change was calculated as the difference in wet mass of the spider before and after the observation period. The number of caught prey and the total time the predators spent feeding on day one vs. day two were analyzed using paired t test, to study the effect of consecutive days. Analysis of covariance was used to study the effect of consecutive days on the predator body mass change. Body mass change was the response variable, and the day was the independent variable. The length of the spider was used as the covariate. Data were analyzed separately for each spider species across prey types using JMP software Version 9. SAS Institute (2010).

B. Prey preference and intraguild interactions between desert predators: experimental design and statistical analysis

Arthropod-free, open net house-grown *Chenopodium murale* (Amaranthaceae) plants were placed in small cages and seeded with prey and desert predators, to study the effect of agricultural prey availability on intraguild interactions between desert predators. The cages were built using transparent 200 ml plastic cups (Fig. 4.1). One cup was used as a pot to hold the plant, and a second one was placed upside-down on top of the first one to create an enclosure to cage the arthropods. Between the two cups, I inserted a Petri dish with a hole in the center, and inserted the plant through it. The hole was sealed with modeling clay around the plant. Modeling clay was also used to seal all parts of the enclosure. The predators and the herbivores were introduced through a hole in the enclosure, which was then closed with transparent tape.

Three experiments were conducted. The first experiment (B.1) examined preference of each predator for whiteflies or thrips. The second experiment (B.2) studied the intraguild interactions when predators were offered different prey types. A third experiment (B.3) was aimed at studying the effect of a competitor on predator feeding behavior. As in the previous experiment, the predators were *Thanatus* sp. and *P. amitai*, and the prey were whiteflies, thrips and fruit flies. Spiders were starved for ten days before being used in the experiments, the changes in predator body mass were calculated, and body size was measured as previously described. Different spiders were used for each experiment.

Fig. 4. 1: Enclosure used to study predator behavior on *Chenopodium murale* plants.

B.1. Prey preference

One individual of each spider species was placed alone in the enclosure. The spiders were offered ten whiteflies and ten thrips simultaneously. Each spider was observed individually for two and a half hours. In total, fifteen *Thanatus* sp. and fifteen *P. amitai* were observed in this experiment. I recorded the number of prey caught of each prey species, as indication of predator prey preference. A χ^2 goodness of fit test was used to compare the observed captures to a null hypothesis of no preference (expected frequency =0.5). The data were analyzed using JMP software Version 9. SAS Institute (2010).

B.2. Intraguild interactions when predators are offered different prey types

I placed an individual of each of the two spider species together in an enclosure, and offered them fifteen whiteflies, fifteen thrips, or three fruit flies. Fruit flies raised on an enhanced diet of fruit fly medium and crushed dog food were included as a control; these flies are a suitable prey for spiders, and allow them to develop, survive, and reproduce optimally (Mayntz and Toft, 2001). I observed each enclosure for two and a half hours, and recorded the following intraguild interactions: chasing the other predator with no physical contact between the spiders, and attacks on the other predator. The outcome of the attacks was also recorded. If the attacked predator was killed, the observation still continued to complete two and a half hours. Fifteen observations were done for each prey type.

The numbers of chasing and attacking events were analyzed separately for each prey type. As data were not normally distributed, one-way non-parametric ANOVA was used to analyze the data. Data were analyzed using JMP software Version 9. SAS Institute (2010).

B.3. Changes in predator feeding behavior in the presence of a competitor

I placed one individual of each spider species together in an enclosure, and one individual of each spider species separately in other enclosures. I offered the predators fifteen whiteflies, fifteen thrips, or three fruit flies. Each enclosure was observed for two and a half hours. I recorded: a) the number of prey caught; b) duration of feeding events; and c) changes in predator body mass. Fifteen observations were done for each prey type and treatment (i.e. presence or absence of competitor).

Data were analyzed separately for each spider species across prey types. One-way non-parametric ANOVA was used to test for the difference in prey intake and in time predators spent feeding in the presence and absence of competitors. Analysis of covariance was used to study the difference in predator body mass change in the presence and absence of competitors when offered different prey. Body mass change was the response variable and the treatment was the independent variable. The length of the spider was used as the covariate. Data were analyzed using JMP software Version 9. SAS Institute (2010).

Results

A. Consumption of agricultural herbivores by desert predators

Thanatus sp ate a similar number of whiteflies and fed for a similar time on both days (Table 4.1). However, they gained significantly more mass on day one than on day two; in fact, they actually lost mass on day two (Fig 4.2, Table 4.2). The body mass change on day one vs. the body mass change on day two of each individual spider was plotted on a day-mass space. The day-mass space showed that most individuals that gained mass on day one lost mass on day two (Fig 4.3A, points in the lower right quarter).

Thanatus sp. consumed a similar number of thrips and spent a similar time feeding on both days (Table 4.1). Predator body mass change did not differ statistically between both days when feeding on thrips (Table 4.2). However, individual spiders responded differently to this prey. In a day-mass space graph, it can be seen that some spiders gained mass on day one and not on day two (or lost mass on day two), and other individuals showed the opposite response (Fig 4.3B; lower right and upper left quarter, respectively).

Thanatus sp. consumed significantly more fruit flies, and spent significantly more time feeding on them on day one than on day two (Fig. 4.4A and Fig. 4.4B, respectively, Table 4.1). *Thanatus* sp. mean body mass change was larger on day one that on day two (Fig. 4.2B, Table 4.2). In a day-mass space graph, it can be seen that several individuals gained mass on both days, while others gained mass only on day one. A few individuals lost body mass on day two (Fig 4.3C; upper and lower right quarter, respectively).

There was no significant change in mass of unfed controls between day one and day two (Table 4.2).

A. Whiteflies
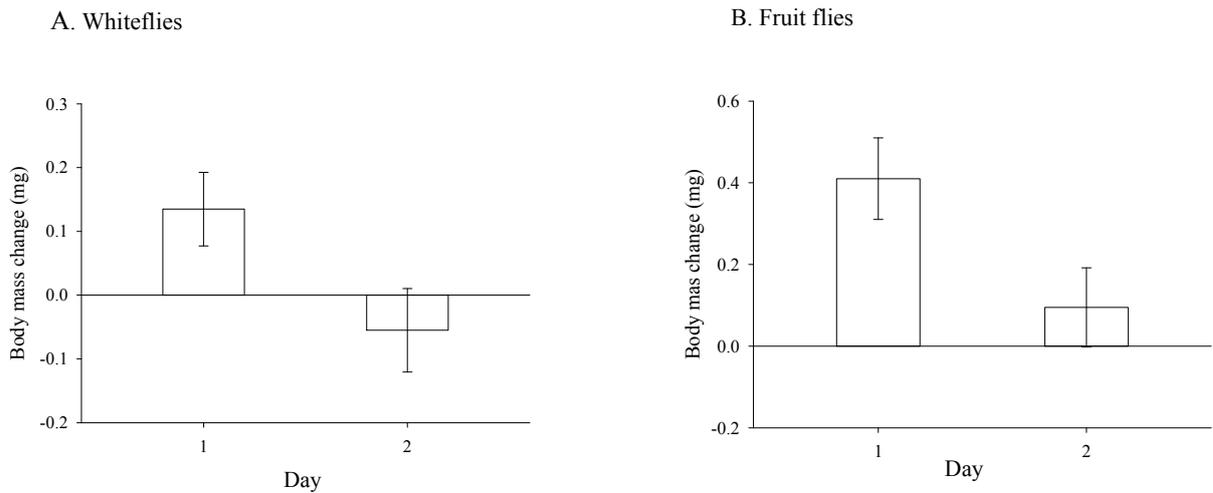
B. Fruit flies

Fig 4.2: Effect of feeding day on change in *Thanatus* sp. body mass (Mean ±SE) when fed on (A) whiteflies or (B) fruit flies for two consecutive days.

A. Whiteflies

B.Thrips
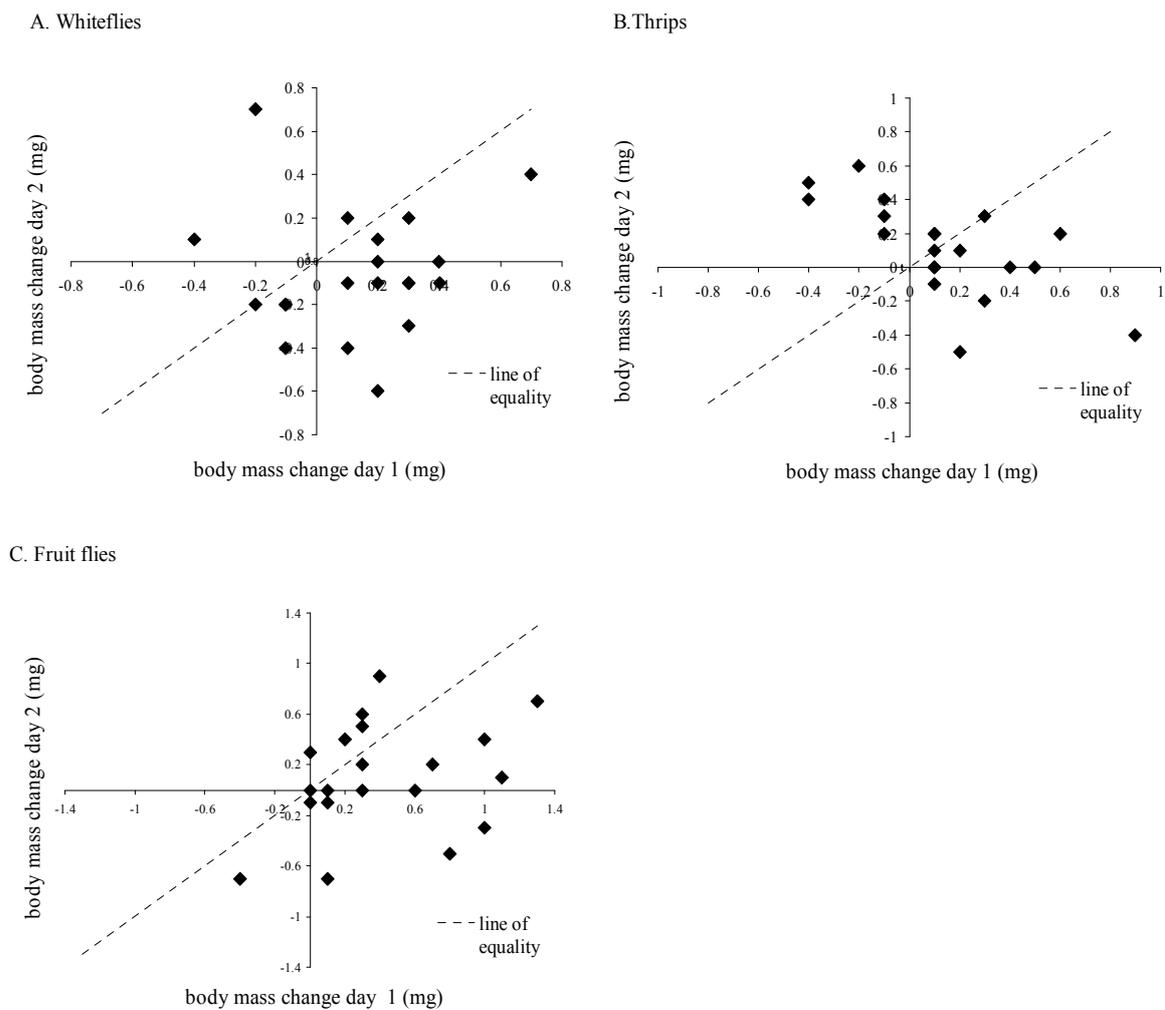
C. Fruit flies

Fig. 4.3: Body mass change on day one vs. body mass change on day two of individual *Thanatus* sp. spiders when feeding on (A) whiteflies, (B) thrips and (C) fruit flies.

A. Number of prey caught

B. Total feeding time
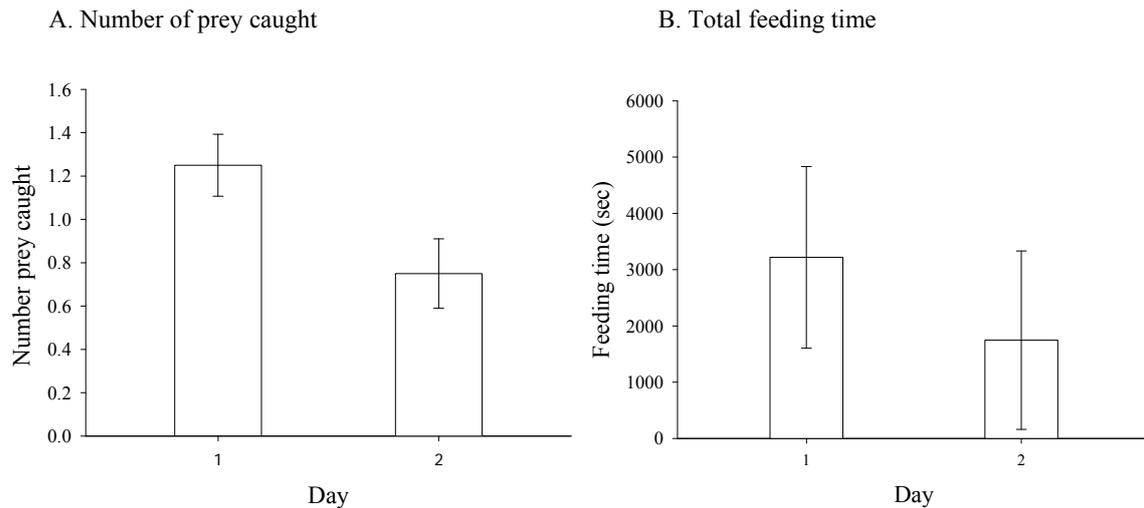
Fig. 4.4: Effect of feeding day on (A) number of prey caught and on (B) total feeding time by *Thanatus* sp. (Mean ±SE) when fed on fruit flies for two consecutive days.

When offered whiteflies, *P. amitai* ate a similar number of individuals on both days, and the total time spent feeding did not differ statistically on both days (Table 4.1). Even though the difference in body mass change between the two consecutive days was not statistically different (Table 4.2), in a day-mass space it can be seen that individuals gained or lost mass consistently on the two days (Fig. 4.5A, upper right and lower left quarter respectively).

P. amitai ate a similar number of thrips on both days and fed for a similar time on both days (Table 4.1). The difference in body mass change between the two consecutive days was not statistically different (Table 4.2). In a day-mass space, it can be seen that most individuals gained mass on day two, even if they lost mass on day one (Fig. 4.5B upper left quarter).

P. amitai consumed a similar amount of fruit flies and spent a similar time feeding on them on both days (Table 4.1). Predator body mass change did not differ statistically between the two days (Table 4.2). In a day-mass space graph, it can be seen that most of the spiders gained mass on both days. The increase in body mass on day one was higher than the increase on day two for the majority of the spiders (Fig 4.5C; upper right quarter).

There was no significant difference in change in mass of unfed controls between day one and day two (Table 4.2).

A. Whitflies

B. Thrips
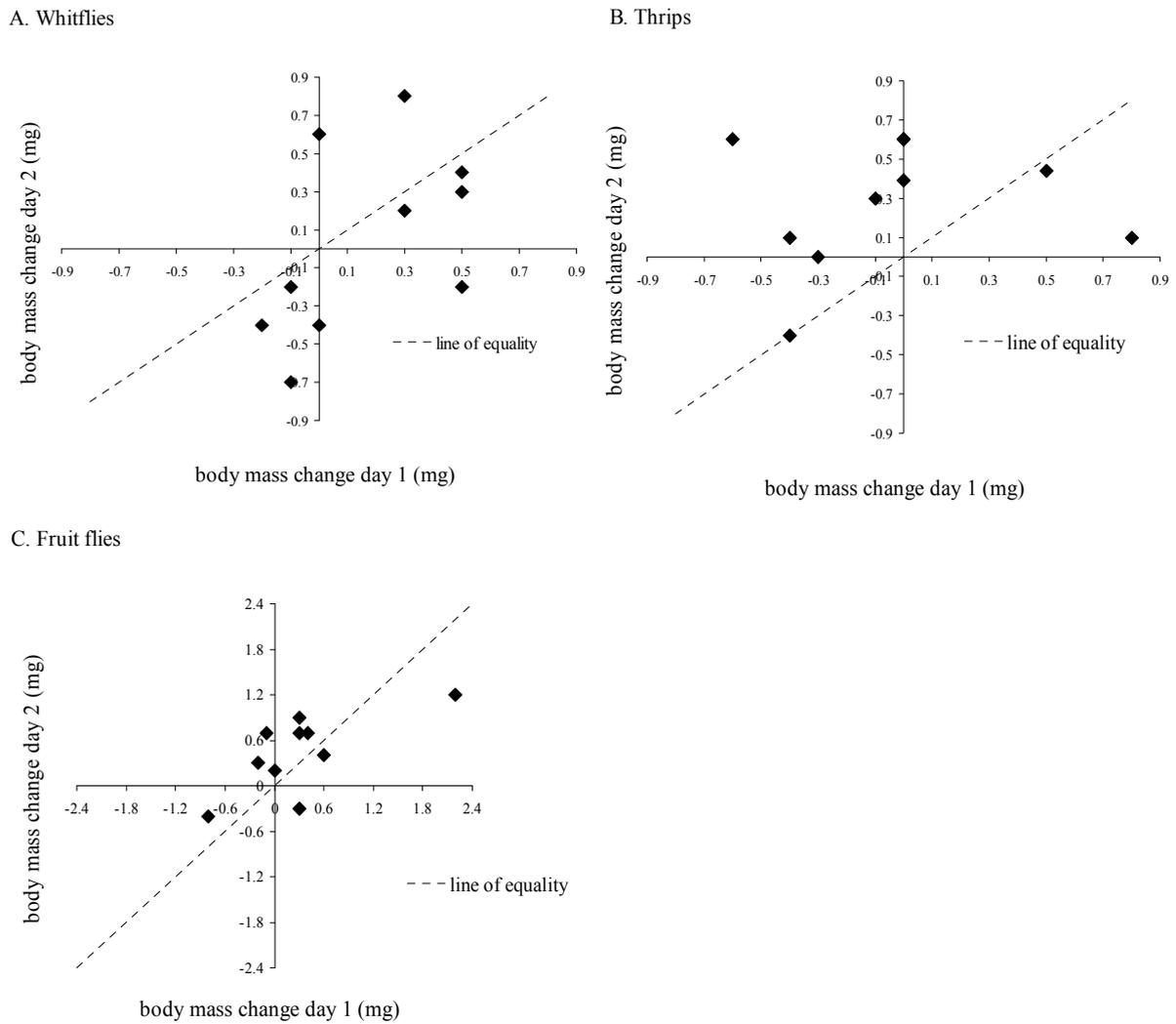
C. Fruit flies

Fig. 4.5: Body mass change on day one vs. body mass change on day two of individual *P. amitai* spiders when feeding on (A) whiteflies, (B) thrips and (C) fruit flies.

Table 4.1: Paired t test showing the effect of day on number of caught prey and total feeding time when *Thanatus* sp. and *P. amitai* where fed with either whiteflies, thrips, or fruit flies for two consecutive days. Significant differences are shown in bold (p< 0.05).

Spider species	Diet	Variable of interest	df	t ratio	p
Thanatus sp.	Whiteflies	Number of caught prey	19	0.661	0.601
		Total feeding time (min)	19	0.531	0.517
	Thrips	Number of caught prey	19	0	1
		Total feeding time (min)	19	1.43	0.169
	Fruit flies	Number of caught prey	19	**4.198**	**<0.001**
		Total feeding time (min)	19	**3.684**	**0.002**

P. amitai	Whiteflies	Number of caught prey	9	-0.518	0.617
		Total feeding time (min)	9	-0.396	0.701
	Thrips	Number of caught prey	9	-0.557	0.591
		Total feeding time (min)	9	0.359	0.728
	Fruit flies	Number of caught prey	9	-0.316	0.76
		Total feeding time (min)	9	-0.241	0.815

Table 4.2: Analysis of covariance showing effect of day on body mass change when *Thanatus* sp. and *P. amitai* where fed with either whiteflies, thrips, fruit flies, or not fed for two consecutive days. The length of the spider was used as the covariate. Significant differences are shown in bold ($p < 0.05$).

Spider species	Diet	Source	df	Sum of Squares	F Ratio	p
Thanatus sp	Whiteflies	Day	1	0.3803	**4.957**	**0.032**
		Length (mm)	1	0.0560	0.730	0.398
	Thrips	Day	1	0.0034	0.037	0.848
		Length (mm)	1	0.0028	0.030	0.863
	Fruit flies	Day	1	0.8864	**4.633**	**0.038**
		Length (mm)	1	0.2689	1.406	0.243
	Unfed	Day	1	0.0044	0.046	0.831
		Length (mm)	1	0.0444	0.468	0.498
P. amitai	Whiteflies	Day	1	0.0689	0.721	0.408
		Length (mm)	1	0.0280	0.293	0.596
	Thrips	Day	1	0.0526	0.442	0.515
		Length (mm)	1	1.7868	**15.021**	**0.001**
	Fruit flies	Day	1	0.0133	0.284	0.775
		Length (mm)	1	0.2873	1.808	0.193
	Unfed	Day	1	0.0062	0.0407	0.843
		Length (mm)	1	0.1260	0.824	0.378

B. Prey preference and intraguild interactions between desert predators
B.1. Prey preference

Neither *P. amitai* nor *Thanatus* sp. showed a preference for thrips or whiteflies (Likelihood ratio test $\chi^2 = 0.125$; p =0.724; $\chi^2 = 0.1$; p =0.752 for *P. amitai* and *Thanatus* sp. respectively).

B.2. Intraguild interactions when predators were offered different prey types

The number of chasing events was significantly different between spider species when they were offered whiteflies and thrips (for whiteflies: Wilcoxon test, $\chi^2 = 4.226$; p = 0.04; for thrips: Wilcoxon test, $\chi^2 = 6.174$; p =0.013). *Thanatus* sp. individuals chased *P. amitai* spiders more times than *P. amitai* chased *Thanatus* sp. individuals with both prey types. In contrast, the number of chasing events was similar in the two spider species when they were offered fruit flies (Wilcoxon test, $\chi^2 = 2.247$; p =0.134) (Fig. 4.6A).

The number of attacks was significantly different when spiders were offered whiteflies (Wilcoxon test, $\chi^2 = 4.217$; p =0.004). *Thanatus* sp. individuals attacked *P. amitai* spiders more times than *P. amitai* attacked *Thanatus* sp. individuals. When offered whiteflies, *Thanatus* sp. individuals killed *P. amitai* individuals on two opportunities, while *P. amitai* did not kill the other predator. However, the number of attacking events was not significantly different when spiders were offered thrips (Wilcoxon test $\chi^2 = 1,2313$; p =0.267) (Fig. 4.6B). When offered thrips, both predator species killed the competitor on two occasions. The number of attacking events was similar for the two spiders species when they were offered fruit flies (Wilcoxon test, $\chi^2 = 2.036$; p =0.154). When offered fruit flies, both predator species killed the competitor once.
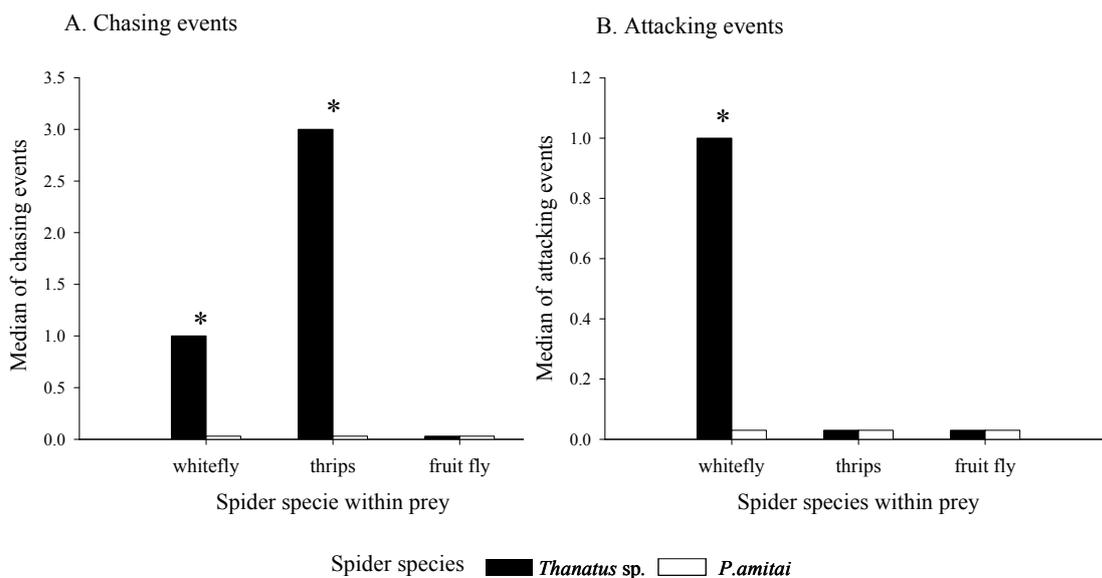
Fig. 4.6: Median number of chasing and attacking events between *P. amitai* and *Thanatus* sp. spiders when offered different prey types. Significant pair-wise comparisons (p<0.05) are indicated by an *.

B.3 Changes in predator feeding behavior in the presence of a competitor
B.3.a. Number of caught prey

The number of prey caught by the two spider species when offered whiteflies, thrips or fruit flies was not significantly different when they were placed alone in the cage or when both predators were placed together (Table 4.3). In other words, the presence of a competitor did not have any effect on the number of prey caught by the predators across the three prey types offered.

Table 4.3: Wilcoxon tests for the difference in number of prey captured in the presence and absence of competitors when offered different prey.

Spider species	Diet	df	χ^2	P
Thanatus sp.	Whiteflies	1	1.127	0.289
	Thrips	1	3.149	0.760
	Fruit flies	1	2.102	0.147
P. amitai	Whiteflies	1	1.511	0.219
	Thrips	1	0.005	0.946
	Fruit flies	1	1.65	0.199

B.3.b. Feeding time

For *P. amitai*, total feeding time was not affected by the presence of *Thanatus* sp. across all prey species (Table 4.4). However, when *Thanatus* sp. fed on thrips, they fed longer when the competitor was absent than when it was present (Fig. 4.7, Table 4.4).
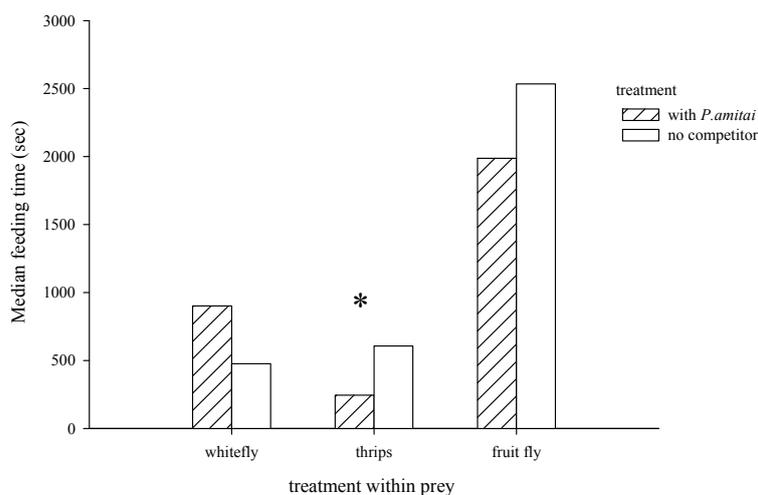
Fig. 4.7: Median feeding time of *Thanatus* sp. on three different prey types in the presence and absence of a *P.amitai* competitor. Significant pair-wise comparisons (p<0.05) are indicated by an *.

Table 4.4: Wilcoxon tests for the difference in time predators spent feeding in the presence and absence of competitors when offered different prey. Significant differences are shown in bold (p< 0.05).

Spider species	Diet	df	χ^2	P
Thanatus sp.	Whiteflies	1	0.6	0.439
	Thrips	1	**6.422**	**0.011**
	Fruit flies	1	0.008	0.979
P. amitai	Whiteflies	1	0.218	0.64
	Thrips	1	0.692	0.405
	Fruit flies	1	1.917	0.166

B.3.c. Body mass change

P. amitai body mass change was significantly affected by the presence of the competitor only when they were offered whiteflies (Fig. 4.8, Table 4.5). *Thanatus* sp. body mass change was not affected by the presence of the other predator across all prey types.
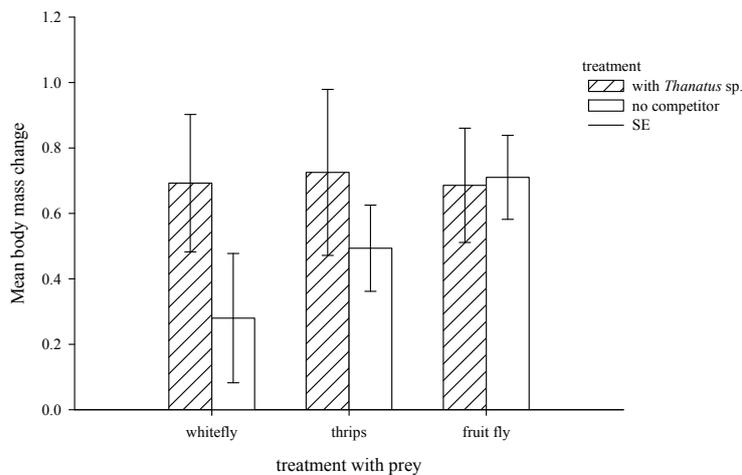
Fig. 4.8: Mean body mass change (mg) in *P. amitai* on three different prey types in the presence and absence of a *Thanatus* sp. competitor. Significant pair-wise comparisons (p<0.05) are indicated by an *.

Table 4.5: Analysis of covariance showing effect of presence or absence of competitors on predator body mass change when offered different prey. The length of the spider was used as the covariate. Significant differences are shown in bold (p< 0.05).

Spider species	Diet	df	Source of variation	Sum of Squares	F Ratio	p
Thanatus sp.	Whiteflies	1	treatment	0.580	1.323	0.264
		1	length (mm)	0.674	1.536	0.225
	Thrips	1	treatment	0.066	0.134	0.718
		1	length (mm)	0.448	0.926	0.325
	Fruit flies	1	treatment	0.071	0.35	0.562
		1	length (mm)	2.289	**11.212**	**0.003**
P. amitai	Whiteflies	1	treatment	2.999	**7.033**	**0.014**
		1	length (mm)	0.684	1.643	0.218
	Thrips	1	treatment	1.18	3.561	0.072
		1	length (mm)	1.086	3.277	0.084
	Fruit flies	1	treatment	0.562	2.219	0.153
		1	length (mm)	1.265	**4.995**	**0.038**

Discussion

Results show that *Thanatus* sp. increase in body mass on two consecutive days when feeding on thrips. However, the response to this prey species was not consistent. Some individuals gained body mass, and some lost. When feeding on whiteflies on consecutive days, these predators lost body mass and showed a consistent decrease in response to this prey. When offered fruit flies, *Thanatus* sp. increased in body mass consistently on both days. The consistent loss of body mass when feeding on whiteflies suggests the existence of a toxic effect when feeding on this prey.

P. amitai was able to increase its body mass when feeding on thrips, even after losing body mass on the first day. When feeding on whiteflies, the response was individual: some lost body mass and some gained body mass. When offered fruit flies, *P. amitai* increased its body mass consistently on both days. In terms of mass gained, *P. amitai* individuals did better than *Thanatus* sp. when offered both pests.

When whiteflies and thrips were offered together, *P. amitai* and *Thanatus* sp. did not show a preference for either prey species. Both spider species consumed the two prey items

equally. However, their body mass changes suggest that for both predator species, whiteflies and thrips may not be as high quality food items as fruit flies.

For spiders that occur in high densities in wheat fields in the Negev desert, intraguild predation was affected by the presence of alternative prey (Gavish-Reveg *et al.,* 2009). The prey type affected the number of intraguild predatory interaction events. *Thanatus* sp chased *P. amitai* more than the other way around when offered both whiteflies and thrips. However, when the predators were offered fruit flies, there was no significant difference in the amount of chasing events between the two spider species. When they were offered whiteflies, *Thanatus* sp. attacked *P. amitai* more often than the other way around, which is consistent with the chasing observations. It seems that the presence of a competitor affected *Thanatus* sp. behavior when offered agricultural prey. No changes in behavior were detected when fruit flies were offered. By contrast, *P. amitai* spiders spent a similar time feeding on each prey item regardless of the presence of the other predator. *Thanatus* sp. spent more time feeding when it was alone. However, both species caught a similar number of prey when they were placed alone in the cage as when they were in the presence of a competitor.

The presence or absence of the competitor did not affect the body mass change across all food types for both predator species. This was consistent with the fact that both predator species caught a similar number of prey in both treatments (when a competitor was present or absent). However, as *Thanatus* sp. spent more time feeding on thrips when it was placed alone in the cage, I expected to see a larger increase in its body mass in this treatment. This observed lack of increase could mean that maybe a physiological process limits assimilation, regardless of the time that the predator spends feeding on the prey.

The hunger level of a predator plays an important role in prey choice (Stephens and Krebs, 1986). Theory predicts that a hungry predator should be less selective, and accept less suitable prey than a satiated predator (Madsen *et al.,* 2004). This might explain why previously-starved *Thanatus* sp. and *P. amitai* individuals consumed thrips and whiteflies on two consecutive days even if they appear to be poor food sources. Although the body mass change response of the predators was not consistent, prey type had an influence on the time predators spent feeding and their body mass change. In food-limited desert conditions, when prey is scarce, both of these spider species are likely to benefit from thrips and whitefly spillovers, even if these prey are not of high quality for the two native predators. Furthermore, subsidies of agricultural prey appear to reduce antagonistic interactions between the two spider species. Taken together, the results suggest that prey subsidies might act to increase predator population size, through both increased resource availability and decreased intraguild

predation. This in turn might increase predation on desert prey. The effect of prey spillover on desert communities was investigated in the work reported in the next chapter.

Chapter V: Effect of herbivore spillover on desert arthropod communities

Introduction

There is no doubt that agricultural activity affects invertebrate communities, and has been associated with population decline of many species (see New, 2005 for a discussion). A variety of agriculture-originating factors may affect arthropod communities in natural habitats. These factors include habitat loss, pollution and pesticide use, introduction of exotic organisms, and spillover of agricultural pests into adjacent natural habitats.

Spillover was defined in the previous chapters as sporadic events of allochthonous resource super-abundance. Consumers in various communities often respond strongly to these allochthonous resources. Despite great variation in the nature of these resources, each represents a brief, infrequent event of high resource availability, and may cause substantial perturbations to the community, with strong effects on consumer populations (Yang, 2004). For instance, spillover of superabundant prey is expected to cause rapid population growth of generalist consumers. However, theory predicts that positive rates of growth and consequent high population density are expected to decline rapidly once the pulsed resource has been depleted (Ostfeld and Keesing, 2000). Such fluctuations in predator abundance might cause changes in the abundance of species with which they interact.

The high productivity of agricultural fields can, at times, make crop fields a source of herbivores that spill over into adjacent natural habitats. The effects of spillover herbivores from agricultural fields on arthropods in surrounding natural habitats have received little attention, in contrast to studies of the movement of herbivores and predators from natural habitats into agricultural fields (Rand *et al*., 2006; Blitzer *et al*., 2012, Tscharntke *et al.* 2012).

The potentially detrimental effects of spillover of large populations of herbivores, subsidized by agricultural fields, on native plants in small semi-natural habitat fragments has only recently been recognized (review in Blitzer *et al*., 2012). Studies have shown the negative effects of agricultural fields on wild organisms, for instance via pathogen infection (Lembo *et al*., 2008) or predator spillover (Batary and Baldi, 2004; Rand *et al.,* 2006). However, the consequences of agriculturally subsidized prey spillover for community structure have scarcely been examined empirically. Models suggest that predation on local prey may increase drastically when the alternative resource declines (Sears *et al.*, 2004). To date, empirical studies of consequences of agricultural prey spillover focused on only one or two taxa (McKone *et al.,* 2001; Kaiser *et al.*, 2008; Squires *et al.,* 2009).

The nature of spillovers across habitat edges is determined by the nature of the matrix, which could impede or facilitate dispersal between patches (Tscharntke and Brandl,

2004; Cronin, 2007). In desert agroecosystems, the contrast in biotic and abiotic conditions between agricultural fields and the desert habitat matrix is much larger than in temperate habitats. In desert systems, spillover effects are not symmetric: arthropods in less productive habitats may be more negatively affected than those in more productive habitats (Polis *et al.*, 1997). In addition, spillover may play a key role in community composition and population dynamics (Tscharntke *et al.*, 2012 and references therein). I was interested, therefore, in the effect of prey spillover on the desert community structure.

In the previous chapters, I showed that thrips and whiteflies move from crop fields into the desert habitats, where they can survive and reproduce on some desert plants. I also showed that desert predators consume these agricultural prey under laboratory conditions. Thus, these agricultural pests may subsidize predators in their natural habitat. The main goal of the work reported in this chapter was to determine whether the spillover of thrips and whiteflies affects desert community structure. If prey spillover has an effect on community structure, changes in species richness, arthropod abundance, and species composition are expected to vary with distance from the crops. If desert arthropods are subsidized by prey spillover, I expect a decrease in species richness and arthropod abundance with increasing distance from the agricultural areas, especially immediately after a spillover event. I predicted i) an increase in abundance of carnivores (predators and parasitoids) near agricultural areas; ii) an increase in carnivore abundance during pre-sanitation and sanitation phenological stages (i.e. after peaks of pest spillover); iii) a positive correlation between abundance of carnivores and agricultural pests during pre-sanitation and sanitation phenological stages; and iv) a higher proportion of the community's carnivores to be found closer to the agricultural areas, due to a numerical response of predators to prey spillover.

Materials and methods

Sampling methods: abundance and species composition of arthropods at increasing distances from agricultural areas

Patches of desert vegetation were sampled for the presence of desert and agricultural arthropods at increasing distances from the agricultural areas. Arthropods were collected on and under desert plants by visual searching and a hand-held suction device (STIHL, SH 55, diameter of the sampling tube is 0.15 m). Arthropods were collected from 18 perennial desert plant species and 24 annual desert plants species (when available) on a total of 9 bimonthly samplings between March 2008 and July 2009.

The sampled plants were situated at 0, 5, 50, 100, 300 and 700 m from the field edge, and up to 15 m from sticky traps that were erected to trap thrips and whiteflies along four line

transects at three different agricultural blocks (see chapter II). Two of the four transects were upwind of the crop fields in two agricultural blocks, and two others were downwind in a third agricultural block. These three agricultural blocks were between 8.5 to 12.5 km apart from each other. In addition, arthropods were collected from plants at four locations between 3000 and 7000 m from agricultural areas (average distance 5500 m).

Statistical analysis

For all analyses, the sampling events were grouped into four sampling periods, which were defined based on crop phenology (hereafter, agricultural phenological stages): planting, growing, pre-sanitation and sanitation phenological stages.

The effects of distance from agricultural fields, agricultural phenological stage, and plant growth type (annual or perennial) on arthropod abundance and species richness, were tested using linear mixed models for repeated measures, with the agricultural phenological stages as the repeated measures (SPSS Software, version 16.0, 2007). As the length of each agricultural phenological stage was different, arthropod abundance at each phonological stage is expressed as mean number per sampling date.

All taxa identified to the species or genus levels, as well as unique morphotypes, were included in species richness analyses. Since ants were not identified to a lower taxonomic level than family, they were not included in the species richness analysis.

To test the effect of distance, plant growth type, and agricultural phenological stage on arthropod abundance and on species richness, six increasing distances were considered: 0, 5, 50, 100, 300 and 700 m.

To study the relationship between distance from agricultural area and arthropod communities in the desert habitat, four functional groups were considered separately: 1) carnivores, 2) herbivores, 3) omnivores (consumers; feeding on both plant and prey materials), and 4) detritivores + scavengers (decomposers). The assignment of species to the different functional groups was done according to what is known about the family and species' feeding habits (McGavin and Lewington, 2001, and references therein). Those individuals that could not be assigned to a functional group were dropped from the analysis (15 % of the total arthropod individuals sampled in the desert areas). To describe the relationship between increasing distance from the agricultural fields (up to 700 m) and the arthropod abundance at each distance, a linear regression analysis was done for each functional group. To determine whether abundance of different functional groups decreased monotonically with distance, or if the relationship was nonlinear, a quadratic term was

included in the regression models. I examined the improvement in fit using a quadratic term with Akaike's Information Criterion corrected for small sample size (AICc).

I used a non-parametric correlation (JMP Software, version 9, SAS Institute, 2010) between abundance of each functional group and of the agricultural pests, whitefly and thrips, up to 700 m from agricultural fields. Linear mixed models for repeated measures, with agricultural phenological stages as the repeated measures (SPSS Software, version 16.0, 2007), were used to test whether desert carnivore abundance increases when pest spillover is greatest. Spillover of whiteflies and thrips peaked during the pre-sanitation and growing stages, respectively.

I used the abundance per sample at each phenological stage for each species to analyze community patterns. For this analysis, 0, 5, 50, 100, 300, 700 and 5500 m distances from agricultural areas were considered. These data were used to build a dissimilarity matrix based on the Bray–Curtis index of similarity, as suggested by Faith *et al.* (1987) with PAST (Paleontological Statistics, Software, version 2.15, 2012, Hammer *et al.*, 2001). The resulting matrix was then used to compare differences in species composition among the increasing distances from agricultural areas, with the non-metric multidimensional scaling (NMDS) ordination technique. This method is frequently used for graphical representation of community relationships. In this technique, a stress function assesses the goodness of fit of the ordination compared with the original sample ranking. Stress values between 0.05 and 0.1 indicate that the ordination adequately represents the data (Clarke, 1993).

Using the dissimilarity matrix built for NMDS, differences in community composition at increasing distances from agricultural areas were tested using one-way analysis of similarity (ANOSIM). ANOSIM is a non-parametric test of significant differences between two or more groups. The test statistic R determines the dissimilarity between groups. If R is close to 1, the composition of the groups is different, while if R approaches zero, the difference is small (Clarke and Gorley, 2001; Rammete, 2007). The one-tailed significance was computed by permutation of group membership, with 9999 replicates (Hammer *et al.*, 2001).

One-way ANOSIM tested the null hypothesis that no change in community structure occurred between distances. ANOSIM only indicates whether the increasing distances differ in species composition, without reference to which species cause these differences. I used the similarity percentage technique, SIMPER (Hammer *et al.*, 2001), to determine the percentage contribution of each arthropod species to the overall dissimilarity among distances (Clarke, 1993).

Results

      A. Effect of distance from agricultural areas on total arthropod abundance and species richness up to 700 m from agricultural fields

      Arthropod abundance was affected significantly by the life form of the plant and by the agricultural phenological stage. The highest arthropod abundance was found during the growing stage and on annual plants. Agricultural stage also had an effect on species richness; the highest species richness was found during the growing stage as well. Distance was not a significant factor for either abundance or richness, and the interaction between distance from agricultural areas and agricultural phenological stage was not significant for either response variable (Table 5.1).

Table 5.1: Effect of distance, plant growth type, and agricultural phenological stage on (A) arthropod abundance at each agricultural phenological stage, and on (B) species richness. Significant differences are shown in bold ($p < 0.05$).

(A) Arthropod abundance

Source	df	F	P
Intercept	1, 0.985	1.621	0.426
Agricultural phenological stage	3, 47.496	**8.642**	**0.000**
Plant growth type	1, 69.166	**4.774**	**0.032**
Distance to agricultural areas	1, 63.655	0.141	0.708
Agricultural phenological stage * distance to agricultural areas	3, 47.973	2.163	0.105

(B) Species richness

Source	df	F	P
Intercept	1, 0.752	31.934	0.168
Agricultural phenological stage	3, 33.458	**10.388**	**<0.001**
Plant growth type	1, 42.647	1.2798	0.264
Distance to agricultural areas	1, 54.746	0.747	0.391
Agricultural phenological stage * distance to agricultural areas	3, 32.744	1.456	0.244

      B. Relationship between distance from agricultural areas and abundance of different trophic groups up to 700 m from agricultural fields

Only carnivore abundance showed a significant decrease with increasing distance from agricultural fields ($F_{(1,332)}$ = 5.203, p=0.023) (Fig.5.1). However, the r^2 is low (0.015). When comparing the linear regression slopes of different functional groups, the slopes are not significantly different from each other ($F_{(3, 987)}$ = 0.271; p=0.8461). There was no improvement in fit of regressions by the inclusion of a quadratic term for any of the trophic groups (Table 5.2).

Table 5.2: AICc values of linear and quadratic models for the effect of increasing distance from agricultural fields on the abundance of arthropods belonging to four functional groups. The better model is the one with the lower AICc value.

Functional group	AICc	
	Linear	Quadratic
Carnivores	1441	3438
Herbivores	1885	4322
Omnivores	127	279
Detritivores +scavengers	1072	2583
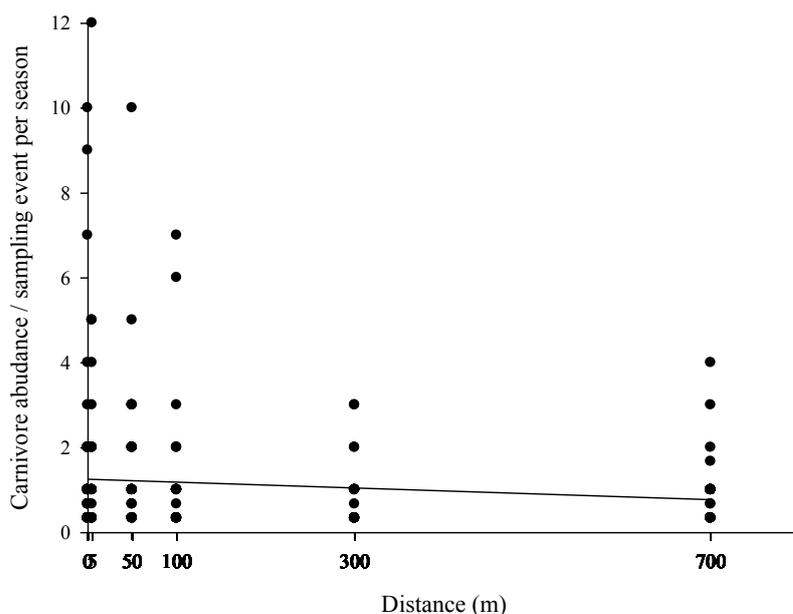
Fig.5.1: Linear relationship between distance from agricultural areas and carnivorous arthropod abundance in desert habitat.

C. Relationship between carnivore abundance, pest abundance, and distance from agricultural areas up to 700 m from agricultural fields

As carnivore abundance decreased significantly with increased distance from the agricultural areas, I analyzed the correlation between carnivore abundance and pest density for each pest species separately. There was no correlation between carnivore and whitefly abundance, and between carnivore and thrips abundance (Spearman's $\rho = -0.187$; n.s; Spearman's $\rho = 0.036$; n.s. respectively). Carnivore abundance was not affected by the agricultural phenological stage ($F_{(3, 14.237)} = 2.764$; $p = 0.08$). However, there was a positive relation between the proportion of carnivores in the sample and the distance of the sample from agricultural areas (Spearman's $\rho = 1$; $p<0.001$) (Fig. 5.2).
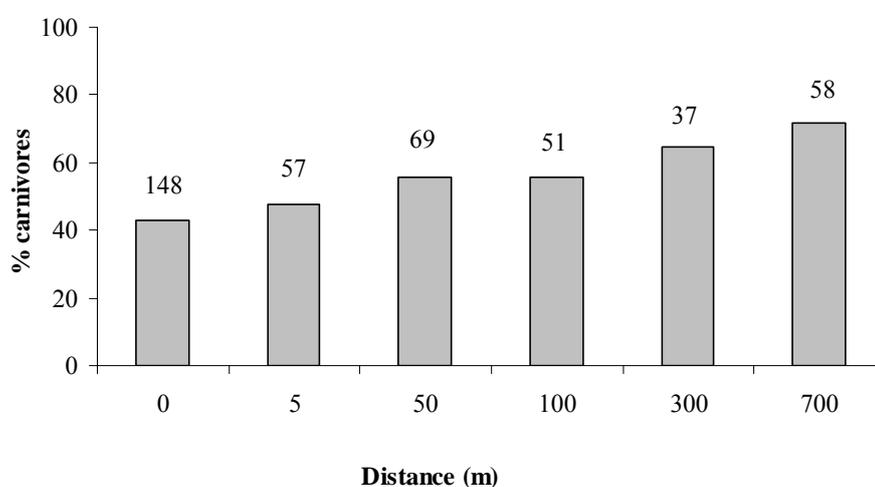
Fig.5.2: Proportion of carnivores out of all sampled arthropods at increasing distances from agricultural fields. Numbers above the bars are total number of arthropods sampled (n).

D. Community composition

One-way ANOSIM showed no significant overall difference in species composition between samples at the different distances (global R = 0.184; p = 0.081). Values of R < 0.25 are usually interpreted as barely separable groups (Clarke and Gorley, 2001; Rammete, 2007). These results are consistent with the three dimensional NMDS plot, (Fig. 5.3) which shows few distinct groups. Samples at 50, 700 and 5500 m collected on annual plants are well-separated from other annuals at closer distances. Perennial and annual samples at 0 m distance, next to the screen houses, fall together and are somewhat separated from other samples. There is no separation between samples collected on annual plants at the remaining distances, or among the perennial plant samples at any distance (Fig. 5.3).
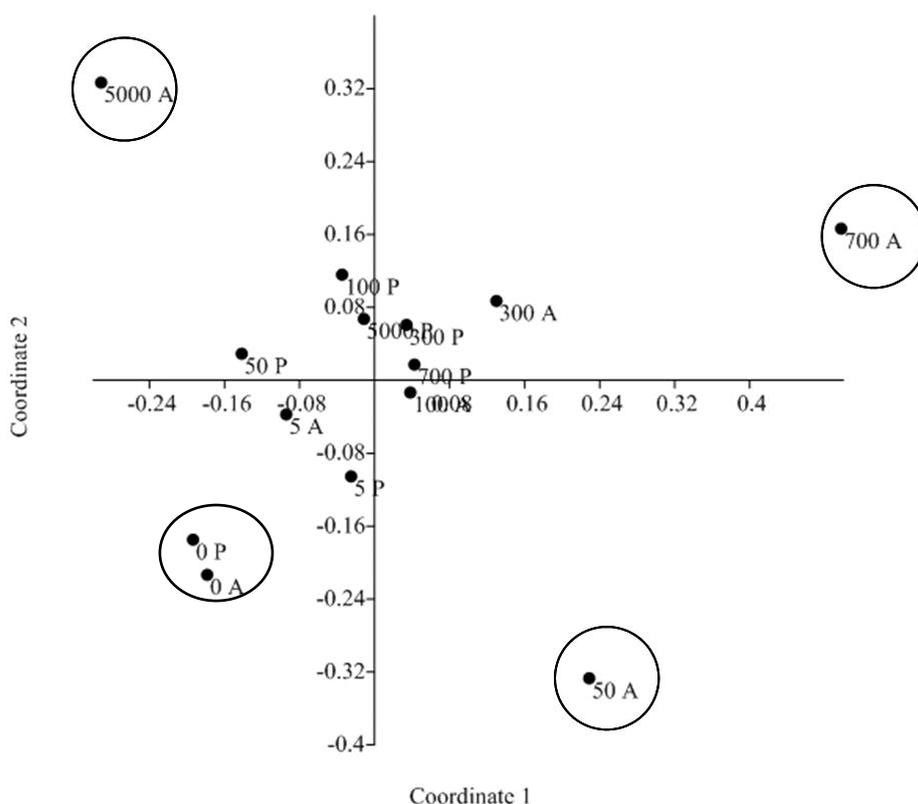
Fig 5.3: NMDS ordination comparing community composition of arthropods at different distances. The stress value (s=0.9) indicates that the map adequately represents the data. A and P stand for annual and perennial plants, respectively. Circles show groups described in the text. Numbers on axes indicate NMDS distance among samples. This distance represents the relative difference in community composition.

During the sampling, 113 species or morphotypes were found. SIMPER analysis showed that 23 species or morphotypes, out of the 113 species found, contributed the most to the overall average dissimilarity among distances when pooling all the groups together. This overall average dissimilarity was estimated at 76.3%. The remaining 90 species or morphotypes contributed together 23.7 % of the overall dissimilarity among distances.

Thanatus spp. spiders (Philodromidae) contributed the most to the dissimilarity (16.5%). However, there was no significant linear relationship between distance from agricultural areas and *Thanatus* spp. abundance in desert habitat ($F_{(1, 88)} = 0.624$; p=0.431). Carnivores contributed 32.6 % of the difference in species composition between distances (nine species of spiders accounted for 29.9 % of the difference). Herbivores contributed 25% of the difference. The two pest species, thrips and whiteflies, were 14.8 % of the total

herbivore contribution. Omnivores contributed 4.7 %, and detritivores and scavengers 2.1 %. Unknown species and unknown morphotypes contributed 11.9 % (Fig 5.4) (Appendix 5.1).
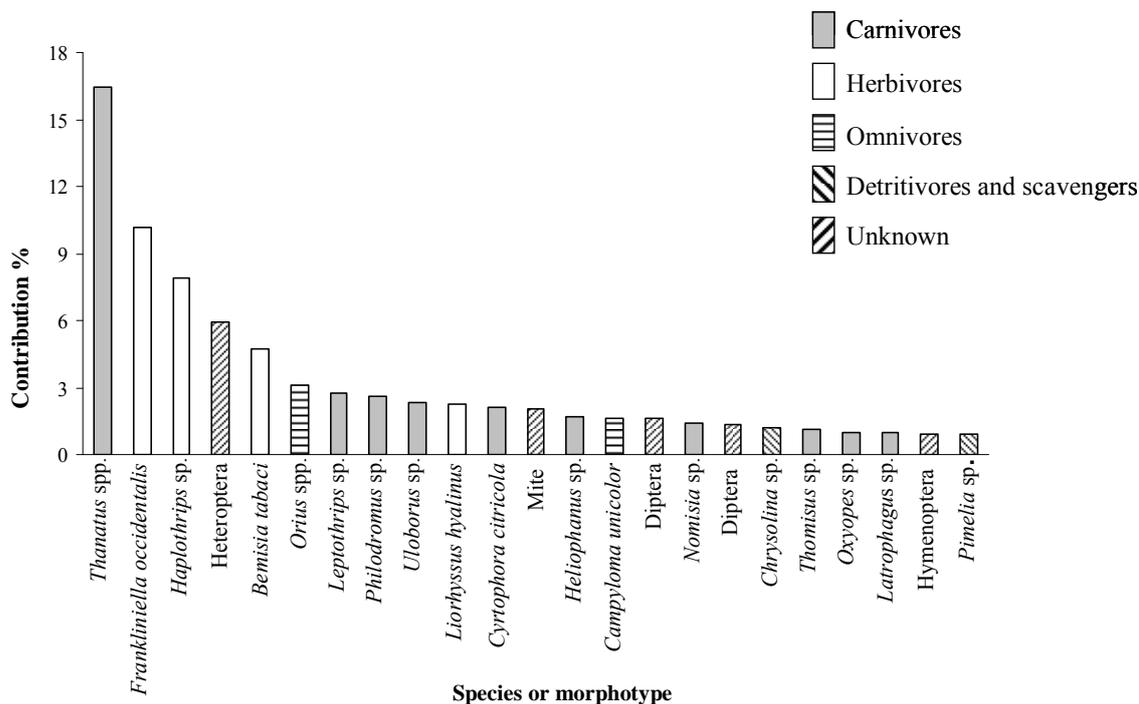
Fig.5.4: Contribution to the overall average dissimilarity by species or morphotype.

Discussion

An earlier study of desert agroecosystems showed that natural habitats contain mainly specialized desert-adapted species (Opatovsky *et al.*, 2010). I expected that the effect of agricultural areas on the desert arthropod community would decrease with the increase in distance from crop areas. I therefore predicted that distance from agricultural areas would affect arthropod abundance and species richness.

This prediction was not overall supported by the data. Only carnivore abundance decreased with increasing distance from the agricultural fields, but contrary to the prediction, the percentage of carnivores out of all arthropods increased with increasing distance. Carnivores contributed the most to the dissimilarity between sampling distances. However, there was no correlation between carnivore abundance and agricultural pest abundance, nor was there an increase in carnivore abundance during any phenological stage. There were few but still clear differences in community composition correlated with a distance gradient from agriculture fields. Samples collected on annual plants at 50, 700 and 5500 m, and those on perennials and annuals at 0 m distance, were well-separated from the other samples.

To provide evidence for a spillover effect, species richness and arthropod abundance are expected to decline with increased distance from the source habitat (Brudving *et al.*,

2009). This study shows that the spillover of agricultural prey did not have an overall effect on species richness, arthropod abundance, or community structure. Carnivore abundance, however, did show the expected pattern. This is consistent with theory that predicts predator abundance to increase locally, as prey subsidies provide additional sources of nutrients and energy (Polis *et al.,* 1997).

The increase in predator proportion with distance could be due to a productivity gradient, not related to the predators themselves. Near agricultural areas, there are patches of weed plants that provide refugia for herbivore species, and thus increase their abundance and their proportion within the arthropod samples. Another possible scenario explaining predator abundance could be that the predator numerical response near agricultural fields could be followed by an increase in species interactions that limit arthropod diversity. However, there was no correlation between predator and pest abundance, which may indicate that predators did not have a rapid numerical response to prey abundance. Alternatively, this could be due to averaging over the season, to predator efficiency in reducing prey numbers, or to scavenger activity.

The carnivores in these samples were dominated by spiders. *Thanatus* spp. spiders consumed both whiteflies and thrips under lab conditions, but both prey types were low quality food for these spiders (Chapter IV). A possible explanation for weak responses to the gradient in other groups may be the overall low density of arthropods in the study area, which makes it difficult to detect changes over the distance gradient. However, during the arthropod sampling, a large proportion of the *Thanatus* spp. was found close to the crop areas, and this group had the largest contribution to the dissimilarity among the communities at different distances. This suggests a strong response by this main predator species to the distance gradient, and this response is likely due to agricultural prey spillover.

The consequences of interactions among organisms moving between natural and agricultural habitats can depend on the distance between agricultural areas and natural habitats, and on subsidy availability as distance from the source habitat increases (Polis and Hurd, 1996; Fahrig, 2003). Few studies to date have considered the fact that allochthonous resource availability can vary with spatial location. Over the spatial and temporal scales of my study, prey spillover effects were noticeable on one group of predators (spiders), but not on the desert arthropod community overall. However, it is important to emphasize that in this chapter, I measured the overall effect of prey spillover. Not finding significant changes in arthropod desert communities after prey spillover may be the result of low population densities, and may introduce the subsequent need to combine samples within season, as well as consider possible counteracting effects that operate to cancel each other.

Appendix 5.1: Species that contributed to the SIMPER overall average dissimilarity percentage (76.3 %). The remaining 90 species or morphotypes contributed all together 23.6% to the overall dissimilarity among distances.

Functional groups	Functional group contribution %	Species or morphotype	Species or morphotype contribution %
Carnivores	32.6	*Thanatus* spp. (Araneae, Philodromidae)	16.5
		Leptothrips sp. (Thysanoptera, Phlaeothripidae)	2.8
		Philodromus sp. (Araneae, Philodromidae)	2.6
		Uloborus sp. (Araneae, Uloboridae)	2.3
		Cyrtophora citricola (Araneae, Araneidae)	2.2
		Heliophanus sp. (Araneae, Salticidae)	1.7
		Nomisia sp. (Araneae, Gnaphosidae)	1.4
		Thomisus sp. (Araneae, Thomisidae)	1.1
		Oxyopes sp. (Araneae, Oxyopidae)	1
		Latrophagus sp. (Araneae, Philodromidae)	1
Herbivores	25	*Frankliniella occidentalis* (Thysanoptera, Thripidae)	10.1
		Haplothrips sp. (Thysanoptera, Phlaeothripidae)	7.9
		Bemisia tabaci (Hemiptera, Aleyrodidae)	4.7
		Liorhyssus hyalinus (Hemiptera, Rhopalidae)	2.2

Omnivores	4.7	*Orius* spp. (Hemiptera, Anthocoridae)	3.1
		Campyloma unicolor (Hemiptera, Miridae)	1.6
Detritivores + scavengers	2.1	*Chrysolina* sp. (Coleoptera, Chrysomelidae)	1.2
		Pimelia sp. (Coleoptera, Tenebrionidae)	0.91
Unkonwn	11.9	Heteroptera	5.9
		Mite (Metastigmata)	2
		Diptera	1.6
		Diptera	1.4
		Hymenoptera	0.9

Chapter VI: Final discussion

Highly productive crop fields, as well as temporal pulses in the crop resource availability from crop emergence until harvest, can at times make crop fields a source of organisms spilling over to adjacent native habitats. Spillover of herbivores from agricultural areas to natural habitats is likely to be an important process affecting prey and predator populations in adjacent natural systems (Tscharntke *et al.*, 2005; Rand *et al.*, 2006). Currently, only a few studies have investigated the impacts at the community level of spillover of agricultural herbivores from agricultural areas to natural habitats. The present study attempted to improve our understanding of the effects of agricultural pests on natural ecosystem diversity.

In areas where the differences in productivity between natural and agricultural areas are extreme, as in desert agroecosystems, the spillover effects are expected to be stronger than in temperate climate areas (Tscharntke *et al.*, 2005). Alternatively, it could be argued that if spillover occurs in high-contrast situations, its impact may be ephemeral, because agricultural prey may not sustain high densities in desert habitats.

Species richness and arthropod abundance were expected to decline with increasing distance from the source habitat as a consequence of prey spillover (Brudving *et al.* 2009). I predicted an increase in predator richness and abundance, as a response to an increase in prey availability close to the more productive habitats.

The results of this study showed that: 1) prey spillover from agricultural fields into adjacent desert habitat clearly occurs, 2) the agricultural pests that spill over can survive on some of the native desert plants, 3) desert predators consume them, even though these pests might be low quality food items, 4) there were clear differences in community structure between communities nearest the crop area and those at the greatest distance, 5) predator abundance decreased with distance, but the proportion of predators out of total arthropods increased with distance, suggesting that they may be subsidized, and 6) the predator species (*Thanatus* spp.) had the highest contribution to the dissimilarity over distances. The largest amount of these predators was found close to the crop areas, suggesting a strong response to the distance gradient that is likely due to agricultural prey spillover.

The low population sizes in deserts may counteract the effects of prey spillover. The two pest species in this study did not maintain high populations on desert plants during most of the year, suggesting that they represent a short-lived subsidy, and that the desert arthropod community probably might revert to its natural state soon thereafter. The numerical response

of predators to prey spillover in desert habitats may not be large enough to produce changes in the community composition.

The poor nutritional quality of agricultural herbivores such as thrips and whiteflies might also play a role in reducing the effects of prey spillover. The dominant predator species sampled in the study system were species of desert spiders that may be unable to use thrips and whiteflies as prey over long periods. There are several predator species that are mass-released in the study area as biological control agents, but these predators were not the most abundant predators in the desert areas. The sampling of arthropods in desert habitats showed that the mass-released predators' contribution to the average dissimilarity across distances is low. Finally, due to the low numbers of arthropods sampled, the data were analyzed at the low resolution of crop stage, which meant combining samples over time. Thus, prey spillover effects could disappear.

A few studies have shown a negative impact of agricultural subsidies (herbivores) on natural habitat (McKone, 2001; Kaiser *et al*., 2008, Squirrel *et al*., 2009). By contrast, our results showed simply little impact, rather than a negative one. However, in these cited studies, the difference in abiotic and biotic conditions between the donor area and the natural recipient habitats were not as extreme as in the Arava hyper-arid agroecosystem.

I showed that both pest species spill over from agricultural areas into surrounding desert habitats and are found in villages close to the agricultural areas throughout the year. These two habitats are likely to play a role in pest persistence, especially during the mandatory sanitation period, acting as reservoirs of pests. Therefore, these two habitat types should be considered when developing pest control programs. For example, ornamental plants that are known to host thrips and whiteflies could be replaced by non-host plant species or, alternatively, treated with selective pesticides. The reduction of suitable non-crop host plant availability should be done before pest population build-up (Norris and Kogan, 2005). In addition, distance to patches of desert host plants should be considered when designing new cropping areas.

The findings of this study contribute to our understanding of how different communities respond to prey spillover. Spillover is a massive short-term perturbation that was expected to have a long-term negative effect on the desert arthropod community. In my study area, there is evidence that prey spillover does occur, and has an effect on desert predator population sizes. In desert areas, the population sizes are low, and therefore it is possible that only a long-term response at the community level would be noticeable. Nonetheless, predators showed a short-term numerical response to prey spillover.

The relative abundance of predators in desert habitats is high, and therefore they are considered to have a significant effect on lower trophic levels (Polis and Yamashita, 1991).

Theoretical work reviewed by Ayal (2007) suggests that predation could be an important mechanism shaping hot desert community structure and species diversity. Therefore, even a short-term response to prey spillover could have an effect on the desert arthropod community. In this study, prey spillover effects were noticeable mainly on one group of predators (spiders), but not on the desert arthropod community overall.

Only recently, the effects of spillover of subsidized agricultural crop herbivores on natural habitats have been recognized. Before this study, there was no empirical evidence on the effect of spillover in arid landscapes. The present study provides the first direct measure of the impact of agriculture on the desert arthropod community.

More studies over a longer time period and of higher temporal resolution should be conducted, to examine the ecological consequences of both prey and predator spillover effects from agricultural areas to adjacent natural habitats. For instance, the short-term numerical response to prey spillover shown by predators could affect the community composition over a longer time period. With greater temporal resolution, spillover movements of other agriculturally subsided prey or predator species might be detected.

Bibliography

Anderson, W., D. Wait, and P. Stapp (2008). "Resources from another place and time: Responses to pulses in a spatially subsidized system." Ecology 89(3): 660-670.

Ayal, Y. (2007). "Tropic structure and role of predation in shaping hot desert communities." Journal of Arid Environments 68(2): 171-187.

Batary, P., and A. Baldi (2004). "Evidence of an edge effect on avian nest success." Conservation Biology 18(2): 389-400.

Benton, T., J.A Vickery, and J.D Wilson. (2003). "Farmland biodiversity: is habitat heterogeneity the key?" Trends in Ecology and Evolution 18(4): 182-188.

Ben-Yakir, D., P. Jasrotia, and M. Chen (2006). "Temporal and spatial distribution of thrips in Israel ". Abstracts of Presentations at the 24th Congress of the Israeli Entomological Society May 17, 2005 ARO, The Volcani Center, Bet Dagan, Israel

Blitzer, E. J., C. F. Dormann, A. Holzschuh, A.-M. Klein, T. A. Rand, and T. Tscharntke (2012). "Spillover of functionally important organisms between managed and natural habitats." Agriculture, Ecosystems and Environment 146(1): 34-43.

Brudvig, L. A., E. I. Damschen, J. J. Tewksbury, N. M. Haddad, and D. J. Levey (2009). "Landscape connectivity promotes plant biodiversity spillover into non-target habitats." Proceedings of the National Academy of Sciences of the United States of America 106(23): 9328-9332.

Byrne, D. N., and T. S. Bellows (1991). "Whitefly Biology." Annual Review of Entomology 36: 431-457.

Casula, P., A. Wilby, and M. B. Thomas (2006). "Understanding biodiversity effects on prey in multi-enemy systems." Ecology Letters 9(9): 995-1004.

Chyzik, R., and O. Ucko (2002). "Seasonal abundance of the western flower thrips *Frankliniella occidentalis* in the Arava valley of Israel." Phytoparasitica 30(4): 335-346.

Chyzik, R. M. K., O. Ucko, and S. Steinberg (1999). "Biological control of Western Flower Thrips (*Frankliniella occidentalis*) by predatory *Orius* spp." Phytoparasitica 27(3): 77

Clarke, K. R. (1993). "Non-parametric multivariate analyses of changes in community structure." Australian Journal of Ecology 18(1): 117-143.

Clarke, K. R., and R. N Gorley (2001). PRIMER v5: User manual/ tutorial, PRIMER-E. Plymouth UK, 91 pp.

Contreras, J., A. Pedro, J. A. Sanchez, and A. Lacasa (1998). "The influence of extreme temperatures on the development of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae)." Boletin . Sanidad . Vegetal. Plagas 24(2): 251-266.

Corbett, A., and J. A. Rosenheim (1996). "Impact of a natural enemy overwintering refuge and its interaction with the surrounding landscape." Ecological Entomology 21(2): 155-164.

Coudriet, D. L., N. Prabhaker, A. N. Kishaba, and D. E. Meyerdirk (1985). "Variation in developmental rate on different hosts and overwintering of the sweet potato whitefly, *Bemisia tabaci* (Homoptera, Aleyrodidae)." Environmental Entomology 14(4): 516-519.

Cronin, J. T. (2007). "From population sources to sieves: The matrix alters host-parasitoid source-sink structure." Ecology 88(12): 2966-2976.

Cui X, Wan F, M. Xie, and T.,Liu. (2008). "Effects of heat shock on survival and reproduction of two whitefly species, *Trialeurodes vaporariorum* and *Bemisia tabaci* biotype B." 10 pp. Journal of Insect Science 8:24, available online: insectscience.org/8.24.

Duelli, P., M. Studer, I. Marchand, and S. Jakob (1990). "Population-movements of arthropods between natural and cultivated areas." Biological Conservation 54(3): 193-207.

Dyer, L. E. ,and D. A. Landis (1997). "Influence of noncrop habitats on the distribution of *Eriborus terebrans* (Hymenoptera: Ichneumonidae) in cornfields." Environmental Entomology 26(4): 924-932.

Fagan, W. E., R. S. Cantrell, and C. Cosner (1999). "How habitat edges change species interactions." <u>American Naturalist</u> 153(2): 165-182.

Faith, D. P., P. R. Minchin, and L. Belbin. (1987). "Compositional dissimilarity as a robust measure of ecological distance". <u>Vegetatio</u> 69(1-3):57–68.

Fahrig, L. (2003). "Effects of habitat fragmentation on biodiversity." <u>Annual Review of Ecology Evolution and Systematics</u> 34: 487-515.

Finke, D. L., and R. F. Denno (2002). "Intraguild predation diminished in complex-structured vegetation: Implications for prey suppression." <u>Ecology</u> 83(3): 643-652.

Gavish-Regev, E., Y.Lubin, and M.Coll (2008). "Migration patterns and functional groups of spiders in a desert agroecosystem." <u>Ecological Entomology</u> 33(2): 202-212.

Gavish-Regev, E., R. Rotkopf, Y. Lubin, and M. Coll (2009). "Consumption of aphids by spiders and the effect of additional prey: evidence from microcosm experiments." <u>Biocontrol</u> 54(3): 341-350

Gerling, D., O. Alomar, and J. Arno (2001). "Biological control of *Bemisia tabaci* using predators and parasitoids." <u>Crop Protection</u> 20(9): 779-799.

Hammer, Ø., D.A.T. Harper, and P. D. Ryan(2001). PAST: Paleontological Statistics Software Package for Education and Data Analysis. <u>Palaeontologia Electronica</u> 4(1): 9pp.

Hilje, L., H. S. Costa, and P. A. Stansly (2001). "Cultural practices for managing *Bemisia tabaci* and associated viral diseases." <u>Crop Protection</u> 20(9): 801-812.

Hoelmer, K. A., D. J. Schuster, and M. A. Ciomperlik. 2008. "Indigenous parasitoids of *Bemisia* in the USA and potential for non-target impacts of exotic parasitoid introductions." Pp. 307-324. *In* J. R. Gould, K. A. Hoelmer and J. A. Goolsby [eds.], *Classical biological control of Bemisia in the United States: a review of interagency research and implementation*. <u>Series: Progress in Biological Control</u>, The Netherlands: Springer, Dordrecht, Vol. 4: 307-324.

Hoelmer, K., and J. Goolsby (2003). "Release establishment and monitoring of *Bemisia tabaci* natural enemies in the United States." *1st International Symposium on Biological Control of Arthropods,* January 14-18, 2002. pp 58-65.

Holt, R.D. (1996)." Food webs in space: an island biogeographic perspective." In: *Food Webs: Integration of Patterns and Dynamics.* G.A. Polis and K.O. Winemiller, eds. London: Chapman and Hall, pp 313-323.

Holt, R. D. (1984). "Spatial heterogeneity, indirect interactions, and the coexistence of prey species." <u>American Naturalist</u> 124(3): 377-406.

Holt, R. D., and M. E. Hochberg. (2001). "Indirect interactions, community modules, and biological control: a theoretical perspective.*" In: Evaluation of Indirect Ecological Effects of Biological Control,* eds. E. Waijnberg, J.K. Scott and P.C. Quimby, CAB Internation*al:* pp 13- 37.

Holt, R. D., and J. H. Lawton (1994). "The ecological consequences of shared natural enemies." <u>Annual Review of Ecology and Systematics</u> 25: 495-520.

Huxel, G.R., G.A. Polis, and R.D. Holt (2004). "At the frontier of the integration of food web ecology and landscape ecology." In: *Food Webs at the Landscape Level.* G.A. Polis, G.R. Huxel, and M. Power, eds. Chicago ,The University of Chicago Press, pp 434-452.

Huxel, G. R., K. McCann, and G. A. Polis (2002). "Effects of partitioning allochthonous and autochthonous resources on food web stability." <u>Ecological Research</u> 17(4): 419-432.

Isaacs, R., M. A. Willis, and D. N. Byrne (1999). "Modulation of whitefly take-off and flight orientation by wind speed and visual cues." <u>Physiological Entomology</u> 24(4): 311-318.

JMP, Version 9. SAS Institute Inc., Cary, NC, 1989-2010.

Kaiser, C. N., D. M. Hansen, and C. B. Mueller (2008). "Exotic pest insects: another perspective on coffee and conservation." <u>Oryx</u> 42(1): 143-146.

Kennedy, G. G., and N. P. Storer (2000). "Life systems of polyphagous arthropod pests in temporally unstable cropping systems." Annual Review of Entomology 45: 467-493.

Kitamura, T., T. Kashio, and M. Matsui (1999). "Effect of high temperature on survival of western flower thrips, *Frankliniella occidentalis* (Pergande)." Proceedings of the Association for Plant Protection of Kyushu 45: 113-115.

Lehman, A., N. O'Rourke, L. Hatcher, and E. J. Stepanski. (2005). JMP for Basic Univariate and Multivariate Statistics: A Step-by-Step Guide. Cary, NC: SAS Institute Inc. 482 pp.

Lembo, T., K. Hampson, D. T. Haydon, M. Craft, A. Dobson, J. Dushoff, E. Ernest, R. Hoare, M. Kaare, T. Mlengeya, C. Mentzel, and S. Cleaveland (2008). "Exploring reservoir dynamics: a case study of rabies in the Serengeti ecosystem." Journal of Applied Ecology 45(4): 1246-1257.

Logarzo, G. A., M. I. Zamar, D. Richman, and O. Bruzzone (2012). "Structure and composition of a thrips community in the Chihuahua Desert, New Mexico, Us." Florida Entomologist 95(1): 35-42.

Lubin, Y. (2006). "Spiders as generalist predators: a dryland agroecosystem perspective." Phytoparasitica 34(4): 327-330.

Madsen, M., S., Terkildsen, and S. Toft (2004). "Microcosm studies on control of aphids by generalist arthropod predators: Effects of alternative prey." Biocontrol 49(5): 483-504.

Mayntz, D., and S. Toft (2001). "Nutrient composition of the prey's diet affects growth and survivorship of a generalist predator." Oecologia 127(2): 207-213

McGavin, G.R., and R. Lewington (2001). Essential entomology: an order-by-order introduction. Oxford, Oxford University Press, 318 pp

McKone, M. J., K. K. McLauchlan, E. G. Lebrun, and A. C. McCall (2001). "An edge effect caused by adult corn-rootworm beetles on sunflowers in tallgrass prairie remnants." Conservation Biology 15(5): 1315-1324.

Mound, L.A. (1983). "Natural and disrupted patterns of geographical distribution in Thysanoptera (Insecta)". Journal of. Biogeography. 10(2): 119-133.

Naranjo, S.E, C. P. C. Ellsworth, and L. Cañas (2007). "Mortality and Population Dynamics of *Bemisia tabaci* within a Multi-Crop System." Fourth International Bemisia Workshop International Whitefly Genomics Workshop. 37 pp. Journal of Insect Science 8:4, available online: insectscience.org/8.04.

Naveed, M., A. Salam, and M. A. Saleem (2007). "Contribution of cultivated crops, vegetables, weeds and ornamental plants in harboring of *Bemisia tabaci* (Homoptera: Aleyrodidae) and associated parasitoids (Hymenoptera: Aphelinidae) in cotton agroecosystem in Pakistan." Journal of Pest Science 80(4): 191-197.

New, T. R. (2005). Invertebrate Conservation and Agricultural Ecosystems. Cambridge, Cambridge University Press, 348 pp.

Norris, R. F., and M. Kogan (2005). Ecology of interactions between weeds and arthropods. Annual Review of Entomology. 50: 479-503.

Opatovsky, I., T. Pluess, M. H. Schmidt-Entling, E. Gavish-Regev, and Y. Lubin (2010). "Are spider assemblages in fragmented, semi-desert habitat affected by increasing cover of agricultural crops?" Agriculture, Ecosystems and Environment 135(4): 233-237.

Ostfeld, R. S., and F. Keesing (2000). "Pulsed resources and community dynamics of consumers in terrestrial ecosystems." Trends in Ecology and Evolution 15(6): 232-237.

Polis, G., W.B .Anderson, and R.D. Holt. (1997). "Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs." Annual Review of Ecology and Systematics 28: 289-316.

Polis, G. A., and S. D. Hurd (1996). "Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities." American Naturalist 147(3): 396-423.

Polis, G. A., and R. D. Holt (1992). "Intraguild predation - the dynamics of complex trophic interactions." <u>Trends in Ecology and Evolution</u> 7(5): 151-154.

Polis, G.A., and T. Yamashita (1991). "The ecology and importance of predaceous arthropods in desert communities." Chapter 7, in*: The Ecology of Desert Communities*. G.A Polis, ed. . Tucson,University of Arizona Press, pp. 180-222.

Ramette, A. (2007). "Multivariate analyses in microbial ecology." <u>FEMS Microbiology Ecology</u> 62(2): 142-160.

Rand, T. A., J. M. Tylianakis, and T. Tscharntke (2006). "Spillover edge effects: The dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats." <u>Ecology Letters</u> 9(5): 603-614.

Rand, T. A., and S. M. Louda (2006). "Spillover of agricultural subsidized predators as a potential threat to native herbivores in fragmented landscapes." <u>Conservation Biology</u> 20(6): 1720-1729.

Ries, L., Fletcher, RJU, Battin, and T. Sisk (2004). "Ecological response to habitat edges: mechanisms, models, and variability explained." <u>Annual Review of Ecology and Systematics</u> 35: 491-522.

Rosenheim, J. A., H. K. Kaya, L. E. Ehler, J. J. Marois, and B. A. Jaffee (1995). "Intraguild predation among biological-control agents, theory and evidence." <u>Biological Control</u> 5(3): 303-335.

Sears, A.L.W., R.D. Holt, and G.A. Polis (2004). "Feast and Famine in food webs: the effects of pulsed productivity." In: *Food Webs at the Landscape Level*. G.A. Polis, G.R. Huxel, and M. Power, eds. Chicago,The University of Chicago Press, pp.359-386.

Sih, A., G. Englund, and D. Wooster (1998). "Emergent impacts of multiple predators on prey." <u>Trends in Ecology and Evolution</u> 13(9): 350-355.

Snyder, W., and E. Evans (2006). "Ecological effects of invasive arthropod generalist predators." <u>Annual Review of Ecology, Evolution and Systematics</u> 37: 95-122.

Snyder, W. E., and D. H. Wise (1999). "Predator interference and the establishment of generalist predator populations for biocontrol." Biological Control 15(3): 283-292.

SPSS Inc. Released 2007. SPSS for Windows, Version 16.0. Chicago, SPSS Inc.

Squires, S. E., L. Hermanutz, and P. L. Dixon (2009). "Agricultural insect pest compromises survival of two endemic *Braya* (Brassicaceae)." Biological Conservation 142(1): 203-211.

Stephens, D.W., and J.R Krebs, (1986). Foraging Theory. Princeton: Princeton University Press. 247 pp

Symondson, W. O. C., K. D. Sunderland, and M. H. Greenstone (2002). "Can generalist predators be effective biocontrol agents?" Annual Review of Entomology 47: 561-594.

Tscharntke, T., J. M. Tylianakis, T. A. Rand, R. K. Didham, L. Fahrig, B. Peter, J. Bengtsson, Y. Clough, T. O. Crist, C. F. Dormann, R. M. Ewers, J. Fruend, R. D. Holt, A. Holzschuh, A. M. Klein, D. Kleijn, C. Kremen, D. A. Landis, W. Laurance, D. Lindenmayer, C. Scherber, N. Sodhi, I. Steffan-Dewenter, C. Thies, W. H. van der Putten, and C. Westphal (2012). "Landscape moderation of biodiversity patterns and processes - eight hypotheses." Biological Reviews 87(3): 661-685.

Tscharntke, T., T. A. Rand, and F. Bianchi (2005). "The landscape context of trophic interactions: insect spillover across the crop-noncrop interface." Annales Zoologici Fennici 42(4): 421-432.

Tscharntke, T., and R. Brandl (2004). "Plant-insect interactions in fragmented landscapes." Annual Review of Entomology 49: 405-430

Ucko, O., S. Cohen, and R. Ben-Joseph (1998). "Prevention of virus epidemics by a crop-free period in the Arava region of Israel." Phytoparasitica 26(4): 313-321.

Wagner, T. L. (1995). "Temperature-dependent development, mortality, and adult size of sweet-potato whitefly biotype-b (Homoptera, Aleyrodidae) on cotton." Environmental Entomology 24(5): 1179-1188.

Wissinger, S. A. (1997). "Cyclic colonization in predictably ephemeral habitats: A template for biological control in annual crop systems." <u>Biological Control</u> 10(1): 4-15.

Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright (2008). "What can we learn from resource pulses?" <u>Ecology</u> 89(3): 621-634.

Yang, L. H. (2004). "Periodical cicadas as resource pulses in North American forests." <u>Science</u> 306(5701): 1565-1567.

Zar, JH (1999). Biostatistical analysis. 4th edidtion. Prentice- Hall Inc. New Jersey.663 pp

Zhang, Z. J., Q. Wu, X. F. Li, Y. J. Zhang, B. Y. Xu, and G. R. Zhu (2007). "Life history of western flower thrips, *Frankliniella occidentalis* (Thysan, Thripae), on five different vegetable leaves." <u>Journal of Applied Entomology</u> 131(5): 347-354.

מעבר פרוקי רגליים משטחים חקלאיים לאזורים מדבריים סמוכים והשפעתם על מבנה החברה המדברית

מחקר לשם מילוי חלקי של הדרישות לקבלת תואר ״דוקטור לפילוסופיה״

מאת
ולריה הוכמן אדלר

הוגש לסינאט אוניברסיטת בן גוריון בנגב

ספטמבר 2012

באר שבע

מעבר פרוקי רגליים משטחים חקלאיים לאזורים מדבריים סמוכים והשפעתם על מבנה החברה המדברית

מחקר לשם מילוי חלקי של הדרישות לקבלת תואר "דוקטור לפילוסופיה"

מאת
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הוגש לסינאט אוניברסיטת בן גוריון בנגב

ספטמבר 2012

באר שבע

אישור המנחה ....

אישור המנחה ....

אישור דיקן בית הספר ללימודי מחקר מתקדמים ע"ש קרייטמן........................

העבודה נעשתה בהדרכתם של

פרופ׳ יעל לובין [1]

פרופ׳ משה קול [2]

[1] **המחלקה לאקולוגיה מדברית ע״ש מיטרני,**

המכונים לחקר המדבר על שם יעקב בלאושטיין,

אוניברסיטת בן גוריון בנגב, ישראל

[2] **המחלקה לאנטומולוגיה,**

הפקולטה לחקלאות, מזון וסביבה ע״ש ר.ה. סמית,

האוניברסיטה העברית בירושלים, ישראל

הצהרת תלמיד המחקר עם הגשת עבודת הדוקטור לשיפוט

אני החתום מטה מצהיר/ה בזאת : (אנא סמן) :

_x___ חיברתי את חיבורי בעצמי, להוציא עזרת ההדרכה שקיבלתי מאת מנחה/ים.

_x_ ___ החומר המדעי הנכלל בעבודה זו הינו פרי מחקרי מתקופת היותי תלמיד/ת מחקר.

____ בעבודה נכלל חומר מחקרי שהוא פרי שיתוף עם אחרים, למעט עזרה טכנית

הנהוגה בעבודה ניסיונית. לפי כך מצורפת בזאת הצהרה על תרומתי ותרומת שותפי   למחקר, שאושרה על ידם ומוגשת בהסכמתם.

תאריך __19 ספטמבר2012_   שם התלמיד/ה   _ולריה הוכמן אדלר

חתימה _____

תקציר

גלישה של פרוקי רגליים מאזורי חקלאות יכולה להשפיע על הדינמיקה של מארגי מזון בסביבה הטבעית.

ניטרתי את ארועי הגלישה של פרוקי רגליים המזיקים מאזורי חקלאות לאזורים בהם אין חקלאות, תזמון הגלישה בהתאם לעונת הגידול, עוצמת הגלישה בהתאם למרחק מהגידול והשפעתה על קהילת פרוקי הרגליים המדבריים באזורים צחיחים. המחקר נערך בערבה התיכונה, ישראל.

הנחת העבודה היא שפרוקי רגליים מזיקים ינועו מבתי גידול בעלי יצרניות גבוהה לבתי גידול בעלי יצרניות נמוכה, וגלישת פרוקי הרגליים המזיקים (מקור) תשפיע על קהילת פרוקי הרגליים המדבריים הטבעיים (מבלע). שטחי החקלאות האינטנסיבית בערבה מספקים הזדמנות נדירה ללמוד את השפעת גלישת פרוקי הרגליים המזיקים. השטחים המעובדים מוקף בבתי גידול מדבריים קיצוניים ויוצרים אזורים בעלי יצרניות גבוהה - "איים" - במטריצה המדברית.

המחקר עסק בארבע שאלות מרכזיות : 1) האם ישנה גלישה של חרקים מזיקים מאזורים חקלאיים לאזורים הסמוכים להם, והאם יש ירידה בכמות המזיקים לאורך מרחק עולה מהאזורים החקלאיים? 2) בהנחה שישנה גלישה, האם המזיקים יכולים לשרוד ולהתרבות באזורי המדבר? הגלישה למדבר רלוונטית אם פרוקי הרגליים המזיקים יכולים לתרום לאוכלוסיות של טורפים או דטריטיבורים מדבריים. 3) האם פרוקי הרגליים המזיקים נאכלים ע"י טורפים מדבריים, והאם הם משפיעים על יחסי גומלין בין פרוקי הרגליים הטורפים המדבריים? ו- 4) האם ישנם שינויים בהרכב המינים של חברת פרוקי הרגליים המדברית כתוצאה מהשפעה של גלישת פרוקי הרגליים המזיקים?

בדקתי את הנחות העבודה ע"י ניטור של השכיחות והתפוצה של פרוקי רגליים מאזורים חקלאיים לאזורים מדבריים הסמוכים להם ואת יחסי הגומלין עם המינים הטבעיים. על מנת לענות על השאלות ; ראשית, ניטרתי את המצאות המזיקים בהתאמה לעונות השונות של הגידול באזורים מדבריים סמוכים ובגנים פרטיים במושבים הסמוכים לחקלאות. שנית, בדקתי האם פרוקי הרגליים המזיקים יכולים לשרוד ו\או להתרבות על צמחי מדבר. שלישית, ערכתי ניסויי מעבדה לבדיקת יחסי הגומלין בין פרוקי הרגליים המזיקים לפרוקי הרגליים המדבריים הטורפים, ובחנתי את הדרכים בהם יכולים פרוקי הרגליים המזיקים להשפיע על חברת פרוקי הרגליים המדברית. לסיום, דגמתי את חברות פרוקי הרגליים לאורך מרחק עולה מאזורי הגידול.

הראתי שלפרוקי הרגליים המזיקים יש את האפשרות לגלוש ולשרוד על צמחייה מדברית מקומית בתוך אזורים טבעיים המשיקים לאזורי החקלאות.בנוסף, פרוקי הרגליים המזיקים נאכלים ע"י פרוקי רגליים מדבריים טורפים, ולכן יכולים לקיים את אוכלוסיית הטורפים. התוצאות הראו שיש הבדלים משמעותיים במגוון המינים באזורים הקרובים לאזורי החקלאות, אך לא היתה התאמה בקשר למרחק מאזורי החקלאות. לעומת זאת, שכיחות הטורפים ירדה בהתאמה למרחק מאזורי החקלאות, מה שמצביע על תגובה של הטורפים לתוספת בשכיחות המזיקים. במספר קטן של מחקרים הראו שיש השפעה חלשה של תוספת בכמות המזיקים הצמחוניים על הטורפים המקומיים באזורים טבעיים לא מדבריים. במחקר זה נמצא כי השפעות גלישת הטרף היו מובהקות על קבוצת טורפים אחת (עכבישים), אך לא על פרוקי הרגליים המדבריים באופן כללי.

יש צורך במחקרים נוספים לטווח ארוך יותר אשר יהיו בעלי תדירות בדיקה גבוהות יותר על מנת שניתן יהיה לבדוק את ההשפעות האקולוגיות של גלישת המזיקים החקלאיים, והטורפים הטבעיים, המוספים מאזורים חקלאיים לאזורים מדבריים טבעיים הסמוכים להם.