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Use of alternative habitats by spiders in a desert agroecosystem

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Abstract. Annual crop fields are short-lived and disturbed environments. Therefore, sustainable populations of natural enemies in these fields must be maintained by repeated colonization each season from habitats outside the crop fields. In desert agroecosystems, unmanaged habitats differ greatly in abiotic and biotic conditions from croplands, creating potentially significant barriers to movement of predators. We asked here: to what extent do predators use non-crop habitats as refuges or breeding sites in the desert agroecosystem of the northern Negev, Israel? We investigated the use of natural desert habitat, planted trees (*Eucalyptus*), and a summer crop (sunflowers) by winter-wheat inhabiting spiders. We collected spiders using pitfall traps and a suction device from wheat fields and adjacent to non-wheat habitats during the wheat season and between seasons. We found that two crop specialist species, *Trichoncoides piscator* (Simon, 1884) (Linyphiidae) and *Thanatus vulgaris* Simon, 1870 (Philodromidae), switched to an alternative crop during the inter-wheat season. Habitat generalist species, such as *Nomisia* sp. (Gnaphosidae), *Enoplognatha* spp. (Theridiidae) and *Alioranus pastoralis* (O. Pickard-Cambridge, 1872) (Linyphiidae) used alternative non-crop habitats as refuges and breeding sites to differing degrees in both seasons. While all habitat generalist species used the desert habitat, none used planted trees exclusively as an alternative habitat. We conclude that crop-inhabiting, desert species may be unable to colonize the wheat fields if nearby desert habitat is supplanted by other crops or by tree plantations.

Keywords: breeding site, colonization, planted trees, refuge

Crop fields may provide high quality habitats for predators that are attracted to the fields by an abundance of prey. Nevertheless, the fields are often short-lived and disturbed habitats owing to crop management practices, qualities that may make them less suitable for predators. Seasonal crops in particular favor herbivore species that can survive and reproduce in spatially and temporally changing environments, and have developed good dispersal abilities and short life cycles that are completed during a single crop season (Ehler & Miller 1978). Many predators, however, have long life cycles relative to the crop cycle. In order to maintain stable populations of predators that can act as natural enemies of crop herbivores, alternative habitats must be available between crop seasons. These habitats may provide refuge, prey and breeding sites, and thus serve as sources of populations that will colonize the crop fields in the following season (Landis et al. 2000).

The suitability of alternative habitats is determined by habitat characteristics such as the abiotic and biotic conditions they provide, their stability over time, and above all by the permeability of their boundary with the crop fields (Burel et al. 2000; Hunter 2002). In spite of the presumed importance of these habitats, relatively few studies have demonstrated the use of multiple alternative habitats by crop-inhabiting predators. Here, wheat fields in a desert agroecosystem serve as a case study of alternative habitat use by spiders that colonize the wheat fields. Spiders are generalist predators with diverse predatory behaviors, habitat preferences and dispersal abilities (Nyffeler & Benz 1987; Uetz et al. 1999). They can be important predators of crop pests in temperate regions (Nyffeler & Sunderland 2003; Symondson et al. 2003) and also in desert crops (Opatovsky et al. 2012). Spiders in annual crops can be divided generally into agrobiont species that are phenologically synchronized with the disturbance regime in the crop fields (Birkhofer et al. 2013) and those with long life cycles that require additional habitats for survival. For the latter species, the presence of alternative habitats to complete their life cycle, and the ability to move between habitats, are essential features of the system that will enable them to sustain activity in the fields.

Desert agroecosystems, unlike temperate ones, are characterized by strong contrasts between the crop fields and neighboring habitats, which may restrict the ability of predators to take advantage of alternative habitats. Nevertheless, Pluess et al. (2008) showed that during the wheat season, more than 50% of the spider species occurring in wheat fields are found also in the adjacent desert habitat. However, while several spider species were shown to immigrate into the wheat fields from habitats outside the crop fields (Gavish-Regev et al. 2008), only a few species were found to move across the boundary into the desert habitat immediately after the wheat harvest (Opatovsky & Lubin 2012). These possibly contradictory results led us to investigate the use of alternative habitats by crop-inhabiting spider species during both crop and inter-crop seasons in this desert agroecosystem. We asked whether desert habitats serve as refuges and breeding sites for wheat-inhabiting spiders between crop seasons. Alternatively, spiders could move to planted trees or other crops as the season progresses. These different possibilities can have important implications for management of the desert agroecosystem, namely whether or not to maintain natural habitat surrounding the crop fields.

The aim of this research was to reveal how different habitats are used by wheat-inhabiting spiders in the crop and inter-crop seasons. We sampled spiders in paired, adjacent habitat patches in the northern Negev desert: wheat fields paired with

Table 1.—Description of substrate and vegetation characteristics in each habitat at each sampling session.

	Jan	Feb	Apr	Jun	Aug	Sep	Nov
Desert	Perennials & green annuals			Perennials & dry annuals	Perennials & sparse dry annuals		
Trees	Moist leaf litter				Dry leaf litter		
Wheat	Green		Dry	Dry stubble	Plowed fields		Newly seeded fields
Sunflowers	-			Young plants	Dry plants	Dry stubble	Plowed fields

adjacent desert habitat or with planted eucalyptus trees, and post-harvest (fallow) wheat fields paired with desert, planted trees or a summer crop (sunflowers). These different habitat types are characterized by different biotic and abiotic conditions and by their degree of stability over the seasons. The wheat fields are covered by homogenous vegetation during the crop season and are bare between seasons, while the natural desert habitat is more stable, but is dry most of the year with a short period with annual vegetation after the rainy season. The planted tree habitat combines the stability of the natural environment with higher vegetation cover and cooler micro-climate also during the summer when the desert habitat and wheat fields are dry. The summer crops (sunflowers in our study) are usually irrigated during the summer and therefore provide moist habitat in this dry environment. The phenology of these different habitats and the environmental conditions provided could determine their availability to wheat-inhabiting spiders.

METHODS

Study sites.—Spiders were sampled in an area of approximately 30 km^2 of agricultural fields of Kibbutz Be'eri, Israel (31° 25′ 37″ N, 34° 29′ 34″ E), an area that is dominated by large annual crop fields. During the winter, the main crop is winter wheat (*Triticum aestivum* L.), which is sown after the first rain (November) and harvested in March for green fodder or in May for grain. Most of the wheat fields are dryland crops that rely on the annual precipitation (ten year average: 271 mm, data from the Israel Meteorological Service). During the summer, the agricultural fields either remain as plowed, bare soil or a summer crop is grown. The sampling was done in 14 sites that included wheat fields adjacent to different non-wheat habitats. Six wheat field sites were adjacent to planted trees ("tree"), four sites were adjacent to natural, desert habitat ("desert") and four fallow wheat field sites were adjacent to sunflowers (*Helianthus annuus* - "sunflower"). The latter sites were sampled during the summer, inter-wheat season. The "wheat", "desert" and "tree" habitats were not irrigated, with the exception of two wheat fields near planted trees, which received irrigation during November right after sowing, while the "sunflower" habitat was irrigated throughout the sampling sessions. The planted trees were non-indigenous *Eucalyptus* (mainly *Eucalyptus camaldulensis*) planted along the dry river-banks to prevent soil erosion (180–330 trees per hectare). The soil cover in the tree habitats was mostly dry leaf litter and sparse shrubs. The cover in the desert habitats was composed of annual vegetation appearing mainly after the rainy season, but dry the rest of the year, and scattered shrubs and perennial grasses (*Asphodelus aestivus*, *Lyceum shawii*, *Stipa capensis*) (Table 1).

Spider sampling.—Three samples were taken during the wheat-growing season (January, February and April, 2011), three samples in the inter-wheat season (June, August and September, 2011) and one sample at the beginning of the following wheat crop season (November, 2011). The spiders were sampled using pitfall traps and a suction device (except the sample in November 2011, which was done only with pitfall traps). Eight pitfall traps were located parallel to the field's edge, 50 m into the field and 50 m into the adjacent habitat respectively (a total of 16 traps for each site) and were separated from one another by 3 m. In the planted tree habitat, the traps were located near the center of the habitat, between 10 and 50 m into the habitat, owing to the restricted width of the *Eucalyptus* habitat at some sites. The traps were 10 cm deep with a 9 cm diameter opening, buried in the ground so the rim was level with the surface, and each contained 100 ml of 50% ethylene glycol with a drop of detergent to break the surface tension. The traps were open for a week each sampling session.

The suction samples were taken using a Stihl SH55 suction device with a tube opening of 65 mm diameter. Samples were taken along five transects in each habitat, 50 m from the habitat edge and parallel to it, except in the planted trees habitat, which was sampled in the center of the habitat (10 to 50 m from the habitat edge). Each transect was 20 m long and the suction device was lowered for 10 s at each 1 m along the transect (total of 20 collections per sample and 10 samples per site). A fine mesh sleeve was inserted into the collecting tube of the device, and after each transect the contents of the sleeve were emptied into a bag that was cooled until the spiders were separated in the laboratory using a hand-held aspirator. The spiders were stored in 70% ethanol until they were identified. Adult spiders were identified to species level using taxonomic keys (Levy 1985, 1988; Roberts 1995; Proszynski 2003). Nomenclature was adapted to the World Spider Catalogue (World Spider Catalog 2016). Immature individuals were identified to genus or family level. Voucher specimens are deposited in the arachnid collection of the Hebrew University of Jerusalem.

Data analysis.—The analysis was done on the lowest taxonomic level possible of the four most common spider families (with more than 10% of the total number of individuals collected). First, the effect of two factors, season (wheat season and inter-wheat season) and habitat (planted tree, desert, summer crop and adjacent wheat fields), was tested. We used a generalized linear model with a Poisson distribution on the average number of individuals per pitfall trap or suction sample, with habitat type and season as fixed categorical factors and the site as a random factor. The response variable (average number of individuals per trap or suction sample) was chosen from the sampling method that collected the largest total number of individuals (Table 2).

Table 2.—The total number of individuals of each spider group collected in each sampling method and the average number of individuals per trap or suction sample. Significant differences between the numbers of individuals collected in each method (t-test) are marked in bold. For analysis of the effects of habitat and season on abundance, we used the data from the sampling method that yielded the largest number of individuals.

Group	Collecting method	No. of individuals caught in each method	Average of individuals per trap/suction sample	t	*P*
Linyphiidae					
Alioranus pastoralis	Pitfall	36	0.07	0.72	0.47
	Suction	10	0.04		
Trichoncoides piscator	Pitfall	34	0.03	1.82	0.07
	Suction	0	0		
Gnaphosidae					
Nomisia	Pitfall	29	0.04	1.42	0.16
	Suction	6	0.01		
Juveniles of *Nomisia*	Pitfall	92	0.09	0.69	0.48
	Suction	36	0.08		
Theridiidae					
Enoplognatha	Pitfall	46	0.14	**2.53**	**0.01**
	Suction	9	0.04		
Juveniles of *Enoplognatha*	Pitfall	16	0.02	**3.1**	**0.002**
	Suction	33	0.1		
Philodromidae					
Thanatus vulgaris	Pitfall	179	0.17	**3.04**	**0.002**
	Suction	15	0.03		
Thanatus fabricii	Pitfall	225	0.25	**2.39**	**0.02**
	Suction	1	0.001		
Juveniles of *Thanatus*	Pitfall	32	0.03	**3.94**	**<0.001**
	Suction	681	1.71		

Second, we tested the differences in spider abundance between the main habitats by using multiple comparisons of the significant factors. In cases where interactions between the habitat type and season were significant, the comparisons were done between habitats in each season separately. To evaluate the importance of the alternative habitats as breeding sites, the analysis described above was repeated for the juvenile stages of the main spider groups. In addition, the abundances of adults and juveniles in the wheat fields and alternative habitats were plotted over the year to examine patterns of change.

The statistical analyses were done using R 3.1.2 (R Core Team 2014) with nlme package (Pinheiro et al. 2016).

RESULTS

A total of 4133 individuals were collected in the two sampling methods in both seasons and in all habitats combined. Of these, 468 individuals belonging to 18 families were collected in the wheat fields during the crop season. The most common families in the wheat fields were Linyphiidae (sheet-web spiders, 25% of the total individuals), Gnaphosidae (ground spiders, 17%), Theridiidae (tangle-web spiders, 14%) and Philodromidae (running crab spiders, 13%).

Linyphiidae.—Adult linyphiids were collected mainly in pitfall traps and no juveniles were found. Of five species, two species dominated the samples: *Alioranus pastoralis* (O. Pickard-Cambridge, 1872) and *Trichoncoides piscator* (Simon, 1884) (28% and 22%, respectively, in the wheat fields).

During the wheat season, *A. pastoralis* was collected in wheat fields and desert habitat only, and it was not found in the inter-wheat season at all (Fig. 1A, $F_{2,61} = 0.83$, $P = 0.41$; Table 3). The seasonal dynamics of *A. pastoralis* show low abundance in the desert habitat and in adjacent wheat fields at the beginning of the season (Fig. 1B). By April, this species disappeared from the desert habitat and appeared in large numbers in wheat fields adjacent to planted trees, but not in the adjacent trees (Fig. 1B).

Trochonchoides piscator occurred during the wheat season in the wheat fields and trees, but not in the desert habitat (Fig. 1C; overall $F_{2,61} = 1.84$, $P = 0.07$; Table 3). In the inter-wheat season, *Tr. piscator* occurred in fallow wheat fields and in sunflowers and was significantly more abundant in the sunflower crop (Fig. 1C; overall, $F_{3,78} = 3.55$, $P < 0.001$, sunflowers vs. wheat, $P < 0.001$; Table 3). The decrease in abundance of *Tr. piscator* in wheat fields at the end of the season was followed by an increase in the sunflower fields (Fig. 1D).

Gnaphosidae.—The genus *Nomisia* Dalmus, 1921 constituted 27% of the gnaphosid individuals collected in pitfall traps in the wheat fields. The only species of *Nomisia* found in all habitats was *Nomisia ripariensis* (O. Pickard-Cambridge, 1872), however, there were too few individuals to analyze habitat preference at the species level, due to the low proportion of adults and the inability to separate juveniles to species. Adults and juveniles were found in both seasons in all habitats except sunflowers. Their abundances did not differ significantly among wheat fields, trees and desert habitat (Adult: Fig. 2A; Season, $F_{1,141} = 0.09$, $P = 0.92$, Habitat: $F_{3,141} = 1.11$, $P = 0.27$; Juveniles: Fig. 2C; Season, $F_{1,141} = 0.04$, $P = 0.97$, Habitat: $F_{3,141} = 0.81$, $P = 0.42$; Table 3). Adults were found in tree habitats at the end of the wheat season while juveniles appeared in low abundances in the tree and desert habitats earlier in the season (Fig. 2B, D).

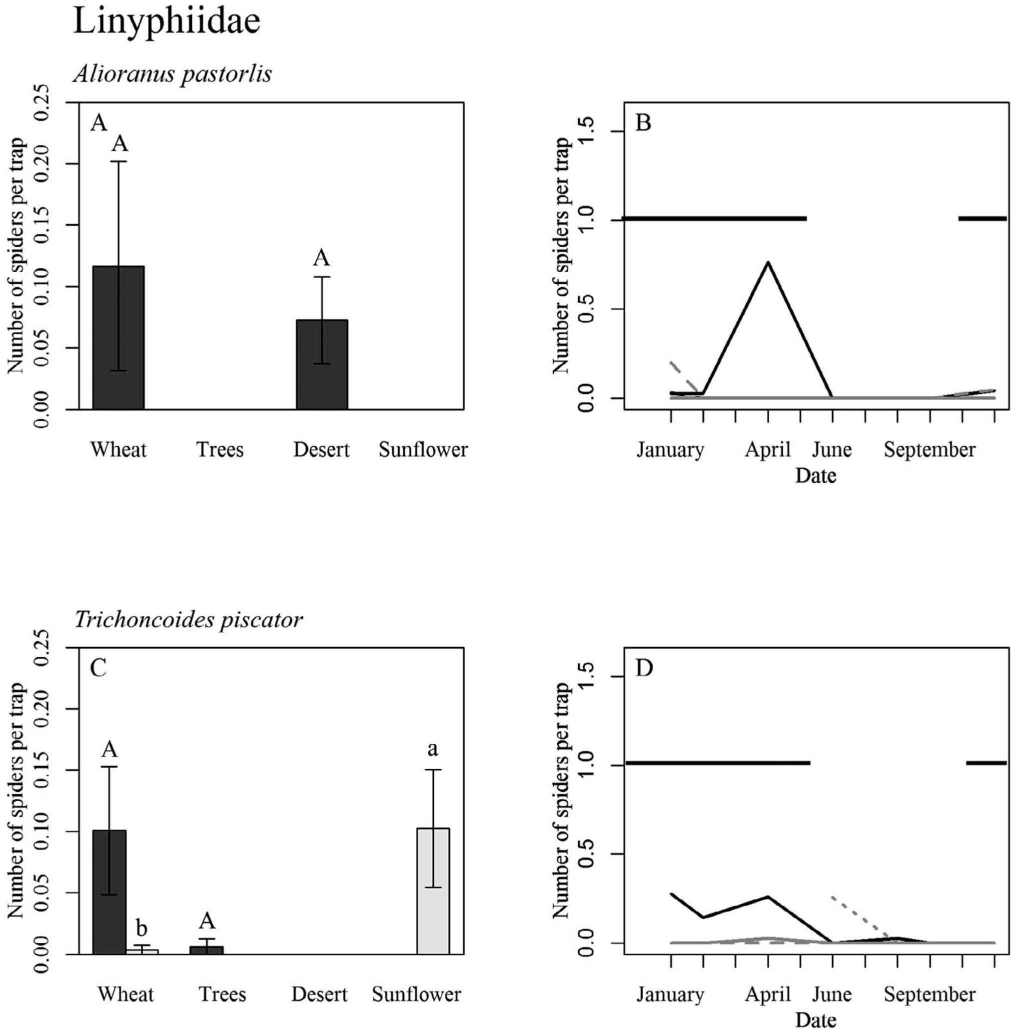

Figure 1.—Abundance of *Alioranus pastoralis* (A, B) and *Trichoncoides piscator* (C, D) (Linyphiidae) across habitat types and seasons (mean number of individuals per pitfall trap ± s.e.). A, C. The average numbers found in the four different habitat types (wheat fields, planted eucalyptus trees, desert and sunflower fields). The black bars represent the wheat season (October–May) and the grey bars represent the inter-wheat season (May–October). The letters above the bars represent significant differences ($P < 0.05$) between habitat types within each season. B, D. Changes in abundance in wheat adjacent to trees (solid black line), wheat adjacent to desert (broken black line), planted trees (solid grey line), and desert (broken grey line). Horizontal lines at the top indicate the wheat season.

Theridiidae.—The genus *Enoplognatha* Pavesi, 1880 constituted 52% of the total theridiid spiders collected in the wheat fields. The adults were collected in pitfall traps and the juveniles mainly by suction device (Table 2). There were two common species, *E. gemina* Bosmans & Van Keer, 1999 and *E. macrochelis* Levy & Amitai, 1981, which were combined, as there were not enough individuals of each species alone to test for habitat use. Adults and juveniles were trapped only during the wheat season, in wheat, planted trees and desert habitat. Adults occurred in significantly lower numbers in the trees than in the desert habitat (Fig. 3A; overall $F_{2,61} = 2.27$, $P = 0.03$; trees vs. desert, $P = 0.04$; Table 3), while juveniles were found in all habitats except sunflowers (Fig. 3C; $F_{2,61} = 1.1$, $P = 0.29$; Table 3). Adults and juveniles were present in the desert habitat and adjacent wheat fields early in the wheat season (Fig. 3B, D).

Philodromidae.—There were two common species, out of five species: *Thanatus fabricii* (Audouin, 1826) (50% of total adult philodromids in pitfall samples) and *Th. vulgaris* Simon, 1870 (45%). Adults were collected in pitfall traps and juveniles by suction device (Table 2). *Thanatus fabricii* was found mainly in the desert habitat with no differences between seasons (Fig. 4A; overall $F_{3,141} = 2.73$, $P = 0.01$, desert vs. wheat $P = 0.001$, desert vs. trees $P = 0.001$; desert vs. sunflowers $P = 0.02$; Table 3).

Thanatus vulgaris dominated the samples collected from the wheat fields (87% of philodromids from wheat fields). *Thanatus vulgaris* was found in higher abundance during the inter-wheat season ($F_{1,141} = 1.96$, $P = 0.04$; Table 3). During this season, *Th. vulgaris* adults were collected mostly in sunflower fields (Fig. 4C; overall, $F_{3,80} = 2.8$, $P = 0.006$, sunflowers vs. trees $P = 0.01$, sunflowers vs. desert $P = 0.01$, sunflowers vs. wheat $P = 0.04$; Table 3). During the wheat season *Th. vulgaris* occurred in all habitats ($F_{2,61} = 1.69$, $P = 0.09$; Table 3), however its abundance increased in the wheat fields toward the end of the wheat season (Fig. 4D)

Juvenile *Thanatus* were found mostly in the inter-wheat season and in higher abundance in the sunflower fields (Fig.

Table 3.—Habitat preference of the main spider groups (family, genus and dominant species) between the wheat fields and adjacent alternative habitats during the wheat season (desert, planted trees) and between fallow wheat fields and a summer crop (sunflowers) between wheat seasons. Significant effects from GLMM and post hoc comparisons are marked in bold.

Group	Factor	F(df)	*P*	Significant differences
Linyphiidae				
Alioranus pastoralis	Season	-	-	Found only in the wheat season
	Habitat (wheat season)	0.83 (2,61)	0.41	
Trichoncoides piscator	Season	**3.35 (1,141)**	**0.001**	**Between seasons>wheat season**
	Habitat	**2.97 (3,141)**	**0.003**	
	Season*Habitat	**3.0**	**0.003**	
	Habitat (wheat season)	1.84 (2,61)	0.07	
	Habitat (between seasons)	**3.55 (3,78)**	**<0.001**	**Sunflower>wheat (<0.001)**
				Sunflower>trees (<0.001)
				Sunflower>desert (<0.001)
Gnaphosidea				
Nomisia	Season	0.09 (1,141)	0.92	
	Habitat	1.11 (3,141)	0.27	
Nomisia juveniles	Season	0.04 (1,141)	0.97	
	Habitat	0.81 (3,141)	0.42	
Theridiidae				
Enoplognatha	Season	-	-	Found only in the wheat season
	Habitat (wheat season)	**2.27 (2,61)**	**0.03**	**Desert>trees (0.04)**
Enoplognatha juveniles	Season	-	-	Found only in the wheat season
	Habitat (wheat season)	1.1 (2,61)	0.29	
Philodromidae				
Thanatus fabricii	Season	1.24 (1,141)	0.21	Wheat season>between seasons
	Habitat	**2.73 (3,141)**	**0.01**	**Desert>wheat (<0.001)**
				Desert>trees (<0.001)
				Desert>sunflower (0.02)
Thanatus vulgaris	Season	**1.96 (1,141)**	**0.04**	**Between seasons>wheat season**
	Habitat	**2.21 (3,141)**	**0.02**	
	Season*Habitat	**2.87**	**0.004**	
	Habitat (wheat season)	1.69 (2,61)	0.09	
	Habitat (between seasons)	**2.8 (3,80)**	**0.006**	**Sunflower>wheat (0.04)**
				Sunflower>trees (0.01)
				Sunflower>desert (0.01)
Thanatus juveniles	Season	**3.19 (1,141)**	**0.001**	**Between seasons>wheat season**
	Habitat	**2.26 (3,61)**	**0.02**	
	Season*Habitat	**2.05**	**0.04**	
	Habitat (wheat season)	**2.45 (2,40)**	**0.01**	**Desert>wheat (0.04)**
				Desert>trees (0.04)
	Habitat (between seasons)	**2.15 (3,73)**	**0.03**	**Sunflowers>wheat (0.04)**

4E; season, $F_{1,141} = 3.19$, $P = 0.001$, habitat, $F_{1,161} = 2.26$, $P = 0.02$, habitat (inter-wheat), $F_{3,73} = 2.15$, $P = 0.03$, sunflowers vs. wheat $P = 0.04$; Table 3). Juveniles increased in abundance in all non-wheat habitats at the end of the summer (Fig. 4F). During the wheat season juvenile abundance was low but was significantly higher in the desert habitat (overall, $F_{2,40} = 2.45$, $P = 0.01$, desert vs. wheat $P = 0.04$, desert vs. trees $P = 0.04$; Table 3).

DISCUSSION

Overall, spider abundance was low in our samples, as is typical of these desert agroecosystems (Pluess et al. 2008; Opatovsky et al. 2010; Opatovsky & Lubin 2012). By comparison, cereal fields and adjacent grasslands in temperate regions of Europe have abundances several times greater than in our samples (e.g., Schmidt & Tscharntke 2005a; Schmidt-Entling & Döbeli 2009). However, in both regions, the natural habitats harbor higher spider abundance and species diversity than the adjacent crop fields (Schmidt & Tscharntke 2005b; Pluess et al. 2008).

The use of two sampling methods, pitfall traps and suction sampling, provided an additional level of information and allowed us to track the different life stages of spiders, as in some instances juveniles and adults were collected by different methods. For example, adults of *Th. vulgaris* and *Th. fabricii* are terrestrial and were collected almost exclusively by pitfall traps, while the juveniles of these species occur in the vegetation layer and were collected mainly by suction sampling. Thus, we were able to determine the presence of juveniles and adults in each of the habitats in each season, as well as the changes in their abundance over time.

Our results indicate differences in the patterns of habitat use in the different spider groups, and also between juveniles and adults. As predicted, crop specialists switched to an alternative crop during the inter-wheat season, while habitat generalist

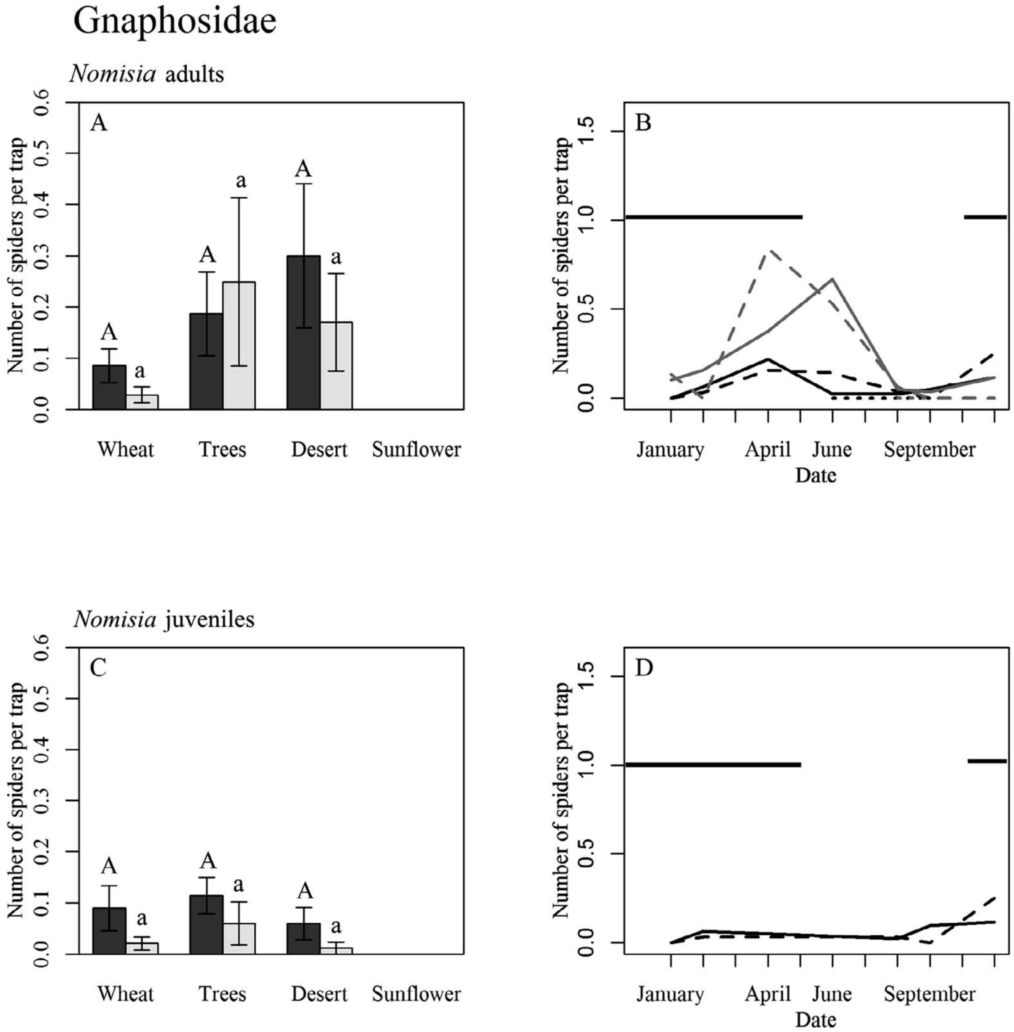

Figure 2.—Abundance of *Nomisia* (Gnaphosidae) adults and subadults (A, B) and juveniles (C, D) across habitat types and seasons (mean number of individuals per pitfall trap ± s.e.). A, C. The average numbers found in the four different habitat types (wheat fields, planted eucalyptus trees, desert and sunflower fields). The black bars represent the wheat season (October–May) and the grey bars represent the inter-wheat season (May–October). The letters above the bars represent significant differences ($P < 0.05$) between habitat types within each season. B, D. Changes in abundance in wheat adjacent to trees (solid black line), wheat adjacent to desert (broken black line), planted trees (solid grey line), and desert (broken grey line). Horizontal lines at the top indicate the wheat season.

species used desert and tree habitats to differing degrees in both seasons. In this system, two species can be considered crop specialists: *Trichoncoides piscator* (Linyphiidae) and *Thanatus vulgaris* (Philodromidae). The former is noted as an agrobiont species in Europe and is associated with different crops (e.g., oilseed rape, Drapela et al. 2008). *Thanatus vulgaris*, to our knowledge, was not previously noted as a crop specialist spider. In Israel, it is recorded throughout the country (Levy 1977). Possibly the species is typical of more mesic habitats, and can survive in the Negev desert only in crop fields.

Trichoncoides piscator disappeared from the wheat at the end of the season and simultaneously appeared in the sunflowers fields. Similarly, *Th. vulgaris* invaded sunflower fields during the inter-wheat season, but nevertheless also remained in fallow wheat fields after the wheat harvest (Opatovsky & Lubin 2012), indicating the possibility of surviving the inter-crop season as adults in the fallow fields. Juveniles may have a broader habitat tolerance than adults, as they were found in the eucalyptus trees and desert during the inter-wheat season as well as in the sunflower fields. However, we could not distinguish juveniles of *Th. fabricii* from those of *Th. vulgaris*. Thus, it is possible that juveniles found in the tree and desert habitats were *Th. fabricii*, while those in the sunflowers were largely *Th. vulgaris*. This interpretation is supported by the fact that during the inter-wheat season *Th. fabricii* adults inhabited the tree and desert habitats, while *Th. vulgaris* adults were infrequent in these habitats.

Spill-over of natural enemies into the surrounding natural environment at the end of the crop season is known in temperate agroecosystems (Rand et al. 2006). Apparently, crop specialist species in the desert agroecosystem are unable to disperse into the desert environment at the end of the wheat season and have to disperse to more mesic environments such as other crop fields. Therefore, the crop specialist spiders such as *Tr. piscator* and *Th. vulgaris* do not necessarily benefit from a diversified agroecosystem with non-crop habitats, as was found also for *Tenuiphantes tenuis* (Blackwall, 1852) (Liny-

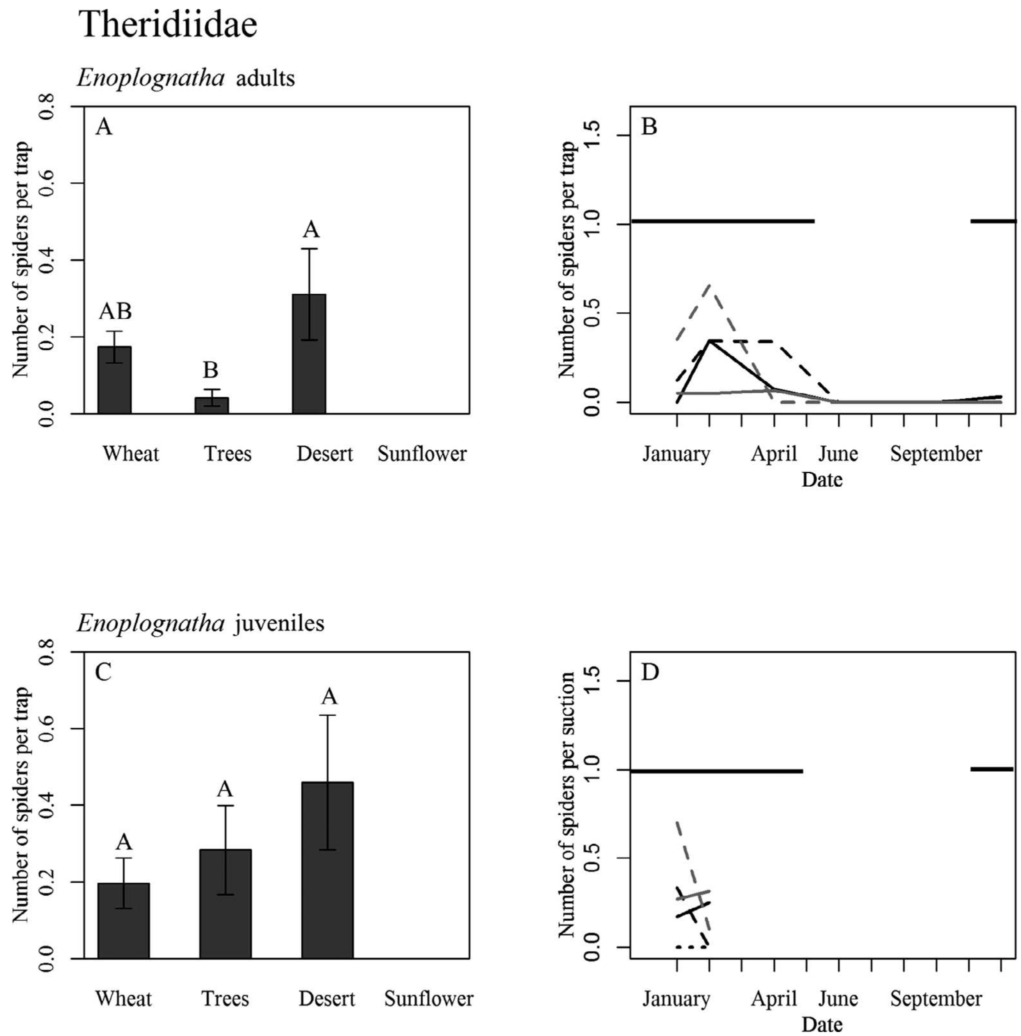

Figure 3.—Abundance of *Enoplognatha* (Theridiidae) adults and subadults (A, B) and juveniles (C, D) across habitat types and seasons (mean number of individuals per pitfall trap/suction sample, respectively ± s.e.). A, C. The average numbers found in the four different habitat types (wheat fields, planted eucalyptus trees, desert and sunflower fields). The black bars represent the wheat season (October–May) and the grey bars represent the inter-wheat season (May–October). The letters above the bars represent significant differences ($P < 0.05$) between habitat types within each season. B, D. Changes in abundance in wheat adjacent to trees (solid black line), wheat adjacent to desert (broken black line), planted trees (solid grey line), and desert (broken grey line). Horizontal lines at the top indicate the wheat season.

phiidae) in the temperate region (Schmidt et al. 2008). While natural habitats provide refuge during the winter in temperate regions (Pfiffner & Luka 2000), we suggest that in desert agroecosystems summer crops are refuges for agrobiont species that cannot survive in the desert habitat during the summer.

Both species of linyphiids (*Tr. piscator* and *A. pastoralis*) occurred in high abundance in the two irrigated wheat fields adjacent to planted trees, leading to large variance in the abundance of these two species in this habitat. *Alioranus pastoralis* was absent from the non-irrigated wheat fields adjacent to trees, and *Tr. piscator* had ten times higher abundance in the irrigated compared to non-irrigated wheat fields adjacent to trees. It is likely that the higher humidity and plant productivity favors these linyphiids (Nyffeler & Sunderland 2003). *Alioranus pastoralis* was not found at all in the inter-crop season, but surprisingly, it occurred in the desert habitat at the beginning of the wheat season, increasing in abundance in the wheat fields only around the middle of the crop season. *Alioranus pastoralis* was observed to lay eggs in the wheat fields (I. Opatovsky, personal observation) and Gavish-Regev et al. (2008) suggested that linyphiid eggs might survive in the soil until the next wheat season. Our results suggest, however, that populations of *A. pastoralis* are resident also in the desert habitat (see also Pluess et al. 2008), and this habitat may act as a dispersal source at the beginning of the wheat season.

Spider groups that used non-wheat habitats to a significant extent during part of their life cycle include the crop residents, *Nomisia* (Gnaphosidae) and *Enoplognatha* (Theridiidae), and desert species such as *Thanatus fabricii* (Philodromidae), and possibly *Alioranus pastoralis* (see above). *Nomisia* are nocturnally active hunting spiders that maintained stable populations of juveniles and adults in the desert and tree habitats and entered the wheat fields at the beginning of the crop season. The generalist habitat preference of these spiders allows each habitat in the agroecosystem to serve as dispersal source. This may explain the early colonization of the wheat fields by

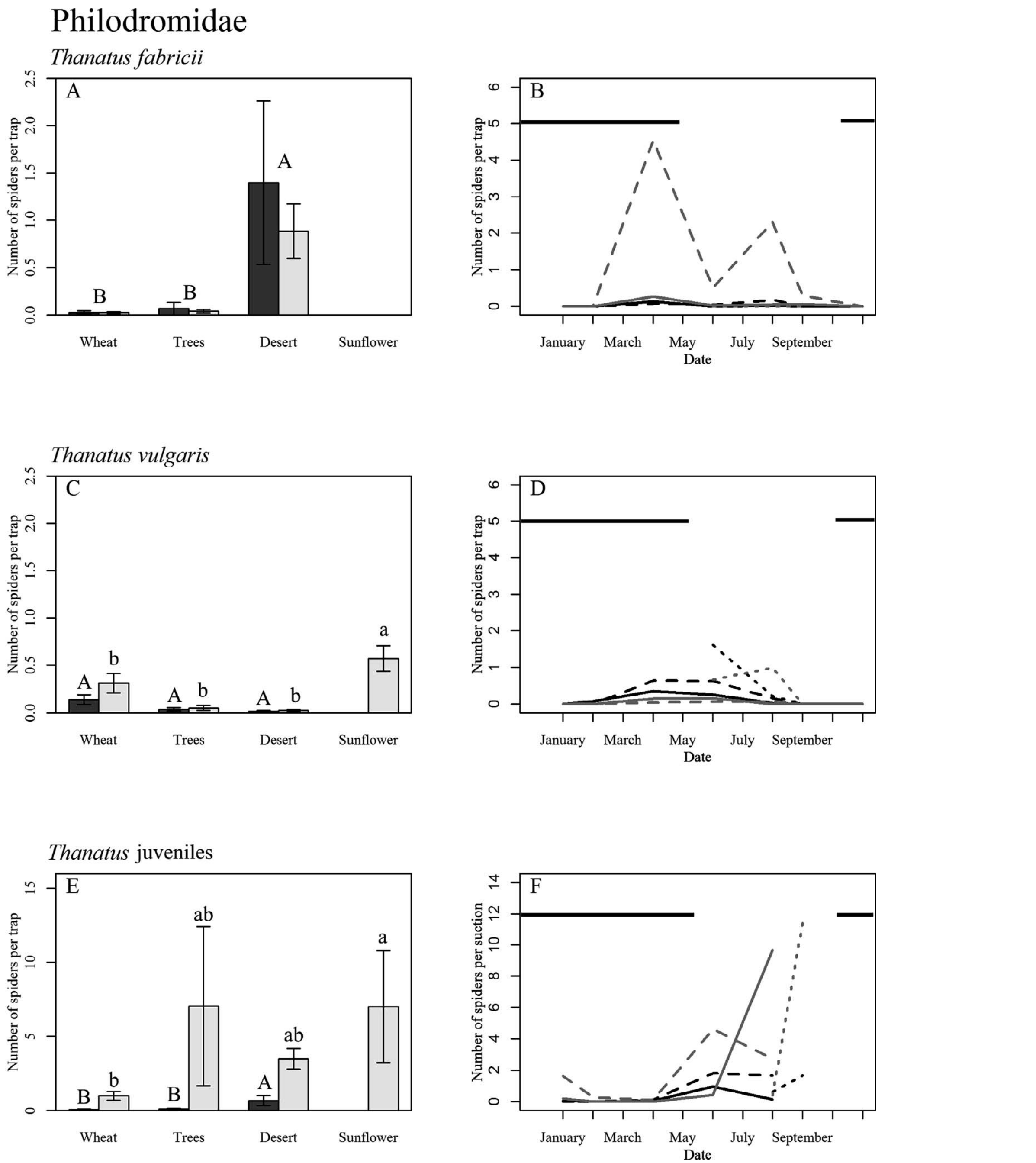

Figure 4.—Abundance of *Thanatus fabricii* adults (A, B) and *T. vulgaris* adults (C, D), and juveniles of *Thanatus* (Philodromidae) (E, F) across habitat types and seasons (mean number of individuals per pitfall trap/suction sample, respectively ± s.e.). A, C. The average numbers found in the four different habitat types (wheat fields, planted eucalyptus trees, desert and sunflower fields). The black bars represent the wheat season (October–May) and the grey bars represent the inter-wheat season (May–October). The letters above the bars represent significant differences ($P < 0.05$) between habitat types within each season. B, D, F. Changes in abundance in wheat adjacent to trees (solid black line), wheat adjacent to desert (broken black line), fallow wheat adjacent to sunflowers (dotted black line), planted trees (solid grey line), and desert (broken grey line) and sunflowers (dotted grey line). Horizontal lines at the top indicate the wheat season.

Nomisia in spite of having cursorial dispersal. Such early immigration into the field from the surrounding habitats may be important in controlling populations of the herbivorous insects early in the season (Birkhofer et al. 2008). Adult and juvenile *Enoplognatha* had a similar distribution pattern to *Nomisia*. Both species of *Enoplognatha* are small spiders that construct sheet webs near the ground. Theridiid juveniles, primarily *Enoplognatha* species, were found to immigrate into Negev wheat fields at the beginning of the crop season, most likely by ballooning, as they appeared simultaneously throughout the field (Gavish-Regev et al. 2008; Opatovsky et al. 2016). *Thanatus fabricii*, unlike the crop specialist *Th. vulgaris*, appears to be mainly a desert species that occurred also in low abundance in the adjacent wheat fields and in eucalypt trees. It is recorded as occurring in sandy habitats in the Middle East and North Africa (Levy 1977).

The planted eucalyptus trees are alien species and are generally thought to harbor lower insect species diversity and abundance in comparison with native trees (Gardner et al. 2008; Gries et al. 2012). However, Herrmann et al. (2015) found that the eucalyptus plantings increase spider species diversity in the semi-desert agroecosystem of Israel. Nevertheless, we found that this habitat was not a uniquely occupied alternative habitat for any of the spider groups that dominated the wheat fields. Some species even avoided the planted trees, for example *A. pastoralis* and adults of *Enoplognatha,* perhaps due to unsuitable conditions for web building. Species that used the tree habitat invariably were found in the desert habitat as well, leading to the conclusion that wheat-inhabiting spiders might not derive special benefit from eucalyptus groves surrounding the crop fields.

With the exception of the two crop-resident species, the linyphiid *Tr. piscator* and the philodromid *Th. vulgaris*, all other species investigated here are most likely desert or disturbed habitat species that invade agricultural fields during the cropping season. In temperate regions, the presence of grassland and forest habitats near cereal fields was shown to have a positive effect on spider species abundance in the crop fields (Schmidt & Tscharntke 2005a, b; Öberg et al. 2007; Hogg & Daane 2010). In general, increasing habitat diversity within the agroecosystem can increase the abundance and diversity of generalist predator species (Sunderland & Samu 2000; Birkhofer et al. 2014). In this desert region, proximity of these natural habitats to the crop fields can facilitate the dispersal of the spiders into the crop, as some crop-inhabiting desert species may be unable to colonize the wheat fields if nearby desert habitat is supplanted by other crops or even by tree plantations. Consequently, in desert agroecosystems, natural or semi-natural habitats should be conserved in order to increase spider abundance and potential biocontrol services provided by them.

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