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Response to selected ecological parameters by *Leptus hringuri* Haitlinger, 2000 larvae (Trombidiformes: Erythraeidae) parasitizing treehoppers (Hemiptera: Membracidae) from Bolivia on two host-plant species

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ABSTRACT

Larvae of *Leptus hringuri* parasitizing families (adult female + offspring) of the treehopper *Alchisme grossa* on two host-plants, *Brugmansia suaveolens* (BS) and *Solanum ursinum* (SU), were studied. The effect of microenvironmental abiotic conditions (luminosity, temperature and relative humidity) and biotic conditions (distance from the soil to a treehopper host and host-plant phenological stage) on this tritrophic interaction was examined. Overall, the results suggest i) intensity of mite infestation (mean number of mites per infested female or family) of treehoppers (insect hosts) was twice on SU than on BS, ii) a preference of L. *hringuri* larvae for places with more luminosity (on both host-plants) and relative humidity (on SU), iii) a negative correlation between larval infestation and distance of the host colony to the ground, and iv) that larvae of L. *hringuri* could detect cues (i.e. chemical) emitted by their insect hosts or the host-plant of the insect host. Results indicate that luminosity, humidity and distance to the ground of the insect-host microenvironment affect both parasitization and prevalence of *Leptus* larvae mites; however, further research will be needed to understand the ecological mechanisms and consequences of these interactions and to test the hypotheses proposed herein under a chemical ecology perspective.

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Acari; habitat preference; mites; parasitism; tritrophic interaction

Introduction

Parasitengona is one of the most diverse groups of mites, comprising more than 9000 species in more than 800 genera. Approximately, 4000 of these species are terrestrial, and a part of them (Trombidiformes) are known as "velvet mites" (Gabryś et al. 2011). The life cycle of velvet mites consists of seven stages: egg, regressive calyptostasic prelarva, ectoparasitic larva, calyptostatic protonymph, free-living predaceous deutonymph, calyptostatic tritonymph, and free-living predaceous adult (Wohltmann 2000; Belozerov 2008). Larval stages of the genus *Leptus* Latreille, 1796 (Trombidiformes: Erythraeidae) parasitize various arthropod hosts (Stroiński et al. 2013; Mąkol and Wohltmann 2012; Muñoz-Cárdenas et al. 2015). Eggs are laid in the soil and then larvae must find a host to feed on its haemolymph until they engorge, detach from the host and return to the soil to continue their development (Zhang 1998; Wohltmann 2000). There are approximately 33 *Leptus* species described for the Neotropical Region (Mąkol and Wohltmann 2012); however, most of the literature on *Leptus* mites focuses almost entirely on taxonomic issues and on mite hosts and distribution (Mąkol and Wohltmann 2012; Pereira et al. 2012), with little or no ecological and natural history considerations. To the best of our knowledge what has been reported on these topics in *Leptus* mites is their time of emergence in the laboratory and their ability to remain in the same attachment site during their parasitic phase (Laydanowicz and Mąkol 2010), that most of the larvae are found near the habitat with the highest relative humidity (Wendt et al. 1992; Wohltmann 1998), and that they are univoltine and semelparous (Wohltmann 2000). The limited knowledge on their ecology and natural history has prevented a deeper understanding of their ecological niche, life history, habitat preferences, and interaction with their hosts (Townsend et al. 2006; Pereira et al. 2012; Cordero-Rivera et al. 2018). We studied parasitization by *Leptus hringuri* Haitlinger, 2000 larvae of the treehopper *Alchisme grossa* Fairmaire, 1846 (Hemiptera: Membracidae) on two of its host-plants in the Bolivian Yungas, *Brugmansia suaveolens* (Humb. and Bonpl. ex Wild) Bercht. and C. Presl, 1823 and *Solanum ursinum* Rusby, 1890 (both Solanaceae). We evaluated the effect of plant microenvironmental abiotic conditions (luminosity, temperature, and relative humidity: RH) and biotic conditions (distance from the soil to a treehopper host and host-plant phenological stage) on *Leptus* parasitism in these two tritrophic interactions.

Materials and methods

Species identification

The species *A. grossa* was previously identified by curator Dawn Flynn from *The Schiele Museum of Natural History* several years ago since we have studied this species for almost 9 years now. Similarly, host-plant species, *B. suaveolens* (BS) and *S. ursinum* (SU), were identified by consulting specialists in Solanaceae plants in Bolivia and by examining the collections in the three main herbaria in Bolivia: *Herbario Forestal Nacional Martín Cardenas* (BOLV), *Herbario del Oriente Boliviano* (USZ), and *Herbario Nacional de Bolivia* (LPB). *L. hinrguri* specimens were collected from the treehopper hosts, transferred to plastic tubes, and then killed by placing the tubes in a freezer at −10°C; they were then immersed in 70% ethanol for preservation. The specimens were mounted in Hoyer's medium (Walter and Krantz 2009) and deposited in the acarological collection of the *Centro de Coleções Taxonomicas da Universidade Federal de Minas Gerais* (CCT-UFMG AC), Brazil. Access numbers of the samples are CCTUFMG AC 180023, 180025, 180027, and 180029. Species were identified by using the taxonomical key of Haitlinger and Šundić (2016).

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Species studied and study area

The species *A. grossa* is a subsocial treehopper that lives on two Solanaceae (*B. suaveolens*: BS and *S. ursinum*: SU) host-plants in the Bolivian Yungas ecoregion. The Yungas ecoregion is characterized by a wide altitudinal cline and approximately 3700 mm of rainfall per year concentrated from October to March (Navarro and Maldonado 2002). The understory vegetation at the study area is composed mostly of small native trees and bushes, BS and SU among them (Torrico-Bazoberry et al. 2014). *A. grossa* females oviposit on the underside of a leaf and exhibit maternal care throughout offspring development. When nymphs hatch, they remain aggregated with their mother until they complete development or at least until the third instar (Torrico-Bazoberry et al. 2014, 2016).

Data of *L. hringuri* larvae parasitizing the treehopper host *A. grossa* on its two host-plants (BS and SU) were collected from mid-December 2012 to early April 2013 during the rainy season at Incachaca (Cochabamba, Bolivia, 17º13'S – 65º49'W; 2450 m a.s.l.), in the Bolivian Yungas forests. During the first field trip, treehopper families (adult female + offspring) that were at similar stages of development (offspring in the egg stage) were chosen. Each plant was tagged with a sequential plant code, and petioles of leaves containing treehopper families were also tagged with a code. Females were also marked on the right side of the pronotum with a permanent marker (Stabilo® write-4-all) by momentarily removing them and then placing them back over their respective egg masses.

All tagged families were monitored once weekly (between 11:00 and 14:00 h) for four months (December–April) until nymphs disaggregated from their original families (Torrico-Bazoberry et al. 2016). Monitoring was performed weekly to avoid re-counting *L. hringuri* larvae; Cordero-Rivera et al. (2018), based on a capture-recapture method, found that *L. killingtoni* Turk, 1945 larvae remained attached to their hosts a mean of 6.7 days, with most of the mites remaining for only a couple of days.

Microenvironmental variables

The abiotic microenvironment of each family's site was characterized by luminosity, temperature, and relative humidity (RH). On each monitoring event, microenvironmental abiotic traits were measured using a light meter (Lutron® LX-101) and a thermocouple (EXTECH®) positioned 2 cm below the underside of tagged leaves for approximately 20 seconds (until measurements were stable). Two measurements of microenvironmental variables per leaf were performed between 11:00 and 14:00 h; the mean of these two values was associated with the monitoring event when data were taken. Comparisons of microenvironmental data between host-plant species and between parasitized vs. unparasitized families were performed using Mann-Whitney tests. All statistical analyses of this work, except variation partition (indicated below), were performed on SigmaPlot 12.0.

The data for abiotic variables were correlated with two variables for mite infestation: the number of *L. hringuri* larvae per treehopper female (when only the female of a treehopper family was parasitized) and the total number of *L. hringuri* larvae per treehopper family when treehopper offspring was also parasitized. The total number of mites on a given female and on its offspring was defined as the sum of the number of mites counted over all monitoring events on that female or on its offspring. The corresponding values of microenvironmental parameters were defined as the mean of values recorded for each female or family over all monitoring events. Correlation analyses were performed between the total number of *L. hringuri* larvae per treehopper female or per family and the mean value of microenvironmental parameters of such female or family over all monitoring events, using Spearman's correlation considering data from both host-plants separately. Thus, a replicate in the correlation analyses corresponded to a treehopper female or family.

Additionally, we used a variation partition analysis (Borcard et al. 1992), a technique used when two or more possible hypotheses are proposed to explain the variation of an ecological variable (Legendre 2008). In this case, the variation partition analysis was used to explain mite abundance on treehoppers based on the abiotic variables measured (HR, temperature, and luminosity). Two different variation partition analyses were performed based on the total number of mites per family, and the total number of mites per female. These analyses were performed using R version 3.4.5 using the vegan package (Oksanen et al. 2006).

Mite prevalence and intensity of mite infestation

On each monitoring event, the number of mites on treehopper females and families was counted. Prevalence of infestation was estimated as the percentage of females or families parasitized with at least one mite larva over all monitoring events. The intensity of mite infestation was measured as the mean number of mites per infested female or families, respectively. Prevalence and intensity of mite infestations were compared between host-plants using Mann–Whitney tests.

Additionally, a correlation analysis was performed between the total number of mites on the treehopper offspring and the number of offspring in the family using Spearman's correlation and considering data from each host-plant separately. To compare if the infestation was higher on adults or on nymphs, *per capita* infestation, defined as the number of mites per number of treehoppers (either adult females or nymphs, respectively) was also compared within each host-plant species using Mann–Whitney tests.

Plant phenological state

The phenology of each plant where treehopper families were found was characterized as vegetative or flowering/fruiting. The number of families that were parasitized or unparasitized on each phenological state was registered and compared using a two-tailed Fisher's exact test. A separate analysis was performed for each host-plant.

Distance of family to the ground

The distance of each treehopper family to the ground was measured as a proxy of the distance that a recently moulted *Leptus* larva must walk before finding a suitable host to attach to and feed, assuming that all *Leptus* eggs are placed on the soil nearby (Zhang 1998). Family distance to the ground was then compared between unparasitized and parasitized families using a Mann–Whitney test. Additionally, Spearman's correlation analyses between family distance to the ground and the total number of *L. hringuri* mites per female and per family were performed for each host-plant separately. All analyses were performed on SigmaPlot 12.0.

Results

Microenvironmental variables

Luminosity significantly differed between host-plants (Mann–Whitney test: $U = 935$; $P = 0.001$) and was higher in SU than in BS (BS: 85.3 ± 54.3 lx; SU: 142.5 ± 97.1 lx; mean ± standard deviation: SD). Likewise, considering data from both hosts and plants together, luminosity was 90.0 ± 61.2 lx on families that were unparasitized and 133.0 ± 93.8 lx on families that were parasitized, with significant differences between them (Mann–Whitney test: $U = 1038$; $P = 0.005$). Luminosity was positively correlated with the total number of mites per family on BS and on SU (Table 1).

RH significantly differed between host-plants (Mann–Whitney test: $U = 849$; $P < 0.001$), the environment of BS plants being more

Table 1. Correlations between the total number of *Leptus hringuri* larvae on treehopper females or families and mean microenvironmental abiotic conditions (luminosity, relative humidity, and temperature) and family distance to ground on (a) *Brugmansia suaveolens* ($N = 69$ families) and (b) *Solanum ursinum* ($N = 43$ families).

	Mean luminosity	Mean RH	Mean temperature	Family distance to ground
a)				
Total number of mites per family	**$r = 0.299$**	$r = -0.072$	$r = 0.113$	$r = -0.145$
	$P = 0.013$	$P = 0.557$	$P = 0.356$	$P = 0.232$
Total number of mites per female	$r = 0.167$	$r = -0.152$	$r = 0.121$	$r = 0.025$
	$P = 0.169$	$P = 0.212$	$P = 0.320$	$P = 0.838$
b)				
Total number of mites per family	**$r = 0.311$**	**$r = 0.520$**	$r = 0.042$	**$r = -0.326$**
	$P = 0.042$	**$P < 0.001$**	$P = 0.786$	**$P = 0.033$**
Total number of mites per female	$r = 0.250$	**$r = 0.415$**	$r = 0.082$	$r = -0.287$
	$P = 0.105$	**$P = 0.006$**	$P = 0.600$	$P = 0.062$

Means were calculated over all monitoring events. Significant correlations are shown in bold. r = correlation coefficient, P = P-value.

humid than that of SU plants (BS: 82.9 ± 4.5%; SU: 78.4 ± 5.6%; mean ± SD). Considering data from both host-plants together, there was no significant difference (Mann–Whitney test: $U = 1238.5$; $P = 0.111$) in RH between sites with unparasitized (80.6 ± 6.5%) and parasitized (82.1 ± 3.1%) families. RH was positively correlated with the total number of mites per family and per female on SU but not on BS (Table 1).

Temperature significantly differed between host-plants (Mann–Whitney test: $U = 812$; $P < 0.001$), the environment being warmer at SU plants than at BS plants (BS: 19.0 ± 1.2°C; SU: 20.1 ± 1.8°C; mean ± SD). Considering data from both host-plants together, there was no significant difference (Mann–Whitney test: $U = 1396$; $P = 0.510$) in temperature between sites with unparasitized (19.4 ± 1.6°C) and parasitized (19.5 ± 1.5°C) families. Correlations with temperature were not significant (Table 1).

Considering the total number of mites per family in the variation partition analysis, 7.2% of the total mite abundance was explained by the RH, temperature, and luminosity data (Figure 1A). Luminosity explained 5.2% of the mite variation when RH and temperature variables were partialled out, RH explained 1.7% of the mite variation when luminosity and temperature were partialled out, luminosity and temperature explained 2.2% of the variation when RH was partialled out, and luminosity and RH explained 0.8% of the variation when temperature was partialled out.

Considering the total number of mites per female in the variation partition analysis, 4.3% of the total mite abundance was explained by RH, temperature, and luminosity data (Figure 1B). Luminosity explained 1.7% of the mite variation when RH and temperature variables were partialled out, temperature explained 1.0% of the mite variation when luminosity and RH were partialled out, luminosity and temperature explained 2.1% of the variation when RH was partialled out, and luminosity and RH explained 0.5% of the variation when temperature was partialled out.

Mite prevalence and intensity of mite infestation

Observations were performed on 112 treehopper females and 4003 treehopper nymphs from 112 treehopper families (69 on BS and 43 on SU) marked during the season. Eighty-seven *L. hringuri* larvae were found on females (37 on BS and 50 on SU) and 130 mite larvae were found on treehopper nymphs (22 on BS and 108 on SU); thus, a total of 217 *L. hringuri* larvae were observed in this study.

Prevalence did not differ between host-plants considering both parasitism of females and of nymphs (Table 2). The intensity of mite infestation of females was 1.5 ± 1.3 (mean ± standard deviation, ranging from 1 to 6) on BS and 3.3 ± 4.2 (mean ± standard deviation, ranging from 1 to 18) on SU, with significant differences between host-plants (Mann–Whitney test: $U = 97$; $P = 0.011$). The intensity of mite infestation of families was 2.1 ± 1.8 (mean ± standard deviation, ranging from 1 to 9) on BS and 9.3 ± 16.7 (mean ± standard deviation, ranging from 1 to 70) on SU with significant differences between host-plants (Mann–Whitney test: $U = 130.5$; $P = 0.009$).

There was a positive correlation between the total number of mites on the offspring and the number of nymphs (offspring) in the family in each host-plant (BS: Spearman $r = 0.587$, $P = 0.001$; SU: Spearman $r = 0.542$, $P = 0.024$). Moreover, the mean over all monitoring events of *per capita* infestation of nymphs and females was significantly different both in BS (Mann–Whitney test: $U = 0$; $P < 0.001$; mean ± standard deviation: 1.7 ± 1.2 for females, 0.05 ± 0.03 for nymphs) and in SU (Mann–Whitney test: $U = 4$; $P < 0.001$; mean ± standard deviation: 3.3 ± 4.2 for females, 0.29 ± 0.40 for nymphs) indicating that *per capita* infestation was higher in female adult treehoppers than in nymphs.

Plant phenological state

L. hringuri larvae were observed on 19 of the 43 (42%) families that lived on a BS plant at its vegetative stage and in 9 of the 24 (38%) families that lived on a BS plant at its flowering/fruiting stage, with no significant difference between the two ratios (Fisher's exact test: $P = 0.8$). However, *L. hringuri* larvae were observed on 15 of the 24 (63%) families that lived on a SU plant at its vegetative stage and in 2 of the 19 (11%) families that lived on a SU plant at its flowering/fruiting stage, the two ratios being significantly different (Fisher's exact test: $P < 0.001$).

Family distance to the ground

Considering data from both host-plants together, the mean height of treehopper families was 111.1 ± 54.5 cm for families that were unparasitized and 91.2 ± 50.6 cm for families that were parasitized, with significant differences between them (Mann–Whitney test: $U = 1151$; $P = 0.035$). A negative correlation between family distance to the ground and the total number of *L. hringuri* larvae per family was observed on SU but not on BS (Table 1).

Discussion

Luminosity of the host microenvironment was positively correlated with parasitization and mite prevalence. The preference of *L. hringuri* larvae for more luminous environments is unclear. More luminous places represent warmer developmental environments due to the incidence of sunlight. Since ectotherm organisms develop faster at higher temperatures (Kingsolver and Huey 2008), the preference of mite larvae for such places could lead to faster development and also to an increase in their survival through avoidance of predator attacks, as it occurs in other arthropods (Brodeur and McNeil et al. 1992; Lagos et al. 2001; Seyahooei et al. 2009; Josso et al. 2011). However, further experimental research will be needed to test this hypothesis, especially considering that no significant correlations between the total number of mites and temperature were found in the present study.

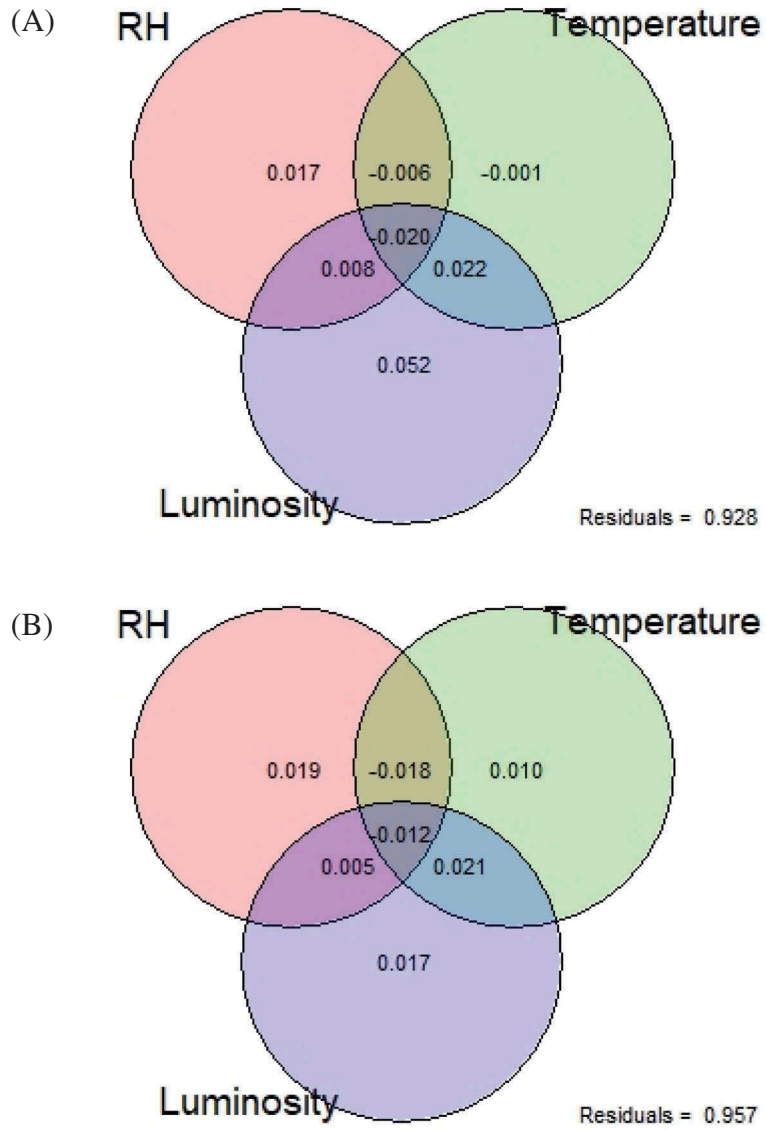

Figure 1. Variance partition of the effects of selected abiotic variables: relative humidity (RH), luminosity, and temperature on mite abundance measured as the total number of mites (a) per family and (b) per female. Values inside the circles represent conditional effects.

Table 2. Prevalence of *Leptus hringuri* larvae on *Alchisme grossa* families (female + offspring) on its two host-plants, *Brugmansia suaveolens* (BS) and *Solanum ursinum* (SU).

	BS	*SU*	Fisher's exact test
Percentage of families parasitized with at least one mite larva on the female or its offspring	40.6% ($N = 28$)	39.5% ($N = 17$)	$P = 0.99$
Percentage of families with the female parasitized (regardless of offspring infestation)	31.9% ($N = 22$)	34.9% ($N = 15$)	$P = 0.99$
Percentage of families with only the female parasitized but not the offspring	24.6% ($N = 17$)	16.3% ($N = 7$)	$P = 0.34$
Percentage of families with the offspring parasitized (regardless of female infestation)	15.9% ($N = 11$)	23.3% ($N = 10$)	$P = 0.45$
Percentage of families with only the offspring parasitized but not the female	8.7% ($N = 6$)	4.7% ($N = 2$)	$P = 0.48$

The positive correlation between RH and the total number of mites per family on SU suggests that *L. hringuri* larvae may need and actively search for a humid environment to develop under field conditions. This preference may be related to the avoidance of desiccation. This interpretation is supported by the study by Wendt et al. (1992) who found a higher abundance of *L. trimaculatus* Hermann, 1804 larvae in the most humid zone (82–100% RH) of their study site, and the study of Wohltmann (1998) who collected *L. ignotus* larvae in very humid zones (that rarely showed RH lower than 100%) and found that when reared under laboratory conditions larvae developed only when RH was higher than 98%. Interestingly, the correlation between RH and total number of mites per family was not significant on BS. This could be related to the fact that SU represents a drier and warmer environment than BS (Pinto et al. 2020) and hence one where the risk of desiccation is higher.

Most of the variation in mite abundance per family (92.8%) and per female (95.7%) cannot be related or explained by the three abiotic microenvironmental variables (HR, luminosity, and temperature) considered in this study, as indicated by the variation partition analyses. Thus, it is possible that other external causes not considered, e.g. biotic factors such as social aggregation (Borcard et al. 1992), may explain mite abundance in this study. Further studies and ecological knowledge of *Leptus* mites are necessary to better understand the factors affecting their abundance and their interaction with their insect hosts. Particularly, knowledge on *Leptus* mites biology is needed to generate new hypotheses regarding their abundance and host interactions (Borcard and Legendre 1994).

The exposure of mites to higher luminosity and temperature on SU than on BS could explain the higher intensity of mite infestation on SU than on BS, both on families and on females. However, this pattern may also be related to differences in semiochemicals such

as cuticular chemical compounds in *A. grossa* (Torrico-Bazoberry et al. 2018), which may vary between host-plants since *A. grossa* has been shown to incorporate alkaloids from BS (Pinto et al. 2016). Thus, cuticular extracts have been observed mediating host searching behaviour in the mites *Grandiella rugosita* Summers and Schuster, 1979 (Sarcoptiformes: Canestriniidae) (Beran et al. 2014) and *Macrocheles saceri* Costa 1967 (Mesostigmata: Macrochelidae) (Niogret et al. 2006).

The difference in mean *per capita* intensity of infestation of treehopper females and nymphs between host-plants suggests the ability of *Leptus* larvae to detect cues emitted by their hosts which exert a differential attractivity towards the mite larvae. As mentioned above, these cues may be related to the chemical nature of the host, itself related to the chemical nature of the host-plant. The difference in *per capita* infestation between females and nymphs on both hosts may be caused by a difference in the amount of signal produced by the (large) female compared to the (relatively smaller) treehopper nymph but may also be caused by a change in the nature of signals along the ontogenic development of the treehopper. This chemical ecological perspective may also explain the higher proportion of parasitized treehopper families observed on vegetative than on flowering/fruiting SU plants. Thus, *L. hringuri* larvae may be able to detect differences in semiochemicals (e.g. volatile organic compounds) which are a function of the phenological state of the host-plant (Kuhn et al. 2004). Further research is needed to assess if volatiles from the insect-host-plant complex can be detected as signals by *Leptus* mites to find a suitable host to feed in analogy to the prey detection behaviour based on semiochemicals suggested for the predatory mite *Phytoseiulus persimilis* Athias-Henriot, 1957 (Mesostigmata: Phytoseiidae) (Dicke 1986).

Since *Leptus* larvae actively search for insect hosts by walking within the vegetation (Lorenzo-Carballa et al. 2011), a negative correlation is expected between the distance of the insect host to the soil and larval abundance on the host (Townsend et al. 2008). In the present study, a negative correlation was found between the distance of each treehopper family to the ground and the total number of mite larvae on such family. Additionally, unparasitized treehopper families were located higher in the host-plant (i.e. further away from the soil) than parasitized families.

This paper has described ecological patterns related to parasitization by *L. hringuri* of phytophagous insects living on sympatric host-plants; further research will be needed to understand ecological mechanisms, patterns, and consequences underlying this multitrophic interaction.

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Author's contributions

DTB, CFP, HMN conceived and designed the study. DTB conducted fieldwork and analyzed the data. JD performed variation partition analyses. DTB and HMN wrote the paper with contributions from CFP. All authors read and improved the manuscript and agreed to its final content.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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