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Adventive *Gryon aetherium* Talamas (Hymenoptera, Scelionidae) associated with eggs of *Bagrada hilaris* (Burmeister) (Hemiptera, Pentatomidae) in the USA

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Abstract

Bagrada bug, *Bagrada hilaris* (Burmeister) (Hemiptera, Pentatomidae), has become a major pest of cole crops (cabbage, broccoli, cauliflower, kale) in California since its arrival in 2008. In this study we documented parasitism of *B. hilaris* eggs at a highly infested site in northern California by deploying sentinel *B. hilaris* eggs and collecting naturally-laid *B. hilaris* eggs in the soil. Two parasitoids, *Gryon aetherium* Talamas (Hymenoptera, Scelionidae) and *Ooencyrtus californicus* Girault (Hymenoptera, Encyrtidae), emerged from sentinel eggs, but only *G. aetherium* was documented attacking eggs in the soil. *Gryon aetherium* is currently being assessed as a classical biological control agent for *B. hilaris* in California, and mating experiments showed that crosses between *G. aetherium* from Pakistan and California yielded viable female offspring. This report marks the first known record of *G. aetherium* in the USA, and further work should be conducted to assess the potential of this parasitoid for biological control of *B. hilaris*.

Keywords

bagrada bug, biocontrol, egg parasitoids, enemy-free space, parasitism rates, sentinel eggs

Introduction

Bagrada bug, *Bagrada hilaris* (Burmeister) (Hemiptera, Pentatomidae), is a damaging pest of cole crops (cabbage, broccoli, cauliflower, kale, and all other cultivated varieties of *Brassica oleracea* L.). It is native to southern Asia and also occurs in eastern and southern Africa (Sforza et al. 2017). The bug quickly spread throughout the major cole crop growing regions of California after being discovered near Los Angeles in 2008, and then moved eastward into Nevada, Utah, Arizona, New Mexico, and Texas (Reed et al. 2013; Palumbo et al. 2016). It also occurs in Chile and Mexico (CABI 2016). Although *B. hilaris* is primarily a pest of cole crops, its host range extends to at least 74 plant species in 23 families (Palumbo et al. 2016). Widespread brassicaceous weeds in California appear to be key hosts of *B. hilaris* until late summer when the plants senesce (Reed et al. 2013; Grettenberger and Joseph 2019) and have likely aided in the bug's spread.

Biological control shows promise as a management option for *B. hilaris*. It appears to be under natural control in its native range in Pakistan, where it is only a sporadic pest (Mahmood et al. 2015). Mahmood et al. (2015) reported that about 35% of naturally-laid *B. hilaris* eggs collected from plant debris in Pakistan were parasitized. Biological control could be particularly helpful in controlling *B. hilaris* in non-crop source habitats that provide seasonal refuge for the pest and are usually out of reach of insecticide treatments, although the bug's unique habit of ovipositing mainly in the soil (Taylor et al. 2014) may provide some protection from natural enemies. Three parasitoid species were collected in Pakistan as potential biological control agents of *B. hilaris* in the US: *Gryon aetherium* Talamas (Hymenoptera, Scelionidae), which was previously misidentified as either *G. gonikopalense* Sharma or *G. myrmecophilum* (Ashmead) (Talamas et al. 2021), *Trissolcus hyalinipennis* Rajmohana & Narendran (Hymenoptera, Scelionidae) and *Ooencyrtus mirus* Triapitsyn & Power (Hymenoptera, Encyrtidae) (Mahmood et al. 2015; Sforza et al. 2019). Of these, *G. aetherium* shows the most promise because it appears to be fairly host specific, in contrast to *T. hyalinipennis* (B. Hogg, unpubl. data) and *O. mirus* (Power et al. 2020), which appear to be generalists. Furthermore, *G. aetherium* is able to parasitize *B. hilaris* eggs under the soil surface, whereas *T. hyalinipennis* either cannot or can at only low levels of efficiency (Tofangsazi et al. 2020), suggesting that *T. hyalinipennis* parasitism may be limited to eggs laid on the soil surface or occasionally on the leaves or stems of plants.

Thus far, all reported parasitoids of *B. hilaris* in the New World have been egg parasitoids from the families Scelionidae and Encyrtidae. In southern California, *Trissolcus basalis* (Wollaston), *T. hyalinipennis*, *T. hullensis* (Harrington), and *T. utahensis* (Ashmead) (Scelionidae) emerged from sentinel *B. hilaris* eggs (Ganjisaffar et al. 2018, 2020), as did *Ooencyrtus californicus* Girault (Encyrtidae) (reported as *O. lucidus* Triapitsyn & Ganjisaffar) (Triapitsyn et al. 2020). *Trissolcus basalis* attacked sentinel *B. hilaris* eggs in Mexico, along with *G. aetherium* (reported as *G. myrmecophilum* Ashmead) and *Telenomus podisi* Ashmead (Scelionidae) (Felipe-Victoriano et al. 2019). *Idris elba* Talamas (Scelionidae) also emerged from field-collected *B. hilaris* eggs in soil in Mexico (Lomeli-Flores et al. 2019). How-

ever, information about parasitoids attacking *B. hilaris* eggs is lacking in north-central California, where most of the cole crops in the US are grown. In this study we assessed attack by parasitoids on both sentinel and naturally laid *B. hilaris* eggs at a heavily infested site in north-central California.

Methods

Study site

The study site consisted of an open field outside Davis, CA (approximately 0.5 km southwest of the campus of the University of California, Davis) that was bordered by farmland to the north and a creek to the south. Plants at the field site consisted largely of weedy grasses and large stands of shortpod mustard (*Hirschfeldia incana* (L.)), a weedy brassicaceous host of *B. hilaris*. Patches of another weedy host, perennial pepperweed (*Lepidium latifolium* L.), were also present. The site was selected because it was heavily infested with *B. hilaris* and other pentatomid species, including *Murgantia histrionica* (Hahn), *Chlorochroa ligata* (Say), *Chlorochroa uhleri* (Stål), and *Thyanta custator* (Fabricius). Shortpod mustard was the focus of sampling because it appears to be the favored host of *B. hilaris* in California; *B. hilaris* is typically present on shortpod mustard until it completely senesces in late summer or fall (B. Hogg, pers. obs.).

Insect colony

Bagrada hilaris were collected for the colony at the study site and maintained in ventilated plastic food containers (25 × 17 × 8 cm) enclosed by organdy mesh, at 28–30 °C, 30–40% RH and a 16L:8D photoperiod. The colony was provided with organic (without pesticide treatment) broccoli florets (*Brassica oleracea* var. *italica* Plenk), kale (*Brassica oleracea* var. *palmifolia* DC), and sweet alyssum (*Lobularia maritima* (L.)). To obtain *B. hilaris* eggs for sentinel cards, two sand-filled, uncovered petri dishes (90 mm diameter) were placed in each container under folded pieces of white cardstock (80 × 80 mm) to provide shade, and eggs were collected daily by sieving the sand using a No. 35 sieve (Humboldt Manufacturing Co., Elgin, IL; mesh size: 0.5 mm).

Sentinel egg cards

Parasitism of *B. hilaris* eggs was assessed using sentinel *B. hilaris* eggs attached to pieces (2 × 14 cm) of white cardstock (Rite in the Rain, Tacoma, WA) using Elmer's Glue-All (Elmer's Products Inc., Westerville, OH) (Fig. 1). To protect the sentinel eggs from sun and precipitation, larger pieces of cardstock were folded to create triangular tubes (14 cm long with 7 cm sides) within which egg cards were attached with paperclips (Fig. 1). Sampling took place in late summer and early

Figure 1. From left to right: A sentinel card with *Bagrada hilaris* eggs; a sentinel card in the field, inside a cardstock triangle to protect it from sun and precipitation; sentinel cards on the ground and in mustard foliage in the field.

fall, when *B. hilaris* numbers are typically highest in north-central California (B. Hogg, pers. obs.). Cards were placed in the field on 10, 17, and 29 September 2020 and on 15, 21, and 28 October 2020, and remained in the field for six to eight days (six days: 17 September, 15 October; seven days: 10 and 29 September, 21 October; eight days: 28 October). Depending on egg availability, either 15 (all September dates) or 10 (all October dates) eggs were glued to each card; eggs on cards were evenly spaced 1 cm apart (Fig. 1).

Cards were placed in two locations on *B. hilaris*-infested shortpod mustard plants: on the ground, where most *B. hilaris* eggs are laid, and in the foliage (~1 m above the ground) (Fig. 1). Cards were placed in foliage to increase the potential pool of parasitoids that were sampled because parasitoids that attack pentatomids other than *B. hilaris* are likely to forage primarily in foliage, where most or all other pentatomids in California lay their eggs. On each sample date, two cards per plant (one on the ground and one in foliage) were placed in eight infested plants, except on 21 October when cards were placed in only six plants due to low egg availability. The same eight plants were sampled through September, but by mid-October four of the original plants had begun to senesce and contained few *B. hilaris*, and on each sample date in October four new infested plants were chosen as replacements, except on 21 October when three original and three new plants were sampled. Sampled plants were at least 9 m apart, and the entire distance from the first to the last sampled plant was 426 m. Cards were placed intact in plastic vials (25 mm diameter × 95 mm high) in the laboratory at 20–24 °C, 40–60% RH and 12L:12D photoperiod and were held for at least four weeks for the emergence of parasitoids, which were identified to species. Any unhatched eggs were dissected to determine whether uneclosed parasitoids were present.

Figure 2. A female *Gryon aetherium* parasitizing an egg (arrow points to the inserted ovipositor).

Soil samples

Eight shortpod mustard plants heavily infested with *B. hilaris* were selected for soil sampling at the site, such that each plant was located within 10 m of a plant bearing sentinel egg cards. Initially, undisturbed soil was sampled from under the infested plants, but few *B. hilaris* eggs were found, likely because the ground was too densely packed. To facilitate egg laying by *B. hilaris* on subsequent sample dates, leaf litter and grass and a ~1 cm-deep layer of soil was removed from a 40 cm diameter area under each plant. The soil was then sieved with a No. 35 sieve and placed back, and loose dried grass collected from the site was placed on top of the soil to provide shade. The soil was left for 6–7 days to allow *B. hilaris* to lay eggs and was then removed with a trowel and placed in resealable plastic bags. Soil samples were collected on four dates: 23 and 29 September and 6 and 15 October.

In the laboratory, the soil was sieved first with a No. 14 sieve (mesh size: 1.41 mm) to remove large debris, and then with a No. 35 sieve to remove soil particles smaller than *B. hilaris* eggs. The remaining soil particles were then examined microscopically for *B. hilaris* eggs, and all eggs that were found were placed in plastic vials (25 mm diameter × 95 mm high) and held at 20–24 °C, 40–60% RH and 12L:12D photoperiod for at least 4 weeks for parasitoid and *B. hilaris* emergence. Any remaining unhatched eggs were dissected.

Interbreeding experiments

Interbreeding tests were conducted with the population of *G. aetherium* currently undergoing host specificity testing in quarantine (originally collected in Pakistan; hereafter the "Pakistani" population) and a wild Californian colony established from individuals that emerged from the sentinel egg cards and soil samples collected in the study described above. Since *G. aetherium* is arrhenotokous (i.e., female progeny cannot be produced by unmated females), the production of female progeny is a sign that females were fertilized by males. A preliminary experiment with five unmated females confirmed the probable absence of thelytoky in the wild population (i.e., the females produced only male progeny).

Experiments were conducted in the USDA-ARS quarantine facility in Albany, CA at 21–26 °C, 40–60% RH, and 14L:10D. The developmental time of *G. aetherium* was about 22 days (range: 16–28) under these conditions, with males usually emerging 1 to 2 days before the females. To ensure the synchronized availability of males and females from both populations, three batches of *B. hilaris* eggs were parasitized by the two *Gryon* populations several days apart. All males and females used in the experiment came from these inoculation batches. After inoculation, the parasitized eggs were kept individually in 2 ml microtubes with honey as a food source for the emerging adults. Within 24 h of emergence, one male was added to the microtubes containing single virgin females. There were four treatments: Pakistani males were paired with Californian females and vice versa, and control treatments were set up by pairing males and females from the same population. If mating was not observed within 10 min of adding the male, 2 to 3 additional males were added to the microtube and left to mate for 24 h. Because parasitism by *G. aetherium* has been reported to be the highest right after emergence (about 12 eggs/female), steadily declining thereafter (Martel et al. 2019), single females were then transferred to glass vials (25 mm diameter × 95 mm high) containing 15 to 20 fresh (< 24 h old) *B. hilaris* eggs glued to a strip of cardstock (20 × 60 mm). After a 24 h exposure to the eggs, the females were removed and preserved in 95% ethanol, and the egg cards were incubated until the emergence of *B. hilaris* nymphs or parasitoids. Unhatched parasitized eggs (blackened) were subsequently dissected and any identifiable male or female *G. aetherium* (based on antennae morphology) were included in the calculation of progeny sex ratio. Ten to twenty replicates were completed for each treatment (Table 2).

Subsequent fertility of female progeny was tested by allowing the progeny resulting from the two crosses (Pakistani males × Californian females and Californian males × Pakistani females) to mate with siblings emerging from the same egg card, or if no males (or not enough) were available, with males emerging from other replicates in the same treatment. A subset of the females was then exposed to *B. hilaris* eggs as above. All females were paired with males within 24 to 48 h of emergence. Pairs could mate for 24 to 48 h and exposure to host eggs lasted 24 or 48 h. The fertility of 57 and 43 female progeny was tested from the Pakistani male × Californian female and the Californian male × Pakistani female crosses, respectively (Table 2).

Progeny sex ratio was calculated for each parental female as the proportion of female progeny produced; proportions were logit-transformed and then compared between treatments using ANOVA and the lm function in R version 4.0.2 (R Development Core Team 2020). Replicates with no parasitism from initial crosses (n = 4 total; n = 1 in the Pakistani male × Pakistani female control and n = 3 in the Californian male × Pakistani female cross) and subsequent fertility tests of female progeny (n = 16 total; n = 5 for the Pakistani male × Californian female cross and n = 11 for the Californian male × Pakistani female cross) were excluded from analyses.

Identification

The taxonomic work undertaken to identify *G. aetherium*, including molecular and morphological studies, is presented and discussed in a companion paper (Talamas et al. 2021).

Results

Parasitism of sentinel eggs

Of the 972 sentinel eggs deployed on 92 cards in this study, 28 (2.88%) on three cards were parasitized by *G. aetherium* and 41 (4.22%) on five cards were parasitized by *O. californicus* (Table 1). Both species parasitized sentinel eggs on the ground and in the foliage, although most eggs attacked by *O. californicus* were on cards in foliage (four cards in foliage versus one on the ground). Egg parasitism by *G. aetherium* only occurred on cards collected on 23 September and 5 November and reached a high of 12.9% on cards on the ground on 5 November. *Ooencyrtus californicus* was present on all of the first four collection dates, and parasitism by it reached a peak of 17.9% on cards in foliage on 23 September (Table 1).

Parasitism of eggs in soil

Of the 154 uneclosed *B. hilaris* eggs that were collected from soil, 37 (24.0%) were parasitized by *G. aetherium* and none were parasitized by *O. californicus* (Table 1). All unparasitized eggs contained *B. hilaris* nymphs that either emerged (n = 97) or died before emergence (n = 20). By mid-October *B. hilaris* had apparently stopped laying eggs; only one egg in soil was recovered on 15 October (Table 1). Parasitism by *G. aetherium* in soil peaked at 46.2% on 6 October (Table 1).

Interbreeding experiments

All treatments produced female progeny (Table 2). The proportion of female progeny differed between treatments (ANOVA, $F_{3,51}$ = 3.58, P = 0.02). Proportions of female progeny were higher in the two treatments that included Californian males (Table

Table 1. Numbers of initial and recovered sentinel *B. hilaris* eggs, numbers of sentinel *B. hilaris* eggs parasitized by *Gryon aetherium* and *Ooencyrtus californicus*, and percent parasitism by *G. aetherium* and *O. californicus*.

Collection		Card		Eggs		*G. aetherium*		*O. californicus*	
date[a]	Type	location	*n*[b]	Initial	Collected	Number[c]	%	Number[c]	%
17 Sep 2020	Card	Foliage	8	120	114	0	0.00	5 (0)	4.39
23 Sep 2020	Card	Foliage	8	120	112	9 (0)	8.04	20 (7)	17.86
6 Oct 2020	Card	Foliage	8	120	108	0	0.00	5 (1)	4.63
21 Oct 2020	Card	Foliage	8	80	75	0	0.00	4 (4)	5.33
28 Oct 2020	Card	Foliage	6	60	36	0	0.00	0	0.00
5 Nov 2020	Card	Foliage	8	80	60	0	0.00	0	0.00
17 Sep 2020	Card	Ground	8	120	87	0	0.00	7 (1)	8.05
23 Sep 2020	Card	Ground	8	120	85	10 (3)	11.76	0	0.00
6 Oct 2020	Card	Ground	8	120	109	0	0.00	0	0.00
21 Oct 2020	Card	Ground	8	80	76	0	0.00	0	0.00
28 Oct 2020	Card	Ground	6	60	40	0	0.00	0	0.00
5 Nov 2020	Card	Ground	8	80	70	9 (3)	12.90	0	0.00
23 Sep 2020	Soil	–	8	–	94	22 (2)	23.40	0	0.00
29 Sep 2020	Soil	–	8	–	33	3 (0)	9.09	0	0.00
6 Oct 2020	Soil	–	8	–	26	12 (3)	46.15	0	0.00
15 Oct 2020	Soil	–	8	–	1	0	0.00	0	0.00

[a] Sentinel egg cards were deployed 6–8 days before each collection date. [b] Numbers of sentinel egg cards deployed or soil samples collected. [c] Numbers outside parentheses are total number of eggs parasitized. Numbers inside parentheses are numbers of *B. hilaris* eggs that contained uneclosed parasitoids. Each egg contained only one parasitoid.

Table 2. Results of the interbreeding experiment between males (m) and females (f) from Pakistani (PK) and wild Californian (CA) populations of *Gryon aetherium*. Data for total progeny and percentage female progeny are means ± SE, and means followed by different letters are significantly different (P < 0.05, Tukey HSD test for the F1 generation and t-test for the F2 generation).

Cross	*n*[a]	Parental females[b]	Fertile females (%)[c]	Total progeny	Female progeny (%)
a) F1 generation					
PKm × CAf	20	20	12 (60%)	16.50 ± 0.74	46.2 ± 9.5b
PKm × PKf	13	12	8 (67%)	17.17 ± 0.96	44.9 ± 10.6ab
CAm × PKf	16	13	12 (92%)	12.69 ± 1.58	73.1 ± 6.9ab
CAm × CAf	10	10	9 (90%)	14.20 ± 1.40	79.8 ± 9.6a
b) F2 generation					
PKm × CAf	57	52	47 (90%)	14.21 ± 0.29	76.7 ± 3.8a
CAm × PKf	43	32	18 (56%)	9.13 ± 0.78	35.2 ± 6.6b

[a] Total number of females that were tested (females that produced no progeny were excluded from analyses). [b] Females that produced male or female progeny. [c] Females that produced female progeny.

2), although the only significant difference was between the control with Californian males and females and the cross between Pakistani males and Californian females (Tukey HSD test, P < 0.05; Table 2). In a 2 × 2 factorial ANOVA, the proportion of female progeny was affected by the origin of male *G. aetherium* (Pakistan/California) ($F_{1,51}$ = 10.49, P = 0.002), but not by the origin of females ($F_{1,51}$ = 0.21, P = 0.65) or by the male*female origin interaction ($F_{3,51}$ = 0.23, P = 0.63).

In subsequent fertility tests, female progeny of both crosses (Pakistani males × Californian females and Californian males × Pakistani females) produced their own female progeny (Table 2). Proportions of female progeny differed between treatments (t-test,

$t_{52} = 5.25$, $P < 0.001$), and again were higher in the treatment that included Californian males. Indeed, because males develop from unfertilized eggs in the haplodiploid system, the treatment that initially included Pakistani males and Californian females would have produced Californian male progeny in the first generation (Table 2).

Discussion

In this study, the scelionid parasitoid *G. aetherium* is reported attacking *B. hilaris* eggs for the first time in the USA. To our knowledge, *G. aetherium* is the fourth adventive scelionid that has been found in the USA while under consideration as a classical biological control agent for invasive stink bugs (Gardner et al. 2013; Talamas et al. 2015; Ganjisaffar et al. 2018). Our mating experiment confirmed that the population of *G. aetherium* in the wild in California can freely mate with the colony from Pakistan that is currently being tested in quarantine. Crossing Californian and Pakistani males and females produced viable female progeny. In fact, the female sex ratio of progeny was most affected by the origin of the parental males, with Californian males producing higher proportions of female progeny than Pakistani males in both the first and second generations. These results are in line with the sex ratios of Pakistani and Californian *G. aetherium* in our laboratory colonies, which tend to be slightly male-biased and heavily female-biased, respectively, and with the sex ratio of field-collected *G. aetherium* in the current study, which was also female biased (59.2%).

Gryon aetherium may be widely distributed in North America. In California, six parasitoid individuals that emerged from *B. hilaris* sentinel eggs placed in the Salinas Valley in 2019 were initially identified as *G. myrmecophilum* but are in fact *G. aetherium* (B. Hogg, unpubl. data). In Mexico, Felipe-Victoriano et al. (2019) documented *G. aetherium* (reported as *G. myrmecophilum*) emerging from sentinel *B. hilaris* eggs, reaching parasitism rates of up to 100% in one sample month. However, they placed sentinel eggs on top of the soil in Petri dishes, where the eggs would have been more accessible to parasitoids than in the soil where *B. hilaris* typically lays its eggs. Some of the eggs collected from the soil in the current study may have been exposed, although most were likely to have been buried. The consistency of the soil (sieved with a no. 35 sieve) was similar to that used in a laboratory study where *B. hilaris* laid 72.3% of its eggs under the soil surface in Petri dishes (Tofangsazi et al. 2020). Regardless of the placement of eggs, we were able to show that *G. aetherium* can attack eggs laid naturally in soil in the field. In fact, the maximum parasitism rate by *G. aetherium* was far higher in soil (46.2%) than on sentinel egg cards (12.9%). These results are consistent with laboratory tests showing that *G. aetherium* (reported as *G. gonikopalense*) parasitized buried *B. hilaris* eggs, and spent more time searching for eggs at lower levels in cages (Tofangsazi et al. 2020). Thus far the only other parasitoid in North America that has been reported to attack *B. hilaris* eggs in soil is the scelionid *I. elba*, which is likely also a parasitoid of spider eggs (Lomeli-Flores et al. 2019). We consider *G. aetherium* to be adventive in North America because we have no records of it prior to the introduction

of *B. hilaris* and because its ability to attack eggs in soil suggests that it co-evolved with *B. hilaris*. No other pentatomids are known to bury their eggs in soil and searching for eggs in soil is likely to be a highly specialized behavior for an egg parasitoid.

In contrast, the other parasitoid recovered from sentinel eggs in the current study, *O. californicus*, was not recovered from eggs in the soil, although it should be noted that soil sampling occurred less often than the deployment of sentinel egg cards. Triapitsyn et al. (2020) reported that *O. californicus* (reported as *O. lucidus*) emerged from sentinel *B. hilaris* eggs in southern California and speculated that it is a native species that switched from pentatomid hosts such as *Chinavia hilaris* (Say) to *B. hilaris*. Several species of egg parasitoids have made a similar switch to the invasive pentatomid *Halyomorpha halys* (Stål) in the US, albeit at very low levels (Abram et al. 2017). As a native species and a likely generalist, *O. californicus* would have no evolutionary history with soil-laid eggs. *Trissolcus hyalinipennis*, another parasitoid of *B. hilaris* eggs that was recently found in California (Ganjisaffar et al. 2018), also appears to be a generalist (B. Hogg, unpubl. data), and seems to be largely or completely incapable of attacking eggs in soil (Tofangsazi et al. 2020). Further testing will be necessary to assess the foraging behavior of *O. californicus*, although its emergence from one sentinel egg card on the ground in the current study suggests that it can at least search at ground level.

The population-level impacts of *G. aetherium* and *O. californicus* on *B. hilaris* remain to be investigated. We suspect that *G. aetherium* and *O. californicus* show an aggregative response to *B. hilaris* density and responded to the extraordinarily high *B. hilaris* densities at the study site. Numbers of *B. hilaris* at the site were higher than at any of the sampled sites in an earlier study in which sentinel eggs were deployed over three years throughout north-central California, including in Solano County where the current study occurred (B. Hogg, unpubl. data). In that study, 35,673 sentinel eggs were deployed but only six *G. aetherium* and 27 *Ooencyrtus* specimens, including nine confirmed *O. californicus*, were recorded. However, adapting to new hosts likely requires between 150 and 10,000 years (Cornell and Hawkins 1993), and native egg parasitoids such as *O. californicus* may have difficulty adapting to *B. hilaris*' unique habit of ovipositing in the soil. To provide consistent suppression of *B. hilaris*, a parasitoid such as *G. aetherium* that co-evolved with this pest in its native range will likely be needed.

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