



# An experimental test of the adaptive host manipulation hypothesis: altered microhabitat selection in parasitized pea aphids

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Received: 23 October 2022 / Accepted: 19 January 2023  
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## Abstract

The behavioral phenotypes of hosts may be altered during parasitism, which could favor either the host or the parasite. Pea aphid *Acyrtosiphon pisum* hosts parasitized by the primary parasitoid wasp *Aphidius ervi* leave the stems or lower leaf surfaces where they are most commonly found and move to upper leaf surfaces before they die and mummify. In order to test whether the change of microhabitat benefits the host or the parasitoid, we transplanted pea aphid mummies reared in the laboratory to three different microhabitats on alfalfa plants in the field: the upper leaf surfaces, the lower leaf surfaces, and the stems. Survival analysis revealed no significant differences in mummy survival to emergence across the microhabitat treatments before an alfalfa harvest, when predation pressure was very high, and 2 weeks after an alfalfa harvest, when predation pressure was very low. In contrast, 5 weeks after an alfalfa harvest, when predation pressure was intermediate differences in predation risk were apparent: mummies transplanted to the upper leaf surface had the lowest mortality rates, mummies transplanted to the lower surface of leaves had intermediate mortality rates, and mummies transplanted to the stems had the highest mortality rates. Furthermore, a laboratory study suggested that, compared to other plant substrates, mummies on stems were more likely to be preyed upon by the ladybeetle, *Hippodamia convergens*, which concentrated its search on stems. Our results support the adaptive manipulation hypothesis, in that parasitized aphids appear to induce their host to move to a region of reduced predator foraging, where their risk of attack is reduced.

**Keywords** Host-parasitoid interactions · Tri-trophic interactions · Adaptive host manipulation · Microhabitat · Pea aphid

## Introduction

Many hosts' behavioral phenotypes change during parasitism (Thomas et al. 2010). In some cases, changes in host behavior represent adaptive host manipulation, in which parasites alter their host's behavior to facilitate their development and dispersal (Holmes & Bethel 1972). For example, the fungal parasite *Ophiocordyceps unilateralis* is able to control worker ants' behavior just prior to their death ("zombie ants"), causing them to lock their mandibles onto the underside of leaves, allowing the fungal fruiting body to grow from the ant, releasing fungal spores that can then fall onto other ants below (Hughes 2014). Infection of snail

hosts by the trematode parasite *Cercaria batillariae* not only increases the size and the growth rate of the host *Batillaria cumingi*, it also drives parasitized snails to migrate to the lower intertidal zone, presumably increasing the transmission of the trematode to its next host, a fish (Miura et al., 2006).

Behavioral modifications of hosts might, however, also reflect responses by hosts to infection that favors the host. For example, *Platyrepia virginialis* caterpillars that are parasitized by the tachinid *Thelaira americana* change their diets, switching to feed on poison hemlock to increase their chance of surviving parasitoid emergence (Karban & English-Loeb 1997). In some cases, host behavioral alteration might also be attempts to protect the host's kin from infection, such as when a clonally reproducing aphid host commits "adaptive suicide" to prevent a parasite from maturing successfully and then attacking the infested aphid's clone-mates (Trail 1980). Alternatively, modified host behavior might not be adaptive for either host or parasite, but merely

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Handling Editor: Heikki Hokkanen.

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represent a side-effect of the pathology resulting from the infection (Klein 2005; Thomas et al. 2005).

Distinguishing the ultimate causes of host behavior change can be difficult without experimentation that reveals which player in the interaction actually benefits from the alteration of host behavior (Poulin 1995). In this study, the fitness consequences of observed alterations in behavior of an infected host, involving a change in microhabitat selection, can be manipulated experimentally by simply transplanting hosts to different microhabitats.

Interactions between the pea aphid *Acyrtosiphon pisum* and their primary parasitoid wasp *Aphidius ervi* provide an example of host behavior modification following infection. Female *Aphidius ervi* insert eggs into pea aphids. Attacked aphids continue to live and feed for a few days as the parasitoid develops. Eventually, successful development of the parasitoid results in the death of the host (Hufbauer 2001), marked by the formation of an aphid “mummy”, which refers to the dried, hardened and inflated exoskeleton remains of the parasitized aphid body. Mummies remain attached to the host plant, and the parasitoid goes through its pupal stage within the aphid mummy. A successfully developed adult wasp emerges from the mummy 5–8 days later by cutting a circular hole in the mummy’s dorsal surface. Live, healthy pea aphids on *Vicia faba* plants were found to spend more than 90 percent of their time feeding on the lower leaf surfaces, and only rarely on upper leaf surfaces or on stems (Salyk & Sullivan 1982), whereas aphids bearing wasp larvae tend to mummify either on the upper surface of the leaves for non-diapausing wasps, or off the host plant altogether for diapausing wasps (Brodeur & McNeil 1989).

Here, our goal was to manipulate the microhabitats occupied by parasitized aphid hosts experimentally by transplanting aphid mummies to different positions on their host plant. In particular, we affixed aphid mummies to three different microhabitats on alfalfa plants: the upper leaf surfaces, the lower leaf surfaces, and the stems. It is uncertain if the modified aphid behavior (i) benefits the parasitoid by increasing the likelihood of successful parasitoid development to the adult stage; (ii) benefits the host, reducing the parasitoid immature’s survival and thereby protecting the aphid’s clone-mates, which often reside on the same plant; or (iii) benefits neither party, with host and parasitoid fitness being the same across different microhabitats. By characterizing the survival of aphid mummies in different microhabitats, we aim to determine which of the interacting organisms might benefit from the modified behavior of parasitized hosts.

Finally, because predation risk experienced by aphid mummies may vary strongly over time (Meyhöfer & Hindayana 2003; Colfer & Rosenheim 2001; Barton & Ives 2014), it may also be that the fitness consequences of altered microhabitat selection are context-dependent. In agricultural systems, disturbances such as harvesting events can alter the

community composition of herbivorous insects and natural enemies. For example, Rauwald & Ives (2001) found that aphid and parasitoid populations dropped after alfalfa harvests and then rebuilt rapidly from aphids and parasitoids that survived harvesting plus immigrating aphids and parasitoids (Rauwald & Ives 2001). Predator populations were also reduced after alfalfa harvests, with the abundance of predators regulated by pea aphid density (Kishinevsky & Ives 2022). Predators found in alfalfa fields interact with aphid parasitoids both indirectly, through competition for aphid prey, and directly, by consuming the immobile aphid mummies (Snyder & Ives 2001). Thus, we hypothesize that the predation risk experienced by aphid mummies in different plant microhabitats may vary over time, relative to harvest (mowing) events. To test this hypothesis, we replicated our experiment over three temporal blocks: pre-mowing, 2 weeks after mowing, and 5 weeks after mowing.

## Materials and methods

### Distribution of live and mummified aphids across plant substrates

A field survey was performed on 11 November, 2019 to describe the distribution of live and mummified pea aphids across different plant substrate microhabitats (stem, lower leaf surface, upper leaf surface). We searched 49 stems on 16 alfalfa plants growing in the Student Experimental Farm on the University of California Davis campus and recorded the microhabitat locations of all live pea aphids and aphid mummies found.

### Field experiment

The purpose of the field experiment was to quantify the predation risk experienced by aphid mummies located in different plant substrate microhabitats.

### Aphid mummy rearing and field site preparation

Pea aphid adults were collected from a local alfalfa field and transported to the laboratory to initiate a colony. The offspring were transferred to another cage to initiate an aphid colony without parasitism. Weekly *Aphidius ervi* shipments from a local commercial insectary (Beneficial Insectary, Redding, CA) were placed inside a cage with pea aphids and potted fava beans (cultivar Broad Windsor; Territorial Seed Company) to establish a parasitoid colony. The colony was inspected daily to collect newly mummified aphids for field experiments, ensuring that all test subjects were less than one day old.

The experimental alfalfa field was located at the UC Davis Plant Pathology Experimental Farm, where alfalfa is periodically harvested by mowing, which transiently suppresses aphid and predator populations. Since we hypothesized that predation pressure might vary over time, we divided the experiment into three temporal blocks: one long after a mowing and harvesting of alfalfa (6 May—13 June, 2020; the alfalfa field had not been mowed for at least 3 months prior), when predator populations had built to high densities; one that began 2 weeks following a mowing event (24 July—1 August, 2020), a period when predator populations were strongly suppressed; and a final block approximately 5 weeks after a mowing (14 August—14 October, 2020), when predator populations had partly rebounded. For each randomly selected alfalfa plant, we labeled three different stems onto which we outplanted laboratory-reared mummies. On each stem, a single aphid mummy was attached to each of three different positions: upper leaf surface, lower leaf surface and stem, by using a tiny droplet of white glue (Elmer's All Multipurpose White Glue) applied to the ventral surface of the mummy. Only a single mummy was attached to a given leaf, and all mummies were affixed to the host plant at approximately the same height above the ground. Leaves whose orientation was parallel to the ground and that were fully expanded were selected. Each alfalfa plant thus had a total of nine mummy outplant replicates spread across three stems, and there were 100, 15 and 96 valid replicates in each of the three temporal blocks.

### Monitoring outplanted mummies

Outplanted mummies were examined daily to record whether they: (i) were intact; (ii) had been preyed upon by predators with chewing mouthparts (i.e., displaying a ragged hole chewed into the mummy, and without the presence of the wasp larva or pupa; in some cases, the entire mummy other than the portion affixed with glue was chewed off the plant); (iii) were missing (i.e., the entire mummy, including the part of the mummy affixed with glue, was gone); or (iv) had emerged (i.e., with a smooth, round emergence hole cut on top of the mummy, indicating the successful exit of the adult wasp). Replicates were excluded when inadvertently, the wrong side of the mummy was attached to the plant surface, or when mummies were accidentally dislodged from the plant during our daily inspections. *Asaphes lucens* is the dominant hyperparasitoid attacking *Aphidius ervi*. Approximately 16 days are required for this hyperparasitoid to emerge from the primary parasitoid within the aphid mummy (Schooler et al. 2003). If mummies remained intact but unemerged for more than 20 days, they were retrieved from the field for dissection in the laboratory. We never detected hyperparasites, and we assigned a survival time of

10 days to these mummies, since healthy wasp larvae generally emerged within 10 days of mummy formation.

### Predator foraging behavior

A laboratory study was conducted to examine the foraging behavior of the predatory beetle *Hippodamia convergens* and its impact on mummies located on the upper and lower surfaces of leaves. Aphid mummies were collected from the laboratory colony, and adult *H. convergens* beetles were purchased from a commercial insectary (NaturesGoodGuys). *H. convergens* is a known predator of aphid mummies in the field (Colfer & Rosenheim 2001). To standardize predator hunger level, *H. convergens* were put into individual plastic vials and held at 25 °C without food for 3 days. Fava bean plants (cv. Broad Windsor; Territorial Seed Company) were grown in plastic pots for approximately 2 weeks and then placed inside a 30 × 20 × 20 cm mesh cage (Bug Dorm, BioQuip). On each fava bean plant, two leaves were selected that were oriented parallel to the ground, each of which received two aphid mummies, one glued to the upper surface and another glued to the lower surface for a total of four mummies per plant. A single adult ladybeetle was transferred to the plant's stem close to the soil, and beetle behavior was observed in a 45-min trial. Behavioral event recorder software BORIS (v.7.9.24; Friard & Gamba 2016) was used to record the times the beetle spent (i) off the plant and not on the soil; (ii) on the soil; (iii) on stems; (iv) on the upper leaf surfaces; and (v) on the lower leaf surfaces. We also recorded the times ladybeetles spent feeding on mummies located on the upper leaf surfaces versus the lower leaf surfaces. The identity and the order of any mummies preyed upon were recorded. Trials were ended if a ladybeetle remained off the plant for 15 min continuously. 27 trials were recorded, and each plant and beetle were used only in a single replication.

### Data analysis

The R package *survival* (v.3.2.10; Therneau 2020) was used to analyze the field data. Mummies that were categorized as preyed upon or missing were considered to have been killed, whereas mummies from which adult parasitoids successfully emerged were considered to have survived. We used Kaplan–Meier non-parametric analysis to test if the survival rates of aphid mummies varied significantly across temporal blocks and across microhabitat treatments; these analyses are based on the number of days until a particular outcome occurs. Mummies successfully emerged are considered censored in this test, and mummies surviving for more than 10 days without being hyperparasitized were terminally censored at their tenth day in the field. Log-rank tests were used to compare survival rates across temporal blocks and

treatments. Cox proportional hazards models were used to estimate hazard ratios among treatment groups. G-tests of independence were used to compare mummy emergence success across different microhabitats.

For the laboratory experiment, we used a G-test of independence to ask if the number of mummies preyed upon on the upper leaf surfaces was significantly different from the number of mummies preyed upon on the lower leaf surfaces. Because the collected data were not normally distributed, we used non-parametric Kruskal–Wallis tests to evaluate whether the time spent by predators foraging on different parts of the plants differed.

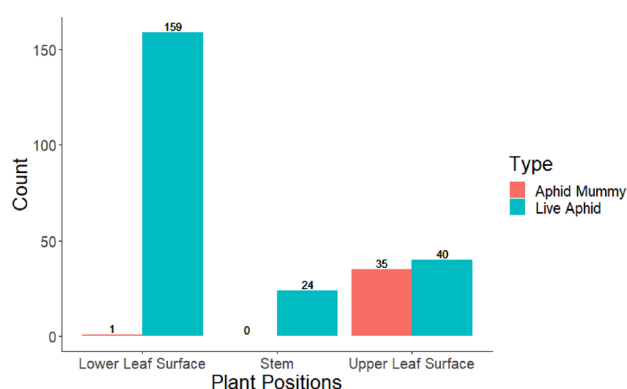
## Results

### Distribution of live and mummified aphids across plant substrates

The field survey showed that the distributions across plant substrate microhabitats were significantly different for live versus mummified aphids ( $G = 33.12$ ,  $df = 1$ ,  $P < 0.001$ ; Fig. 1). Specifically, live aphids were found mostly on the lower sides of leaves (159 out of 223 aphids, 71%), mummified aphids were found almost exclusively on upper leaf surfaces (35 out of 36 mummies, 97%). 24 out of 223 (11%) live aphids were found on stems, whereas no mummies were found on stems.

### Field experiment

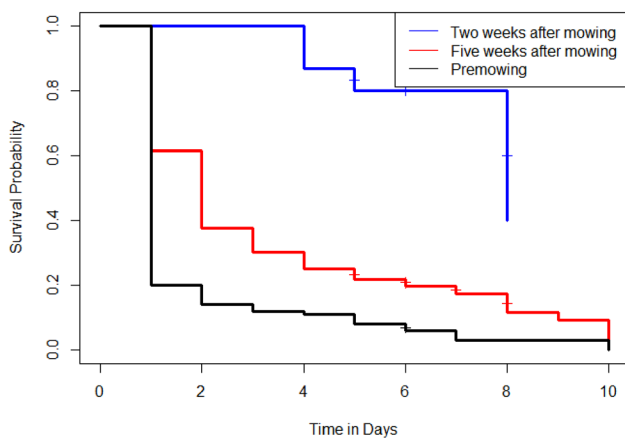
The probability of aphid mummy survival to parasitoid emergence varied substantially across the three temporal blocks of the field experiment ( $G = 38.4$ ,  $df = 2$ ,  $P < 0.001$ ). During the first temporal block (pre-mowing),



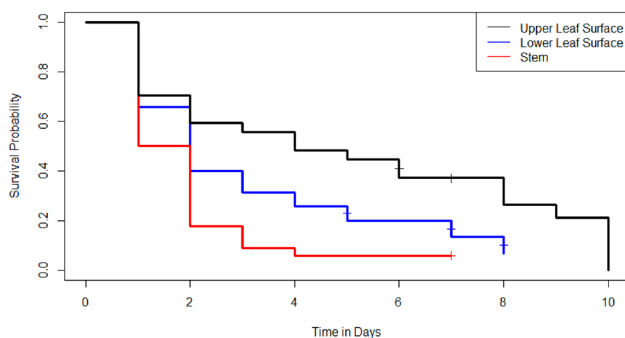
**Fig. 1** The distributions of live aphids ( $N = 223$ ) and mummified aphids ( $N = 36$ ) on three plant microhabitats: upper leaf surfaces, lower leaf surfaces, and stems

the predation pressure experienced by aphid mummies was very high, with only 4 out of 100 outplanted mummies (4%) surviving long enough for an adult parasitoid to emerge. No significant differences in mummy survival to emergence were found across the microhabitat treatments (survival on upper leaf surface, 1 of 34 mummies; survival on lower leaf surface, 1 of 32 mummies; survival on stems, 2 of 34 mummies;  $G = 0.42$ ,  $df = 2$ ,  $P = 0.81$ ). During the second temporal block (2 weeks after mowing), the predation pressure experienced by mummies was greatly reduced, with 11 out of 15 mummies (73%) surviving to adult emergence. There was again no significant difference in mummy survival to emergence across microhabitat treatments during this period (survival on upper leaf surface, 3 of 4 mummies; survival on lower leaf surface, 4 of 5 mummies; survival on stems, 4 of 6 mummies;  $G = 0.04$ ,  $df = 2$ ,  $P = 0.98$ ). In the third temporal block (5 weeks after mowing), predation pressure was intermediate, with 10 of 96 mummies surviving to emergence (10%), and no significant differences across treatments (survival on upper leaf surface, 4 of 27 mummies; survival on lower leaf surface, 4 of 35 mummies; survival on stems, 2 of 34 mummies;  $G = 1.16$ ,  $df = 2$ ,  $P = 0.56$ ). Informal observations confirmed that predatory beetles (family Coccinellidae) were abundant in the field before the mowing. Predators were almost completely absent from the field immediately after the mowing, and the population rebuilt across several weeks after the mowing. No hyperparasitism was discovered during the field experiment, as all mummies in the field emerged or were found to be dead when dissected after 20 days.

Survival analysis was applied to assess treatment effects on mummy survival times. The survival rates of aphid mummies varied significantly across the temporal blocks of the experiment, with the lowest survival rates observed before the alfalfa mowing and the highest survival rates observed 2 weeks after the mowing ( $\chi^2 = 46.4$ ,  $df = 2$ ,  $P < 0.001$ , Fig. 2). There was no significant difference across treatments during the first temporal block, prior to the mowing ( $\chi^2 = 1.4$ ,  $df = 2$ ,  $P = 0.5$ ) or the second temporal block, 2 weeks after the mowing ( $\chi^2 = 0.1$ ,  $df = 2$ ,  $P = 0.9$ ). The third temporal block, 5 weeks after the mowing and during which mummies experienced intermediate predation pressure, showed significant differences across treatments ( $\chi^2 = 13.6$ ,  $df = 2$ ,  $P < 0.001$ , Fig. 3), with mummies transplanted to the upper leaf surfaces having the smallest mortality rates. Relative to the hazard experienced by mummies affixed to lower leaf surfaces, the hazard rate for mummies on upper leaf surfaces was reduced by 44% ( $HR = 0.556$ ,  $SE = 0.297$ ,  $P = 0.048$ ), whereas the hazard rate for mummies on stems was increased by 66% ( $HR = 1.662$ ,  $SE = 0.257$ ,  $P = 0.048$ ), with the overall



**Fig. 2** Survival of outplanted pea aphid mummies in the field across three temporal blocks ( $\chi^2=46.4$ ,  $df=2$ ,  $P<0.001$ ). Censoring of observations is indicated by tic marks

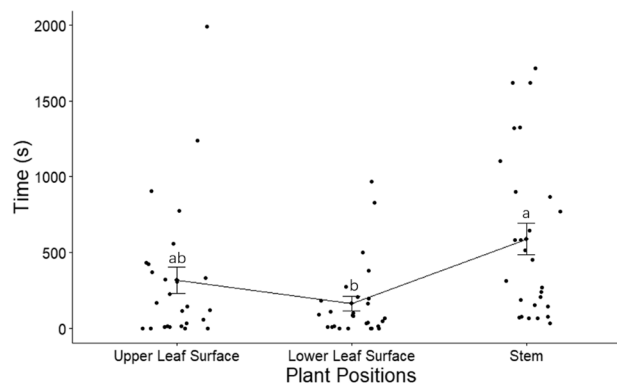


**Fig. 3** Survival of mummies outplanted to different microhabitats during the third temporal block of the field experiment, 5 weeks after the alfalfa mowing (14 August–14 October, 2020; ( $\chi^2=13.6$ ,  $df=2$ ,  $P<0.001$ )). Censoring of observations is indicated by tic marks

differences among the three treatments varied significantly (HR = 1, LR = 13.53,  $df=2$ ,  $P=0.001$ ).

**Lab experiment**

Eight mummies were preyed upon by ladybeetles across 27 replications, including 6 mummies affixed to upper leaf surfaces and two mummies affixed to lower leaf surfaces; this difference across treatments in predation was not significant ( $G=2.36$ ,  $df=1$ ,  $P=0.12$ ). Ladybeetles spread their foraging time unequally across plant substrates ( $\chi^2=9.26$ ,  $df=2$ ,  $P=0.01$ , Fig. 4), spending significantly more time foraging on the stems, whereas the upper and lower leaf surfaces received similar foraging times ( $\chi^2=2.26$ ,  $df=1$ ,  $P=0.13$ , Fig. 4).



**Fig. 4** Time ladybeetles ( $N=27$ ) spent foraging on each of three plant microhabitats: tops of leaves, bottoms of leaves, and stems during a 45-min trial ( $\chi^2=9.26$ ,  $df=2$ ,  $P=0.01$ ). Different letters indicate statistically significant differences between variables

**Discussion**

The significant variation in aphid mummies’ survival rates across the different temporal blocks of our field experiment support the hypothesis that predation risk is changed by the disturbance associated with the alfalfa harvest. Aphid mummy survival 5 weeks after the alfalfa mowing, when overall predation risk was intermediate, supports the hypothesis that the shift in host aphid behavior after parasitism is a result of adaptive parasitoid manipulation: parasitoid wasp immatures (larvae and pupae) experienced lower rates of predation when occupying the upper leaf surfaces, compared with mummies affixed to either lower leaf surfaces or, especially, plant stems. However, the impacts of microhabitat choices were context-dependent, as treatment effects were not apparent when the overall predation risk was either extremely high (first temporal block, prior to alfalfa mowing) or very low (second temporal block, 2 weeks after mowing).

Our results join several previous studies demonstrating strong temporal variation in the impact of mummy predators and hyperparasitoids. Brodeur and McNeil (1992) documented substantial variation in the impact of hyperparasitoids on potato aphid mummies in different microhabitats, both within and between years (Brodeur & McNeil 1992). Higher predator densities were correlated with lower adult emergence of aphid parasitoids (Chacón & Heimpel 2010). *H. convergens* were found to consume up to 98–100% of immature aphid parasitoids as localized aphid populations were extirpated by predators (Colfer & Rosenheim 2001).

Plant stems appeared to be the most dangerous place for mummies during the third temporal block, with the hazard rate for mummies located on stems 66% greater than the hazard rate on the lower leaf surfaces. In the laboratory, ladybeetles spent significantly more time foraging on stems

than on other parts of the plants, suggesting that the high mortality of mummies on stems may reflect the predator's foraging behavior. However, it is unclear whether predators spend more time on stems simply because fava bean plants have higher total stem surface area compared to leaf surface area, and it also remains unclear whether the observed foraging patterns would also be observed in the alfalfa system. Ladybeetles in the laboratory consumed three times more mummies on lower leaf surfaces, mirroring the field results where mummies on the upper leaf surfaces experienced the lowest predation risk. This might be a result of live aphids being more likely to be found on the lower leaf surfaces, and since predators exhibit partial feeding preference for unparasitized aphids over aphid mummies (Meyhöfer & Klug 2002; Prado et al. 2015; Colfer & Rosenheim 2001), parasitoids could benefit by causing their hosts to move away from lower leaf surfaces to avoid predators' attention. In the laboratory, however, ladybeetles did not show a preference for foraging on the lower leaf surfaces of leaves compared to the upper leaf surfaces (Fig. 4). Future research could further examine the predation risk experienced by mummies on upper/lower surfaces of the leaves and explore why predators might express foraging preference for particular microhabitats.

Abiotic factors such as exposure to ultraviolet radiation and other sunlight components, elevated temperatures, and moisture (rainfall or dew) might also have differential impacts on the survival of mummies located in different microhabitats. Mummies on the upper sides of the leaves are more exposed to direct sunlight than mummies on the lower sides of the leaves. During cooler periods of the year, the increased temperature could be beneficial for the development of parasitoids, as the mortality rate of *Aphidius ervi* decreased with increasing temperature up until 25 °C (Sigsgaard 2000). Direct solar radiation could also accelerate parasitoid development and thus reduce the duration of exposure to natural enemies.

Our results suggest that the altered behavior of host aphids was likely a result of adaptive manipulation of the aphid host by its primary parasitoid wasp. This behavior modification does not favor the survival and reproduction of host aphids, since parasitized aphids do not mummify until they are close to death. The adaptive suicide theory is also not supported, given that the altered host behavior enhances the survival of mummies and thus may actually increase the risks of parasitism for aphid clone-mates inhabiting the same or nearby plants. Predation appears to be a dominant factor favoring alteration of microhabitat selection: the hazard rates of aphid mummies were not linked to microhabitat selection when the predator density was either extremely high or low, whereas under intermediate predation pressure parasitized aphid on upper leaf surfaces were least likely to be preyed upon.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s11829-023-09947-y>.

**Acknowledgements** We would like to thank Bryan Pellissier for offering an alfalfa field at UC Davis Plant Pathology Experimental Farm where the field study was conducted. We are thankful to Beneficial Insectary (CA) for providing us with a free supply of *Aphidius ervi* mummies. We would also like to thank Xinqiang Xi and Xiaoli Hu for their comments on this manuscript. We are grateful for insightful comments from a reviewer that greatly improve the quality of this manuscript.

**Funding** This work was supported by the United States Department of Agriculture, regional research project W4185. United States Department of Agriculture, W4185, Jay A. Rosenheim

**Data Availability** The data that supports the findings of this study are available in the supplementary material of this article.

## Declarations

**Conflict of interest** The authors have no competing interests to declare that are relevant to the content of this article.

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