

## ARTICLE

# Longevity of hymenopteran parasitoids in natural versus agricultural habitats and implications for biological control

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**Funding information**

United States-Israel Binational  
 Agricultural Research and Development  
 Fund; Vaadia-BARD Postdoctoral  
 Fellowship Award, Grant/Award Number:  
 FI-589-2019; Rothschild Family  
 Foundation; Steenbock Professorship  
 Award

**Handling Editor:** Nicolas Desneux

**Abstract**

Agricultural habitats are frequently disturbed, and disturbances could have major effects on species in upper trophic levels such as hymenopteran parasitoids that are important for biological control. A strategy for conservation biological control is to provide a diversified agricultural landscape which increases the availability of resources such as sugar required by parasitoid biological control agents. Here, we ask whether parasitoids occurring in agriculture benefit from sugar resources more or less than parasitoids occurring in natural habitats surrounding agricultural fields. We collected parasitoids from agricultural alfalfa fields, field margins, and natural prairies, and in the lab we randomly divided them into two treatments: half were given a constant supply of a sugar source to test their residual lifespan, and half were given neither sugar nor water to test their hardiness. Collected individuals were monitored daily and their day of death recorded. Parasitoids receiving a sugar source lived substantially longer than those without. Parasitoids collected in prairies lived longer than those from alfalfa fields in both the residual lifespan and hardiness treatments, with parasitoids from field margins being intermediate between them. Furthermore, the benefits of a sugar source to increase longevity was lower for parasitoids collected in agriculture than in natural habitats. This suggests that, even though parasitoid biological control agents benefit from sugar resources, their short lifespans make the benefit of sugar resources small compared to parasitoids that occur in natural habitats and have longer lifespans, and are adapted to consistent sugar sources.

**KEYWORDS**

*Aphidius ervi*, hardiness, lifespan, lucerne, prairies, senescence, traits

**INTRODUCTION**

Frequent disturbances, chemical toxin applications, and low plant diversity make agricultural systems harsh

environments for most insects (Matson et al., 1997; Tsoraeva et al., 2020). This is especially true for species that occupy upper trophic levels, such as predators and parasitoids, which require more resources than a conventional

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agricultural plot might provide (Begg et al., 2017; Root, 1973). These resources include alternative prey or hosts, shelter and habitat for diapause, and sugar sources for adults (Heimpel & Jervis, 2005; Landis et al., 2000). Conservation biological control consists of a suite of strategies that are designed to foster predator and parasitoid biological control agents by decreasing disturbances in agricultural fields or augmenting resources within the agricultural landscape. The success of many of these strategies depends on increasing the survival of biological control agents, thereby increasing their lifetime attacks on target pests. Thus, understanding factors that determine the survival of biological control agents across the agricultural landscape is important for designing and assessing conservation biological control.

Many of the most successful biological control agents are hymenopteran parasitoids whose high specificity to target pests both increases the likelihood that their dynamics are tightly coupled to those of the pests and decreases the chances of negative impacts on non-target species. Most parasitoid species require a sugar source as adults which they get mainly in the form of floral nectar or honeydew secreted from sap-feeding insects (Doutt, 1964; Mockford et al., 2022; Russell, 2015; Siekmann et al., 2001; Tena et al., 2018). Sugar meals increase parasitoid longevity, allow for higher oviposition rates, and increase dispersal (Heimpel, 2019; Landis et al., 2000), and parasitoids actively feed on sugar sources in the field (Jervis et al., 1993). Some parasitoid species have low feeding rates in agricultural habitats (Segoli & Rosenheim, 2013), while others have high feeding rates (Lee & Heimpel, 2008) due to honeydew feeding in agricultural habitat (Luquet et al., 2021; also see Heimpel & Jervis, 2005, tab. 9.1 for more examples of different rates of feeding). In studies of multispecies parasitoid communities, higher rates of sugar feeding have been found in natural than in agricultural habitats (Kishinevsky et al., 2018; Kishinevsky & Keasar, 2021). Even though evidence for sugar limitation in agricultural systems is often lacking, a commonly proposed strategy for conservation biological control for parasitoids is to increase floral resources in natural habitats within an agricultural landscape, with the expectation that this will increase parasitoid longevity.

Measuring adult insect lifespan under field conditions is difficult (Nussey et al., 2013), especially for small hymenopteran species. Nonetheless, for some parasitoid biological control agents, longevity may depend on sugar resources in the habitat. Lee and Heimpel (2008) found that the parasitoid species *Diadegma insulare* (Ichneumonidae) survived longer when floral resources were added to an agricultural field. Greater longevity was also found in cage experiments for the parasitoid *Eriborus terebrans*

(Ichneumonidae), an important natural enemy of the European corn borer *Ostrinia nubilalis* (Lepidoptera), when cages were set in natural habitats compared with agricultural plots (Dyer & Landis, 1996).

Natural and agricultural habitats may have substantial differences in insect community composition (Derocles et al., 2014; Shapira et al., 2018) causing systematic differences among communities in the traits of their constituent species. Parasitoids found in agricultural habitats must be capable of maintaining populations in the presence of disturbances such as insecticide use and harvesting. These disturbances may kill parasitoids directly, and they may also lower sugar availability by decreasing the abundances of flowers and sap-feeding insects that produce honeydew (Lee et al., 2006; Tena et al., 2013). Trait-based predictions for hymenopteran parasitoids are premised on the assumption that the agricultural habitat will contain species that are adapted to harsh environments. For example, a generalist feeding strategy, small body size, and relatively longer activity periods are associated with intensified agricultural environments (Gámez-Virués et al., 2015; Perović et al., 2018). Furthermore, differences in senescence are often associated with differences in environmental conditions; habitats with higher adult mortality risk often contain species with lower adult longevity and earlier senescence (Bryant & Reznick, 2004; Stearns et al., 2000; Williams, 1957). Thus, if agricultural habitats are harsh compared with natural habitats, parasitoid species with shorter lifespans might be expected to be more common in agricultural habitats. If senescence is rapid, increased sugar resources may not increase longevity substantially enough to improve biological control, and this might explain in part the lack of improvement in biological control following habitat diversification found in many studies (Karp et al., 2018).

Here, we investigate the longevity of hymenopteran parasitoids in three different habitats. We collected parasitoids from alfalfa (lucerne) fields, their field margins and nearby prairies, and returned them to the lab where we measured how long they lived either with or without a sugar source. We refer to the days to death with a sugar source as residual lifespan; this is not the total length of time they lived, because they were collected from the field where their ages were unknown. We refer to the days to death without sugar as hardiness. While lack of resources is only one type of environmentally harsh condition, it is biologically relevant for parasitoids that must survive the disturbances of alfalfa crops, specifically mowing and harvesting that create hot and dry conditions. We expected natural habitats to be less harsh than alfalfa fields and field margins to have intermediate harshness. We had this expectation because the tallgrass prairies have a high diversity of plant species, so both

floral nectar and honeydew are available as sugar sources for parasitoids. Alfalfa fields are monocultures, and the only sugar source potentially available for parasitoids is honeydew produced by aphids, at least when aphids are present. Using residual lifespan and hardiness measured from 1590 individuals from 21 hymenopteran families, we asked: (1) Do residual lifespan and hardiness differ among habitats? and (2) Would parasitoids from agricultural fields gain more from access to sugar sources than parasitoids from prairies and field margins? We expected that hardiness would be greater for parasitoids collected from agricultural fields, whereas residual lifespan would be greater for parasitoids collected from prairies, with field margins intermediate for both traits. Because we expected the lifespan of parasitoid species found in agriculture to be lower than species in natural habitats, we expected sugar sources to be of less benefit to those parasitoids from agriculture.

## METHODS

### Study system

Our study was conducted in and around the Arlington Agricultural Research Station, the West Madison Agricultural Station, and the Goose Pond restored tallgrass prairies; these sites were in Dane and Columbia Counties, Wisconsin, USA. Alfalfa fields make up roughly 20% of land area (Kishinevsky & Ives, 2022). The restored prairies are embedded in the agricultural area, resulting in close proximity of natural and agricultural habitats. Alfalfa is a perennial crop and is harvested roughly every 30 days, usually three times during the growing season. Alfalfa field margins have naturally occurring plants and are cut at a frequency similar to alfalfa harvesting. Many insects inhabit alfalfa fields, including herbivores, predators, and parasitoids. A dominant herbivorous insect in alfalfa is the pea aphid (*Acyrtosiphon pisum*), and its primary natural enemy is the parasitoid *Aphidius ervi* (Braconidae) which itself is attacked by several parasitoid species (hyperparasitoids). Other key herbivorous insects in alfalfa include the potato leafhopper (*Empoasca fabae*) and the alfalfa caterpillar (*Colias eurytheme*). We have little comprehensive information about the insect composition in the restored tallgrass prairies.

Alfalfa fields are a good system to study the effects of harsh environments on the traits of natural enemies because they are frequently harvested. Harvesting leaves fields with almost no leaf material and hence minimal shelter and moisture. Harvesting also causes high direct mortality of hosts, specifically pea aphids and other aphid

species that are abundant in this system (Kishinevsky & Ives, 2022). This, in turn, decreases sugar resources by decreasing honeydew production. Parasitoids were previously shown to switch between honeydew and nectar as sugar sources (Lee et al., 2006), both of which are removed by harvesting. Finally, although alfalfa is a perennial crop, it is harvested regularly and grows quickly. Therefore, in terms of factors affecting parasitoid populations, alfalfa is more similar to common annual crops than perennial systems such as fruit orchards.

### Sampling design

Adult parasitoids were sampled using sweep nets from alfalfa fields, margins of alfalfa fields, and prairies. Altogether, samples were collected from 13 alfalfa fields, nine in Arlington Agricultural Research Station and four in West Madison Agricultural Station. Field margins were sampled next to seven of the sampled alfalfa fields in Arlington and all four fields in West Madison. We sampled five restored tallgrass prairies, all in proximity to the Arlington Agricultural Research Station, with the distance between sampled fields and prairies ranging from 0.04 to 2.2 km. Some of the locations were sampled more than once. All samples were collected during the summer of 2021, from early June to mid-September. Samples were taken weekly when rain permitted the use of sweep nets. Sampling was standardized to 1-h duration. In the alfalfa fields, pea aphids captured by sweep netting were counted. Captured adult parasitoids were transferred to 20-mL tubes and kept in a cooler until arriving at the lab. Each individual parasitoid was then transferred to a 100 × 15-mm petri dish.

### Treatments and longevity monitoring

Longevity of insects in the field is hard to measure (Nussey et al., 2013). One method that is increasingly used is the residual lifespans method, first proposed by Müller et al. (2007) and used by Carey et al. (2008) for a wild Mediterranean fruit fly population; subsequent studies have compared different fruit fly species (Behrman et al., 2015) and geometrid moths (Holm et al., 2016; Tasnin et al., 2021). This method measures longevity under controlled conditions, making it possible to compare the potential survival of groups collected at different times (Carey et al., 2008) or in different environments. Measuring residual lifespan is performed on organisms captured in the field, so their ages at capture are not known. Because some senescence (increased probability of death with age) is expected, we compared our results

with those of studies on longevity in the lab from the literature (see [Reference data from the literature](#)).

We estimated residual lifespan and hardiness as follows. All collected parasitoids on a given sample date were randomly divided between two treatments: half had a drop of honey placed in the middle-upper part of the petri dish and no water (honey treatment—residual lifespan), and half had no honey or water (no-honey treatment—hardiness). This design is similar to that in the handbook of protocols from Moretti et al. (2017), although to measure hardiness rather than starvation resistance, we did not provide water. Water has been previously shown not to have a large effect on hymenopteran parasitoid longevity (Grosch, 1950; Lee & Heimpel, 2008). Petri dishes with wasps were kept under the same conditions in the lab at  $25 \pm 1^\circ\text{C}$ , 60% relative humidity and a 14-hour light/10-hour dark cycle. All petri dishes were checked daily, and honey was also checked daily and replenished if needed. Dead parasitoids were transferred to 1.5-mL centrifuge tubes and kept in a freezer for identification.

## Parasitoid identification

Parasitoid identification and sex determination was done under a dissecting microscope. Parasitoids were identified to the finest level practical: all were identified to family, some to genus, and some to species. Members of the Aphidiinae (Braconidae) sub-family were identified to genus, except members of the genus *Aphidius* which were identified to species. Hyperparasitoids of *A. ervi* were also identified to species. We used the identification keys of Eady (1969), Ghaliow et al. (2018), and Gibson et al. (1997).

## Reference data from the literature

Our data represent the hymenopteran parasitoid community at our field sites. To compare to a broader representation of species, we selected the five most abundant families in our collection and compared our estimates of family-level residual lifespan to lab-longevity data from the literature for 153 species in the same families compiled by Professor Tim Blackburn (Blackburn, 1991).

## Statistical analyses

We computed Kaplan–Meier survival curves for parasitoids, and statistical comparison between habitats was performed with a log-rank test (Harrington & Fleming, 1982). Parasitoids in the two treatments (with or without a sugar

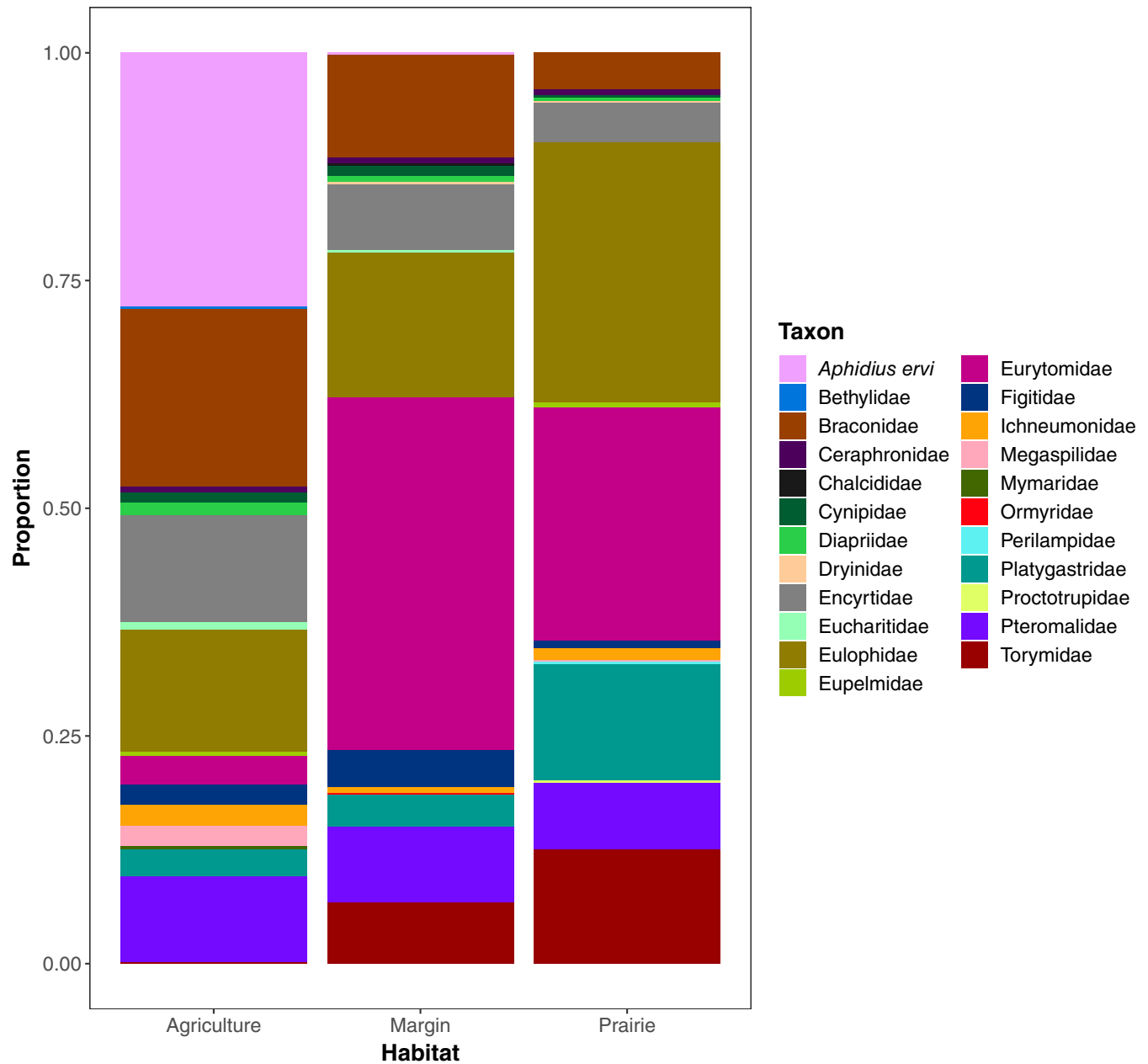
source) were analyzed separately, and family was used as a stratifying factor. Because the analyses included three groups (habitats), three analyses were performed for each group to allow pairwise comparisons, and a Benjamini–Hochberg *p*-value adjustment was used to account for multiple comparisons. We used the function “survdiff” in the package “survival” (Therneau & Lumley, 2015) in the R programming language (R Core Team, 2013).

To analyze parasitoid residual lifespan and hardiness, we used phylogenetic linear regression. We built the family-level taxonomic tree from Blaimer et al. (2023), with missing families of Chalcidoidea added from Zhang et al. (2020). The number of days parasitoids survived in the lab was used as the dependent variable, with treatment (residual lifespan vs. hardiness) and habitat (agriculture, margin, or prairie) as independent variables. We performed the phylogenetic regression using the family-level taxonomic tree with branch lengths standardized to give a contemporaneous (ultrametric) phylogeny. We calculated the relative increase in longevity from sugar feeding (survival with sugar divided by survival without sugar). We analyzed the correlation between lifespan recorded in the current study and data from the literature while accounting for phylogenetic correlations at the family level (Zheng et al., 2009). Analyses were performed using `pglm()` and `cor_phylo()` in the `phyr` package (Li et al., 2020) in R.

## RESULTS

### Parasitoid community

We collected 1590 hymenopteran parasitoids, 900 from the agricultural fields, 346 from field margins, and 344 from the prairies. The collection represented 21 hymenopteran families. Community composition at the family level differed among habitats (Figure 1), with the family Braconidae most abundant in the agriculture (47%, 11%, and 4% of individuals collected from agriculture, field margins, and prairie, respectively). Eurytomidae was the most abundant in field margins (3%, 39%, and 25%), and Eulophidae was most abundant in the prairies (13%, 16%, and 28%). The most abundant species was *A. ervi*, which was collected exclusively from the agricultural fields ( $n = 252$ ), while other Aphidiinae species were rarely found. Pea aphid hyperparasitoids were also collected from agriculture ( $n = 68$ ). In addition, *Cotesia medicaginis*, a parasitoid of the alfalfa caterpillar, was found in agriculture ( $n = 31$ ). Because *A. ervi* was common, we could ask more detailed questions: specifically, residual lifespan and hardiness were not affected by pea



**FIGURE 1** Proportion of each family collected from the different habitats. *Aphidius ervi* is presented separately because it was the most abundant species, but note that it belongs to the family Braconidae (in brown).

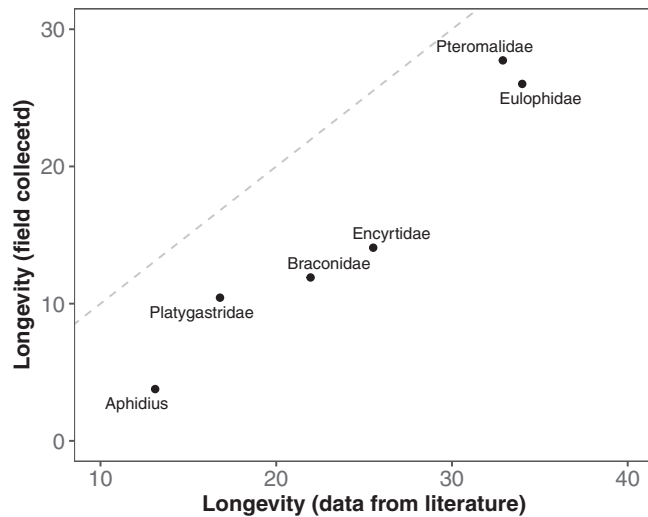
aphid abundance or the time since last harvest of agricultural fields (Appendix S1).

The most abundant families, with at least 50 collected individuals, were chosen for comparison with the dataset of longevity under laboratory conditions (Blackburn, 1991). Seven families met that criteria, but two (Eurytomidae and Torimidae) were not included in the Blackburn dataset. In addition to the five families, we also included *Aphidius* separately due to the frequency of *A. ervi* in our dataset. For all the families, longevity recorded under lab conditions was higher than residual lifespan for parasitoids collected from the field and fed sugar (Figure 2). The correlation

between groups was high: Pearson correlation was 0.92 and 0.94 accounting for phylogeny.

### Effects of treatment and habitat on longevity

Parasitoids with sugar lived much longer than those without sugar (Figure 3). Residual lifespan with sugar was 1–190 days, with a mean and median of 15.1 and 6, respectively. Lifespan in the hardiness treatment (without sugar) was 1–17 days with a mean and median of 2.6 and



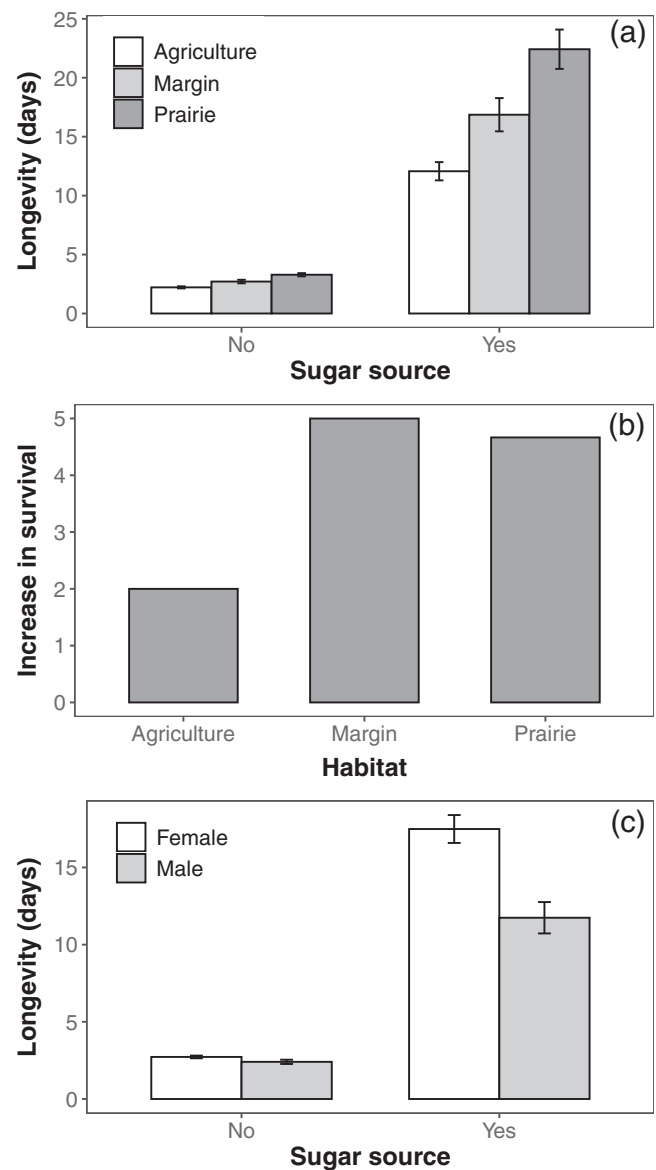
**FIGURE 2** Longevity in days (mean) of the most common parasitoid hymenopteran families collected, with *Aphidius* genus separated from other Braconids. On the x-axis gives data collected from the literature on mean longevity of parasitoids under laboratory conditions with a sugar source compiled by Blackburn (1991). On the y-axis are longevity averages of all the individuals collected from the field in the current study (both sexes and all habitats) which were in the sugar-fed treatment. The 1-to-1 line is shown as gray dashes.

2, respectively. Many of the parasitoids died in the first day: 17% and 34% of individuals with and without sugar.

Parasitoids collected from natural habitat (prairie and field margins) survived longer than those from agriculture (Figure 3a). Furthermore, the relative benefit from sugar feeding (survival with sugar divided by survival without sugar) was higher for parasitoids collected from natural habitats (Figure 3b). Sex could be determined for 1450 of the collected parasitoids, and for these, females had higher residual lifespan than males ( $17.49 \pm 0.9$  vs.  $11.74 \pm 1.0$ ) but hardiness was similar ( $2.73 \pm 0.09$  vs.  $2.41 \pm 0.1$ ) (Figure 3c).

Survivorship curves were roughly negative-exponential (Figure 4), and parasitoids collected from agriculture and prairie were significantly different in both feeding treatments (residual lifespan:  $p = 0.03$ ; hardiness:  $p = 0.0024$ ), while comparisons between agricultural and field margins, and between field margins and prairie, were not significant ( $p > 0.05$ ) in both treatments.

The phylogenetic linear regression showed a large difference between feeding treatments in the log days individuals survived (phylogenetic regression,  $p < 0.001$ , full results not shown). To understand the effect of habitat, we analyzed data for residual lifespan and hardiness separately (Table 1). For both residual lifespan (with sugar) and hardiness (without sugar), survival of parasitoids from prairies was greater than agricultural fields, although field margins

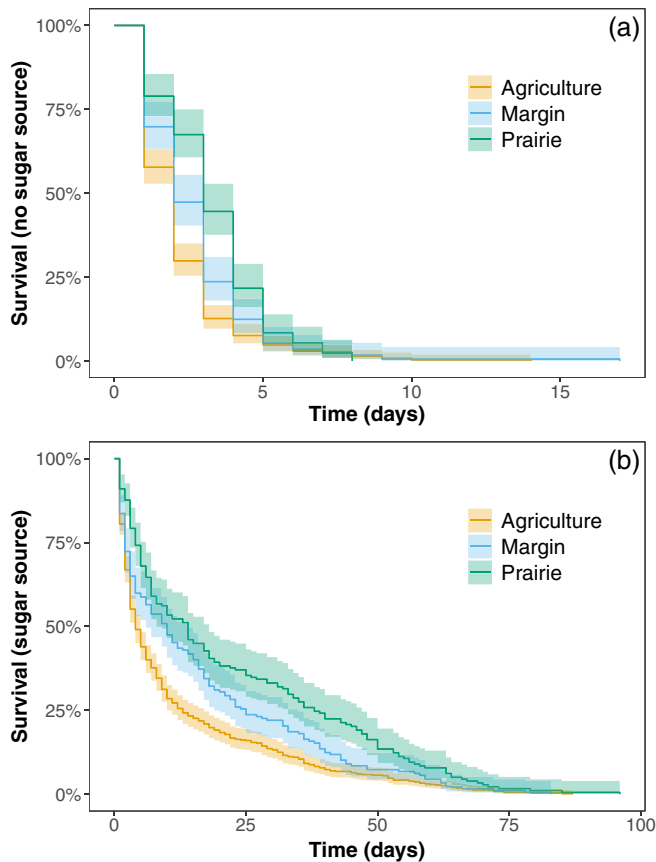


**FIGURE 3** (a) Longevity (mean  $\pm$  SE) of the parasitoids collected at the different habitats with and without a sugar source. (b) The relative increase in longevity (potential lifespan/hardiness) of all parasitoids collected from every habitat. (c) The longevity of female and male parasitoids with and without a sugar source, including only the 1450 parasitoids whose sex could be determined.

did not differ from agriculture. In both cases, there were large differences among families (Figure 5), and although the magnitude of the phylogenetic component of family random effect was large, it was not statistically significant.

## DISCUSSION

We investigated the length of time hymenopteran parasitoids survived after being collected from agricultural



**FIGURE 4** Kaplan–Meier survivorship curves for the parasitoids collected in the different habitats (a) without a sugar source and (b) with a sugar source. Shaded areas represent 95% CIs of the Kaplan–Meier estimator. One individual (“Dracula”) that lived for 190 days in the sugar source treatment is excluded from the figure.

(alfalfa), field margins, and prairie habitat. Parasitoids lived longer when they were given a sugar source regardless of the habitat where they were collected (Figure 3a). This is consistent with lab studies on parasitoids showing a large increase in longevity with a sugar source (Heimpel & Jervis, 2005). Among habitats, individual parasitoids ( $n = 1590$ ) collected from natural habitats had greater residual lifespan (with sugar) and hardiness (without sugar) than parasitoids collected from agriculture, with field margins being intermediate. Importantly, parasitoids collected from agriculture had a lower relative increase in longevity from sugar feeding (survival with sugar divided by survival without sugar) than parasitoids from natural habitats (Figure 3b). From a biological control perspective, this suggests that increasing sugar sources in agricultural fields might not give a substantial benefit to the short-lived parasitoid community.

Differences in residual lifespan and hardiness among habitats could potentially be caused by differences in the condition of individuals when collected; for example, if

prairies had easily accessed sugar sources, then individuals collected from prairies might have had greater sugar reserves when initially brought into the lab. However, parasitoids need frequent sugar meals to avoid starvation (Azzouz et al., 2004; Fadamiro & Heimpel, 2001), making it unlikely they had sugar stores that affected their residual lifespan and hardiness. Therefore, differences among habitats were likely caused by differences in community composition (Figure 1); for example, species more likely to be found in prairies may have had longer intrinsic lifespans, which increased residual lifespan and hardiness. Nonetheless, the patterns we found for residual lifespan and hardiness could not simply be caused by prairies having species from families with longer intrinsic lifespans, because benefits from sugar were greater in the natural habitat across families (Figure 5). This suggests that compositional differences among communities lead to species with different residual lifespan and hardiness occurring in different habitats, yet the compositional differences cannot be simply summarized by the relative representation of different parasitoid families.

Other studies using the residual lifespan method found differences in longevity between habitats, particularly due to abiotic conditions at different altitudes (Duyck et al., 2010), although biotic conditions such as predator pressure were not ruled out. In the current study, particular abiotic and biotic conditions were not measured. Furthermore, we did not measure death in the field, and we are not aware of any studies comparing adult death of a parasitoid community under field conditions in agricultural and natural habitats. Therefore, we do not know whether parasitoids do experience higher mortality in agriculture than in natural habitat. Nonetheless, given that agricultural practices (harvesting, insecticides) will kill parasitoids, it is likely that agriculture represents a harsher environment than prairies. A harsher agricultural environment could explain the community of inherently short-lived parasitoids in agricultural plots compared with prairies. This explanation is consistent with theory about early senescence in environments with high adult mortality (Bryant & Reznick, 2004; Williams, 1957). The different habitats measured are all very close geographically, and some of the species are probably found in all habitats. Nonetheless, species with better adaptations to the agricultural environment are more likely to be found there. Differences in longevity between males and females were also found, which is consistent with other studies on parasitoids under lab conditions (Benelli et al., 2017; Lee et al., 2004; Olson et al., 2000).

The results obtained from random collection of parasitoids in the field are place and time specific, because parasitoids were collected in a particular area during one season. Despite this limitation, comparison with

**TABLE 1** Phylogenetic regression for the log number of days hymenopteran parasitoids survived after collection on the habitat from which they were collected.

Treatment	Effect	Value	SE	SD	p-value
Residual lifespan (sugar source)	Fixed effects				
	Intercept	1.53	0.24		<0.001
	Field margin	0.09	0.12		0.49
	Prairie	0.41	0.12		0.0008
	Random effects				
	1 family_non-phylo			0.23	<0.001
	1 family_phylo			0.39	0.25
Hardiness (no sugar source)	Fixed effects				
	Intercept	0.68	0.10		<0.001
	Field margin	-0.00	0.06		0.99
	Prairie	0.15	0.06		0.017
	Random effects				
	1 family_non-phylo			0.18	<0.001
	1 family_phylo			0.13	0.26
	Residual			1.20	

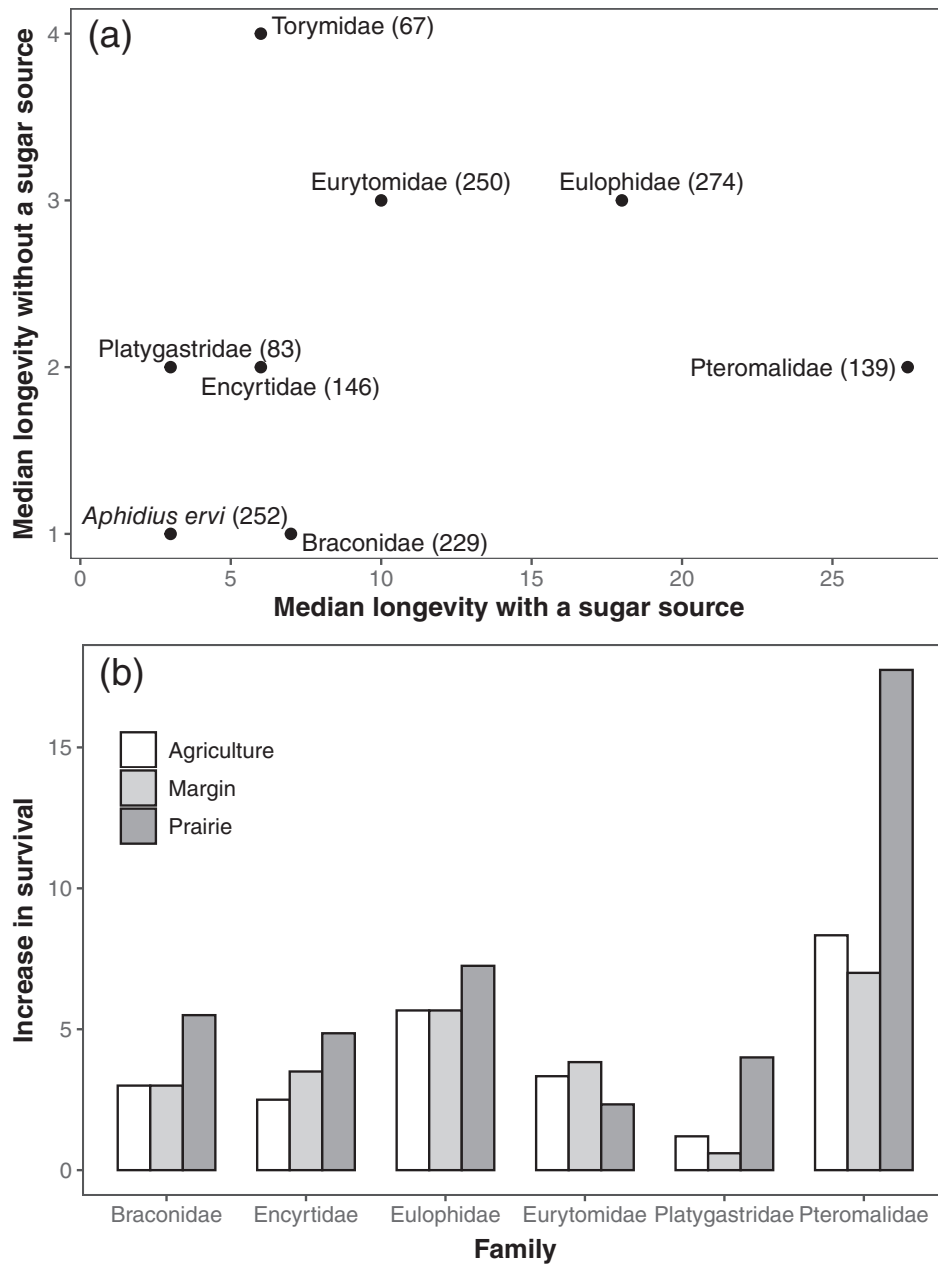
*Note:* Data are split by sugar-source treatment. The base level is the agricultural habitat, so values for field margins and prairies gives differences from agriculture. The random effects capture variation among families either excluding (1|family\_non-phylo) or including (1|family\_phylo) the taxonomic relationships among families; *p*-values associated with (1|family\_non-phylo) compare models with and without the family random effect, whereas *p*-values associated with (1|family\_phylo) compare models with and without the phylogenetic component of the family random effects, with *p*-values calculated using likelihood ratio tests.

longevity data from the literature shows that our results are consistent to what is known about the main families of parasitoids collected (Figure 2). In all the families, longevity with sugar was lower than what is recorded in the literature, which could result from the fact that this comparison was done at the family level, and species composition is probably different. Nonetheless, due to the consistency across families, this difference is probably mainly caused by the residual lifespan method used in the current study. Since adult parasitoids of unknown ages were captured, this lower lifespan compared to data of parasitoids from eclosion is expected if parasitoids senesce. In addition, while capturing parasitoids with sweep nets, transferring them to the laboratory and placing them separately in petri dishes, some of the parasitoids were probably injured. While upon identification we excluded individuals with clear injuries, it is probable that some injuries were not detected. This might be the reason for the high mortality in the first day after collection (17% of sugar-fed individuals). Conditions at early development could also affect aging rates, with temperature and humidity, among other things, different in the field than in the lab (Carey et al., 2008). Kawasaki et al. (2008) showed that Neriidae flies live substantially shorter under field

conditions than in the lab. In addition to starvation and desiccation, under field conditions parasitoids may die from predation, although predation on adult parasitoid wasps is not often discussed and might not be substantial (Heimpel et al., 1997; Tena et al., 2022). Actual longevity in the field probably lies between the longevity found in the no-sugar and sugar-fed treatments.

Our collection showed large differences in family-level composition of parasitoids among habitats, and this could have several explanations. First, differences in plant composition and diversity could lead to differences in herbivorous insect composition. Since most of the wasps collected are parasitoids of herbivorous insects, this could explain compositional differences. In addition, traits apart from lifespan can affect adult success in the different environments. For example, in a different study (Kishinevsky & Keasar, 2021), species which were found to more frequently feed on sugar sources in the field were more likely to be found in natural habitats. Longevity is also associated with other life-history traits: short-lived species are more likely to concentrate reproductive efforts earlier (pro-ovigenic) (Jervis et al., 2001). Such is the case for *A. ervi*, the most frequently collected species in the alfalfa fields (Figure 1). Females from this species have many of their eggs mature upon emergence and are





**FIGURE 5** (a) Relationship between potential lifespan and hardiness (with and without a sugar source) for the most abundant families collected, which make up 90% of the individuals collected; the total number of individuals is given in brackets. (b) Increase in survival calculated as potential longevity/hardiness in each habitat is shown for each of the abundant families.

highly fecund (Moiroux et al., 2018), and we found *A. ervi* to have a very low hardiness and residual lifespan, even compared with other species from the same family (Figure 5a). *A. ervi* is a very successful biological control agent, effectively controlling pea aphids and other aphid species in this system and around the world (Boivin et al., 2012; Schellhorn et al., 2002). From a biological control perspective, in a highly disturbed system like agricultural plots, short longevity and low hardiness are not necessarily disadvantages if longevity and hardiness are traded-off against early adult reproduction.

### Implication for conservation biological control

The relative benefit of sugar feeding was lower for parasitoids collected from agriculture than for those collected from natural habitats (Figures 3b and 5b). This suggests that parasitoid species which are adapted to harsher environments are more common in the agricultural habitats. Having a shorter intrinsic lifespan could be particularly advantageous in a highly disturbed, resource-poor environment, as some agricultural environments are (Bryant &

Reznick, 2004). This result can have implications for conservation biological control programs, as many focus on trying to enhance parasitoid activity by increasing sugar sources in the agricultural field, sometimes not successfully (Heimpel & Jervis, 2005; Lee & Heimpel, 2005). It has been previously shown that one reason for this lack of increase is that parasitoids rely on honeydew as a main source of sugar in agricultural plots, and they are therefore not lacking sugar sources. In addition, sugar feeding by parasitoids may also lead to increased dispersal, which can decrease biological control in the feeding area (Heimpel, 2019). Our results add a third, complementary explanation for the failure of conservation biological control programs to increase sugar sources. Since the relative increase in longevity from an unlimited sugar source in the current study was much lower for the community of parasitoids found in agriculture, supplementation of nectar-providing plants in agricultural systems might not be effective. Furthermore, adding sugar sources can change the composition of the parasitoid community, not necessarily to the advantage of pest control (Miall et al., 2021). For some agricultural systems, the addition of floral sugar sources might not enhance biological control by parasitoids just because the benefit from feeding is low, but could still have other non-agricultural related benefits, like increasing biodiversity (Grass et al., 2016).

#### AUTHOR CONTRIBUTIONS

Miriam Kishinevsky designed and executed the study. Miriam Kishinevsky and Anthony R. Ives analyzed results. Miriam Kishinevsky led the writing of the manuscript.

#### ACKNOWLEDGMENTS

We greatly thank Professor Tim M. Blackburn for sharing his dataset with us. We thank Calvin Sinclair and Karuna Bhat for help with fieldwork, and the staff of the Arlington Agricultural Research Station. This work was funded by a United States-Israel Binational Agricultural Research and Development Fund Award to Miriam Kishinevsky; a Vaadia-BARD Postdoctoral Fellowship Award (FI-589-2019) to Miriam Kishinevsky, a Rothschild Family Foundation grant to Miriam Kishinevsky, and a Steenbock Professorship Award to Anthony R. Ives.

#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

#### DATA AVAILABILITY STATEMENT

Data (Kishinevsky & Ives, 2024) are available in Dryad at <https://doi.org/10.5061/dryad.kwh70rzck>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Kishinevsky, Miriam, and Anthony R. Ives. 2024. "Longevity of Hymenopteran Parasitoids in Natural versus Agricultural Habitats and Implications for Biological Control." *Ecological Applications* e3009. <https://doi.org/10.1002/eap.3009>