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Effect of the eucalypt lerp psyllid *Glycaspis brimblecombei* on adult feeding, oviposition-site selection, and offspring performance of the bronze bug, *Thaumastocoris peregrinus*

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Abstract Oviposition-site selection may be greatly affected by competitive plant-mediated interactions between phytophagous insects but these interactions have been poorly investigated on trees. Here, we evaluated the potential interaction between two invasive pests of *Eucalyptus* trees, the red gum lerp psyllid, *Glycaspis brimblecombei* Moore (Hemiptera, Sternorrhyncha: Aphalaridae), and the bronze bug, *Thaumastocoris peregrinus* Carpintero et Dellapé (Heteroptera: Thaumastocoridae). We assessed the effect of the co-occurrence of *G. brimblecombei* on the selection of feeding and oviposition sites by *T. peregrinus* females using dual-choice bioassays. We compared developmental time and survival of the first instar of nymphs reared on healthy *Eucalyptus tereticornis* Smith (Myrtaceae) leaves and on leaves infested with the lerp psyllid, either with or without lerps (i.e., white conical sweet-tasting structures, secreted during the nymphal stage). Bronze bug females prefer to oviposit on lerp-carrying leaves but we found no difference in feeding preference when compared to healthy leaves. Infestation with the lerp psyllid hampered nymphal performance in terms of developmental time and survival, although the presence of lerps reverted the effect in survival and shortened the duration of the initial instar. These results display an interaction between these two insect species that affects both the oviposition preference of *T. peregrinus* females and the nymphal performance. Although there seems to be a discrepancy between mother preference and offspring performance, feeding on the lerps may prove beneficial to the offspring under long-term conditions and multiple infestation by other pests and diseases.

Introduction

Interspecific competition is an important factor affecting the fitness of phytophagous insects (Kaplan & Denno, 2007). Competitive interactions are often indirectly mediated by induced changes in plant chemistry, morphology, and/or physiology that result from herbivore attack and affect the fitness of a competitor (Karban & Baldwin, 1997; Ohgushi, 2005; Stam et al., 2014). Oviposition-site selection of phytophagous insects is heavily affected by such indirect plant-mediated interactions (Kaplan & Denno, 2007). Plant-mediated interspecific interactions have been reported in insects from the same feeding guild (Denno et al., 2000; Karban et al., 2012) and across feeding guilds (Kessler & Baldwin, 2004; Soler et al., 2012). Furthermore, the outcome of the interaction can change depending on the sequence of arrival of the herbivores onto the plant (Poelman et al., 2008; Soler et al., 2012; Kroes et al., 2016; Huang et al., 2017).

Most of the studies on interspecific competition among phytophagous insects deal with annual plants (Kaplan

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et al., 2011). Unlike annual plants, trees are exposed to many insect species, occurring either simultaneously or subsequently during the years needed for a rotation cycle in commercial plantation forestry. The study of competitive interactions among phytophagous insects in such long-term systems is particularly interesting, although challenging. Assessing changes in oviposition behaviour of an insect due to the co-occurrence of a potential competitor may be a good starting point to determine the effect of interspecific competition among phytophagous insects in these ecosystems.

Among the many insects that attack eucalyptus trees (Myrtaceae), two that have become important pests worldwide are the red gum lerp psyllid and the bronze bug. The red gum lerp psyllid, *Glycaspis brimblecombei* Moore (Hemiptera, Sternorrhyncha: Aphalaridae), is a small-winged sap-sucking insect that usually lives beneath a white conical sweet-tasting structure called lerp, which is secreted during the nymphal stage (Firmino-Winckler et al., 2009). Although they can feed on other eucalypt species, they are particularly abundant on adult shoots and leaves of red gum trees (*Eucalyptus tereticornis* Smith, *Eucalyptus camaldulensis* Dehnh.), on which they perform better than on other commercial species like the blue gum (*Eucalyptus globulus* Labill., *Eucalyptus maidenii* Muell.) and the rose gum (*Eucalyptus grandis* Hill ex Maiden) (Hollis, 2004; FAO-MGAP, 2006; de Santana & Burckhardt, 2007; Firmino-Winckler et al., 2009). Although it is regarded as an important pest in other parts of South America (de Santana & Burckhardt, 2007; Benítez Díaz et al., 2013), it has remained a pest of relatively low importance in Uruguay since its detection in 2004 (Bianchi & Sánchez, 2004). In Uruguay, *G. brimblecombei* is multivoltine, with population peaks between August and December (FAO-MGAP, 2006). The bronze bug, *Thaumastocoris peregrinus* Carpintero et Dellapé (Heteroptera: Thaumastocoridae), is an invasive pest of *Eucalyptus* species that has dispersed during the past decade from Australia, its centre of origin, to the main eucalypt forestry areas in the world (Nadel & Noack, 2012). In Uruguay, this species displays a preference for red and blue gums and exhibits seasonal dynamics with population peaks from March to late April (Martínez & Bianchi, 2010; Martínez & Gómez, 2014; Martínez et al., 2014). Both insect species exhibit epiphytic oviposition and usually lay eggs in batches. Bronze bug females often select oviposition sites elevated from the leaf surface, such as the central nerve of the leaf, deformations on the leaf blade, twigs, or even debris (Wilcken et al., 2010; Nadel & Noack, 2012). Thus, it is common to find bronze bug eggs on eggs of the psyllid, or on the lerps themselves (Ide et al., 2011), which are also frequently fed upon by adults and juveniles (Figure 1). To our knowledge, no study has yet investigated the effect of eucalypt infestation with *G. brimblecombei* on preference and performance of *T. peregrinus*.

The goal of this study was to evaluate the potential intraguild interaction between these two invasive pests of eucalypt trees, by assessing the effect of the presence of *G. brimblecombei* on the selection of feeding and oviposition sites by bronze bug females, and on the performance of their offspring. We hypothesized, based on field observations, that the co-occurrence of the lerp psyllid provides the bronze bug with an alternative food source that may be beneficial to both the female and her offspring.

Material and methods

Insects

Adults of *T. peregrinus* (1–2 days old) were obtained from a permanent mass rearing at INIA Tacuarembó, Uruguay. They were set to mate in communal mating cages consisting of an aluminium frame (35 × 50 × 70 cm) covered with voile mesh. Each mating cage contained ca. 80 females and 60 males. They were provided with fresh shoots of *E. globulus* in Erlenmeyer flasks. Experimental females were collected from the mating cages after a week, and were assumed to have mated based on previous research on the life cycle of *T. peregrinus* (cf. Martínez et al., 2014, for details on rearing procedure).

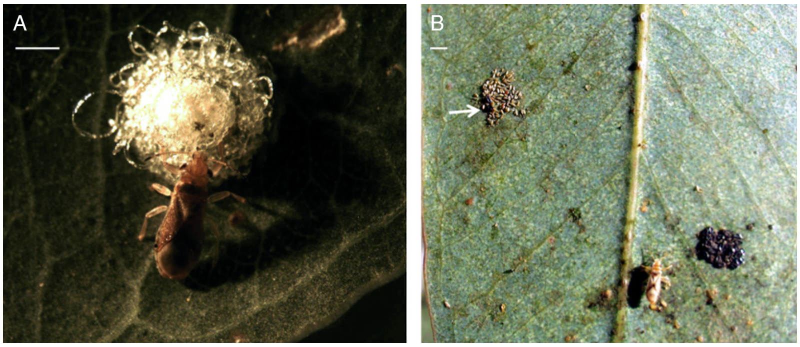

Figure 1 (A) Female of *Thaumastocoris peregrinus* feeding on a lerp. (B) Eggs of *T. peregrinus* (arrow) close to *Glycaspis brimblecombei* ovipostures. Scale bars indicate 1 mm.

Lerp-carrying leaves were collected in a shelter plantation of *E. tereticornis* infested with the lerp psyllid (10–20 lerps per leaf), located at the INIA experimental station (31°44′19.24″S, 55°58′43.75″W).

Preference

Feeding and oviposition preference of mated females was assessed in an experimental arena consisting of a Petri dish (5.5 cm diameter) filled with water and containing two leaf squares (2 × 2 cm) cut out from adult *E. tereticornis* leaves as treatment options. A cotton swab was cut into two halves and attached with adhesive tape to the bottom of the dish to provide a base to the leaf squares and prevent them from floating and touching the walls of the dish (Figure 2A). The leaf squares were then joined by one edge with adhesive tape affixed to the abaxial side, and placed onto the cotton stick at the centre of the dish. Finally, an adhesive label (1.5 × 0.8 cm; Rotola, Montevideo, Uruguay) was fixed between the leaf squares as a neutral release area (Figure 2B). One bronze bug female was enclosed in each experimental arena and left in a rearing chamber at 25 ± 5 °C, 55 ± 10% r.h., and L12:D12 photoperiod, to assess feeding and oviposition preference. Treatments consisted of a leaf square carrying one lerp of *G. brimblecombei* and a square cut from a healthy leaf collected from the same tree stand as control. After 2 days, oviposition and feeding by the bronze bug were assessed by counting eggs and faecal droplets on each leaf square.

Nymphal performance

Recently laid bronze bug eggs (24–48 h old) were placed on a leaf square (3 × 3 cm) floating on water inside a Petri dish as explained above. Immediately after hatching, bronze bug neonates were individually transferred to leaves belonging to one of the following treatments: healthy *E. tereticornis* leaves, leaves infested with 10–20 *G. brimblecombei* lerps, and leaves similarly infested after removing the lerps with a needle. The distal part of the leaves was previously cut to a length of 5 cm, and their petiole was enclosed in cotton and inserted in a test tube filled with water (Figure 3). The tubes were then incubated at 25 ± 5 °C, 60 ± 10% r.h., and L12:D12 photoperiod. As a measure of performance, nymphal survival was recorded daily until the nymphs had either moulted or died. We chose to assess the performance during the first instar based on previous studies showing that mortality is highest during this period (Martínez et al., 2014, 2017). In addition, a shorter experimental time prevented potential artefacts derived from the degradation of leaf sections.

Data analysis

Female preference was analysed by calculating the proportion of faecal drops and eggs in the tested treatment with respect to the total number of faecal drops and eggs (treatment + control), following Grostal & Dicke (1999). Hence, feeding and oviposition preference indices were established for each replicate, so that zero represents a complete preference for the control (*E. tereticornis* healthy adult leaves), 0.5 represents no preference, and 1 means a complete preference for the treatment under evaluation. The calculated indices were then transformed by the arcsine $\sqrt{x}$ transformation, and the resulting data were analysed by a Student's t-test, under a null hypothesis of no preference.

For performance data, the duration of the first instar for each individual was compared among treatments by a one-factor ANOVA, after $\sqrt{x}$ transformation. Tukey's test was employed for post-hoc comparisons among treatments, under a 95% family-wise confidence level. Survival curves of nymphal development were compared in pairs with the log-rank test (Peto & Peto, 1972). All tests were run in R v.3.4.0 (R Development Core Team, 2009).

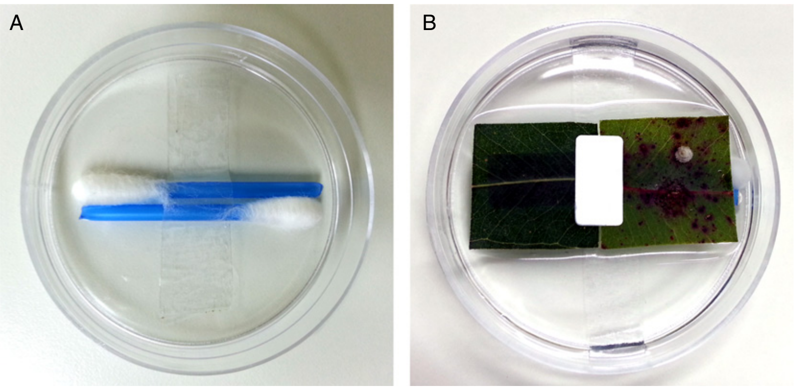

Figure 2 Experimental arena: (A) cotton swab cut in halves and attached at the bottom of the Petri dish; (B) arena ready for the bioassay with the two treatments and a paper label as neutral area.

Figure 3 Setup for *Thaumastocoris peregrinus* nymphal performance bioassays. A typical leaf infested with *Glycaspis brimblecombei* lerps is shown. The lighter spots correspond to either lerps on the other side of the leaf or former lerps on the same side.

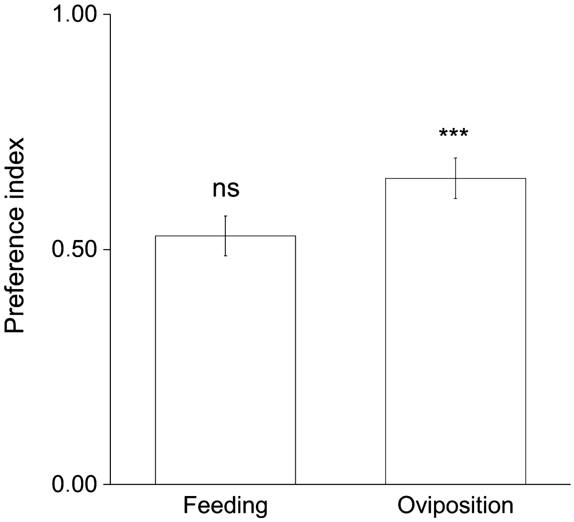

Figure 4 Mean (± SEM) feeding (n = 92) and oviposition (n = 87) preference index of *Thaumastocoris peregrinus* females in dual-choice bioassays with lerp-carrying vs. healthy *Eucalyptus tereticornis* leaf squares. An index above 0.5 indicates preference for the lerp-infested leaf square. The asterisks indicate a significantly different index from 0.5 (Student's t-test: ***P<0.001; ns, P>0.05).

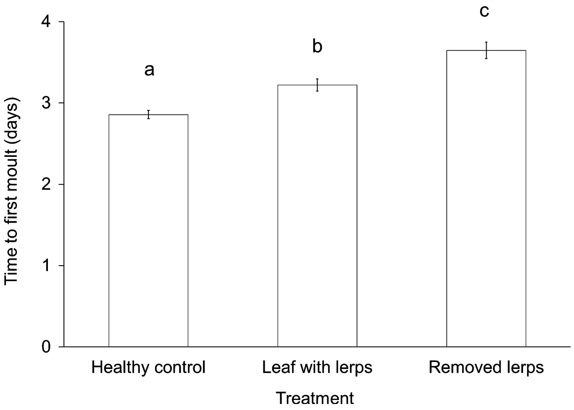

Figure 5 Mean (± SEM; n = 100 nymphs per treatment) duration (days) of the first instar of *Thaumastocoris peregrinus* nymphs reared on leaves of *Eucalyptus tereticornis*. The leaves were either healthy (control), with 10–20 lerps of *Glycaspis brimblecombei*, or with lerps removed before the assay. Means capped with different letters are significantly different (Tukey's test: P<0.05).

Results

Preference

In total 200 females were tested, equally divided over the oviposition and feeding preference tests. Females preferred to oviposit on lerp-carrying leaves over healthy leaves (t = −3.6935, d.f. = 86, P = 0.0004; n = 87) but did not discriminate between these two treatments for feeding (t = −0.7804, d.f. = 91, P = 0.43; n = 92) (Figure 4). Females that died or did not oviposit were not included in the analysis (13 and 8 for the oviposition and feeding preference tests, respectively). Females laid a total of 556 eggs, 374 on lerp-carrying leaves (4.1 ± 0.3 eggs per female), most of them adjacent to a lerp (all but three eggs). In contrast, only 182 eggs were laid on healthy leaves (2.0 ± 0.3 eggs per female). During the experiment, several females were observed feeding next to or directly on the lerps.

Nymphal performance

The duration of the first instar was different among treatments: nymphs reared on healthy leaves moulted earlier than those reared on leaves infested by *G. brimblecombei*. Between infested leaves, the first instar was longer when lerps had been previously removed (Figure 5). During the daily observations, nymphs reared on lerp-carrying leaves were frequently found on or adjacent to a lerp. Nymphal survival rate on lerp-removed infested leaves (67%) was significantly lower than on healthy leaves (84%), whereas lerp-carrying leaves resulted in survival rates (76%) not different from either treatment (Table 1).

Table 1 Log rank test for survival rates of *Thaumastocoris peregrinus* first-instar nymphs reared on *Eucalyptus tereticornis* healthy leaves, lerp-carrying leaves, and leaves whose lerps were previously removed (n = 100 nymphs per treatment)

Pair-wise comparison	χ^2	d.f.	P
Lerps vs. healthy	1.5	1	0.22
Lerps vs. lerps removed	2.6	1	0.11
Lerps removed vs. healthy	7.8	1	0.005

Discussion

We evaluated potential competitive interactions between two sucking phytophagous insects that occur on *Eucalyptus* trees. Our experimental results demonstrate an oviposition preference by the bronze bug for sites already colonized by the lerp psyllid, and a reduced performance of the nymphs on these sites, partially mitigated by the actual presence of lerps. The lower performance of nymphs as a result of lerp psyllid co-occurrence suggests some form of competition between the two species, most likely mediated by the plant. However, our results also show that the nymphs increase their survival rates and shorten their initial development in the presence of lerps. Together, these findings indicate that these two insects interact.

Our study was conducted outside the natural area of these species. To our knowledge, no information has been published on interactions between the bronze bug and the lerp psyllid in Australia. However, it is likely that this interaction occurs also in areas where their natural distributions overlap (Nadel & Noack, 2012; de Queiroz et al., 2013).

Bronze bug females laid more eggs on psyllid-infested leaves, but no such preference was observed for feeding. Among insects in which juveniles and adults share similar feeding habits, the selection of optimal oviposition sites may be difficult to take apart from the selection of optimal feeding sites (Scheirs & De Bruyn, 2002). In our study, we found a preference for lerp-carrying leaves over healthy leaves only regarding oviposition-site selection. Similarly, oviposition but not feeding preference was previously found in this insect with respect to conspecific-infested plants (Martínez et al., 2017). This study confirms that *T. peregrinus* females also include the co-occurrence of *G. brimblecombei* as a criterion to discriminate between oviposition sites.

At first glance, the selection for lerp-infested leaves as oviposition sites by female bronze bugs does not seem to result in an increased performance by their offspring. Indeed, nymphs feeding on healthy leaves developed faster than those feeding on leaves colonized by the lerp psyllid. The worst performance was observed on infested leaves from which all lerps had been removed, resulting in the slowest development and the lowest survival. A negative impact of *G. brimblecombei* co-occurrence may result from induced changes in plant chemistry or an overall decrease of resources available to the bronze bug as a result of competition. In fact, psyllids affect their host plants by removing sap and reducing photosynthesis as a consequence of both the construction of lerps and the excretion of honeydew that facilitates sooty mould growth (Hollis, 2004). Species within the genus *Glycaspis* have been reported as phloem feeders (Moore, 1964; Sharma et al., 2013). Feeding by the related genus *Cardiaspina* induces premature senescence in leaves of *Eucalyptus moluccana* Roxb. (Steinbauer et al., 2014). Likewise, in our study system we observed chlorotic spots on the leaf surface below the lerps, suggesting senescence induced by *Glycaspis*. All these changes may explain the poorer performance of the bronze bug nymphs on plants exposed to the lerp psyllid shown by our study.

The presence of lerps improves nymphal performance. Although nymphal duration was longer on leaves exposed to the lerp psyllid than on healthy leaves, we found no effect on survival if lerps were left on the leaves. In our experimental setup, we used leaf sections containing lerps cut out from leaves with moderate to heavy infestation, so it may be assumed that induced plant responses to *G. brimblecombei* herbivory should be present in such treatment, regardless of lerp removal. However, a counteracting positive impact may be in place, given the rich sugar contents of the lerp. For instance, the use of lerps as food sources has been documented for birds (Oliver, 1998; Florence, 2005) and native Australian human populations (Turner et al., 1994), but we found no previous evidence in the literature for lerp feeding by insects. Nevertheless, we often observed bronze bug adults and nymphs feeding on lerps, a behaviour that has also been observed in the field (Carlos Wilcken, pers. comm.). Moreover, we recorded that eggs laid on lerp-carrying leaves were almost exclusively laid next to a lerp. So, it is likely that feeding on the lerps resulted in improved performance of the nymphs in comparison with those reared on leaves attacked by *G. brimblecombei* but from which the lerps had been removed.

Analysing seasonal dynamics may provide new insights to interpret the link between mother's preference and nymphal performance observed in our study. We conducted our experiments between December and February, after the population peak of *G. brimblecombei* and before the population peak of *T. peregrinus*. We specifically avoided the end of summer (March) because this is the period in which the trees are exposed to most leaf-disease causing pathogens in Uruguay (Balmelli et al., 2013; Soria et al., 2014). Therefore, the performance of bronze bug nymphs was evaluated under two scenarios: healthy leaves as an ideal resource, and a potentially sub-optimal situation with the co-occurrence of another herbivore, the lerp psyllid. During the population peak at the end of summer, with a reduced leaf nutritional quality due to the co-occurrence of several pests and pathogens, the apparent contradiction between the mother's choice for oviposition sites and the performance of the nymphs may be resolved differently. In such a scenario, the extra source of sugars provided by the lerps may be more important for nymphal performance. This hypothesis deserves further experimentation.

Leaf structure may be another factor contributing to the preference of bronze bug females for lerp-carrying leaves. Bronze bug females usually select for oviposition sites elevated from the leaf surface (Wilcken et al., 2010; Nadel & Noack, 2012), and lerps provide an elevated structure. In our experiment, 371 out of 556 eggs were laid in direct contact with the lerp, suggesting that the observed preference for lerp-carrying leaves may be, at least in part, explained by the choice of leaf structural features. Other species in the Heteroptera select plants for oviposition according to particular structural features (Lundgren, 2011; Martínez et al., 2013), but in general these preferences have been related to a better offspring performance due to bottom-up (Lundgren et al., 2008) or top-down effects (Udayagiri & Welter, 2000). Further studies are needed to assess the role of the lerps' physical attributes on oviposition-site selection by the bronze bug.

In conclusion, our study provides evidence for interactions between the bronze bug and the lerp psyllid that not only play a role in the oviposition preference of *T. peregrinus*, but also affect the performance of the immature stages. Initially, these results suggest a competitive interaction between these two species. A more realistic scenario with leaves affected by other pests and pathogens, and including a longer observation time frame, may shed light on the potential benefits of oviposition-site selection observed in the bronze bug, to assess whether 'mother knows best'.

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