BioControl (2023) 68:131–142
https://doi.org/10.1007/s10526-023-10191-9

Host specificity and performance on different hopper species of the egg parasitoid *Anagrus virlai*

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Received: 26 September 2022 / Accepted: 17 February 2023 / Published online: 6 March 2023

Abstract The performance of *A. virlai* on six Cicadellidae and three Delphacidae (Hemiptera) species was assessed under laboratory conditions to clarify its host specificity. In addition, the influence of host egg size on the body size and egg load of the emerging parasitoids was investigated. The Deltocephalinae (Cicadellidae) *Amplicephalus marginellanus* (Metcalf), *Amplicephalus dubius* Linnavuori and *Dalbulus maidis* (DeLong & Wolcott) were the most parasitised species. Wasps were unable to parasitise the eggs of the Cicadellinae (Cicadellidae) *Hortensia similis* (Walker), *Plesiommata mollicella* (Fowler) and *Scopogonalia subolivacea* (Stål) or successfully develop in the eggs of *A. marginellanus*. The parasitism and emergence rates recorded in *Delphacodes kuscheli* Fennah, *Metadelphax propinqua* (Fieber) and *Peregrinus maidis* (Ashmead) (Delphacidae) were lower than in the other parasitised species. Of all the Cicadellidae tested, *S. subolivacea* laid the largest eggs and *D. maidis* the smallest. The Delphacidae deposited the smallest eggs of all hopper species evaluated as hosts. Parasitoids emerged from the eggs of *A. dubius* were larger and carried higher egg loads than the other wasps reared in *A. marginellanus* and *D. maidis*. There was no correlation between most measured morphometric variables and the egg load of wasps. Our results provide valuable insights into the host specificity of this egg parasitoid, but further studies are desirable to fully understand how target and non-target hosts affect the population dynamics of *A. virlai* in the field.

Keywords *Anagrus virlai* · *Dalbulus maidis* · Cicadellidae · Delphacidae · Mymaridae · Maize agroecosystem

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Handling Editor: Josep Anton Jaques Miret.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10526-023-10191-9.

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Introduction

Natural enemies provide a valuable agroecosystem service by controlling pest population densities through predation and parasitism. Most parasitoid hosts are herbivorous insects that can use more than one plant species as hosts of different taxonomical groups, constituting an intricate trophic network (Volf et al. 2017). As a result, parasitoids have evolved the ability to exploit different host species, resulting in a diverse host range determined by behavioural responses to hosts and their environment (Antolin et al. 2006).

Egg parasitoids are the most important natural enemies of leafhoppers (Cicadellidae) and planthoppers (Delphacidae) in rice and maize agroecosystems (Liu et al. 2010; Torres Moreno and Moya Raygoza 2020). Most are considered generalist species moving towards host patches driven by volatile signals released by their hosts during feeding and egg laying (Lou et al. 2005; Krugner et al. 2008a). Furthermore, leafhopper and planthopper species can migrate from overwintering places to the crop when conditions become favourable, resulting in a bottom-up influence on mobile organisms like parasitoids (Corbett and Rosenheim 1996; Hu et al. 2017).

The presence of wild vegetation in and around the crops provides parasitoids with refuge and alternative hosts, potentially assisting in pest control. This is particularly desirable from a conservation biological control (CBC) perspective, where crops with high connectivity with uncultivated areas can facilitate parasitoid movement and recolonization over large areas (Tscharntke et al. 2008). In addition, the use of alternative hosts can be advantageous for CBC because parasitoids with broader host ranges are more likely to successfully survive in agroecosystems in the temporal absence of the target pest (Raymond et al. 2016). However, host specificity may play an ambivalent role for biological control. For moderately generalist species, broad host plasticity might guarantee long-term control, whereas specialist parasitoids would instead display higher parasitism rates, beneficial for short-term control programs (Raymond et al. 2016).

Egg parasitoids of the genus *Anagrus* Haliday (Hymenoptera: Mymaridae) are frequently classified as generalists. Most of their hosts are Hemiptera Auchenorrhyncha, specifically species belonging to the Cicadellidae and Delphacidae families (Triapitsyn 2015). Nevertheless, the host range of several species remains unknown. The New World egg parasitoid *Anagrus virlai* Triapitsyn is a common and generalist species whose host range includes nine species of Cicadellidae: *Agalliana ensigera* Oman (Magophtalminae); *Ciminius platensis* (Berg), *Dechacona missionum* (Berg), and *Hortensia similis* (Walker) (Cicadellinae); *Chlorotettix fraterculus* (Berg), *Dalbulus elimatus* (Ball), *Dalbulus maidis* (DeLong & Wolcott), and *Exitianus obscurinervis* (Stål) (Deltocephalinae); and *Xerophloea viridis* (Fabricius) (Ledrinae); and two species of Delphacidae: *Delphacodes kuscheli* Fennah and *Peregrinus maidis* (Ashmead) (Delphacinae) (Luft Albarracin et al. 2009; Triapitsyn et al. 2019). All of them, except for *D. elimatus*, are native species inhabiting maize agroecosystems in subtropical Argentina (Marino de Remes Lenicov et al. 2004; Luft Albarracin et al. 2009).

Crop seasonality plays a key role in the population dynamics of pests and their natural enemies. In the case of maize, in its centre of origin (Mexico) and other tropical regions, this crop is cultivated either year-round during both the wet season and the dry season or only during the wet season (Moya Raygoza et al. 2005). In contrast, in more temperate zones such as subtropical regions, maize is only cultivated during the wet season (spring and summer) (Virla et al. 2013). Consequently, herbivorous species that are present in maize in the limit areas (i.e., southernmost areas in the Southern Hemisphere) exhibit a wide variety of strategies to increase their tolerance to cold and to overwinter on either non-crop habitats (weeds and edge grasses) or winter crops (Pinedo Escatel and Moya Raygoza 2015; Brentassi et al. 2019; Rodríguez Juárez et al. 2020). These changes in maize availability and its herbivorous hosts might affect parasitoid's communities (Prischmann et al. 2007). In the subtropics of Argentina, the Auchenorrhyncha (Hemiptera) community that inhabits maize crops and the vegetation that surrounds them is made up of at least 21 species of leafhoppers (Cicadellidae) (Luft Albarracin et al. 2009) and 13 planthoppers (Delphacidae) (Marino de Remes Lenicov et al. 2004).

Hoppers have become a serious phytosanitary problem among maize pests for a variety of reasons: they cause direct damages to host plants by feeding from phloem and xylem tissues, by laying their eggs endophytically in different organs of the host plant, and some species by removing the cell contents from mesophyll cells (Virla et al. 2021). Additionally, they cause crop damage by transmitting several phytopathogens such as viruses and bacteria. For example, the corn leafhopper *D. maidis* is an efficient vector of several maize pathogens, such as "maize rayado fino virus" (Tymovirales: Marafivirus), "corn stunt spiroplasma" (Mollicutes: Spiroplasmataceae: *Spiroplasma kunkelii* Whitcomb), "maize bushy stunt phytoplasma" (Mollicutes: Acholeplasmataceae: *Candidatus Phytoplasma ateris*), and the recently described *Mastrevirus* that causes "maize striate mosaic virus" (Giménez Pecci et al. 2012; Vilanova et al. 2022). Members of the Cicadellinae subfamily are vectors of *Xylella fastidiosa* Wells et al., a gram-negative bacterium that produces several plant diseases (Alves et al. 2008; Dellapé et al. 2016; EFSA Panel on Plant Health (PLH) et al. 2019). The planthoppers *D. kuscheli, Metadelphax* (=*Toya*) *propinqua* (Fieber) and *P. maidis* transmit the "Mal de Río Cuarto Virus" (MRCV), one of the most important pathogens affecting maize in Argentina (Mattio et al. 2005; Giménez Pecci et al. 2012; Dumón et al. 2018).

The host specificity of a natural enemy has long been a critical issue in biological control. The spectrum of action of a biological control agent has evolutionary, environmental, and economic implications (van Lenteren et al. 2006). Specificity first establishes the intrinsic potential of a given species to become an efficient natural enemy of a target pest, but empirical evidence showed that parasitoid species may suffer a trade-off between host-range breadth and host-use efficiency (Rossinelli and Bacher 2015). The relevance of *A. virlai* as a potential biocontrol agent has been largely recognized because it is able to parasitise *D. maidis* eggs and potentially control its populations in different maize fields in the Americas (Moya Raygoza et al. 2012; Virla et al. 2013; Luft Albarracin et al. 2017; Torres Moreno and Moya Raygoza 2020). Furthermore, *A. virlai* exhibits a certain degree of specificity for Cicadellidae hosts, attacking only occasionally some Delphacidae species (Hill et al. 2019). Although there are reports on *A. virlai* biology and its field parasitism, its performance on different host species has been scarcely studied. Furthermore, its proposed broad host range was mistakenly based on the Palearctic species *Anagrus incarnatus* Haliday or its synonym *Anagrus breviphragma* Soyka (Triapitsyn et al. 2019), providing unclear data that needs revision. Clarification on this matter is especially important for biological control assessment, as in the case that *A. virlai* is too specialized and could not exploit alternative hosts when the target pest is absent, it might result in slower recolonization of the crop. In this work, we evaluated the performance (parasitism and emergence rates) of *A. virlai* on six Cicadellidae species [*Amplicephalus dubius* Linnavuori, *A. marginellanus* (Metcalf), *D. maidis*, *H. similis*, *Plesiommata mollicella* (Fowler), and *Scopogonalia subolivacea* (Stål)] and three Delphacidae species (*D. kuscheli, M. propinqua* and *P. maidis*) using maize as host plant. Additionally, we analysed if host size and egg clustering may have affected parasitoid host selection. Furthermore, we tested if the host eggs of the three most parasitised species influenced both morphometric characters and the egg load of emerged parasitoids. Finally, we carried out a multivariate analysis to investigate if the host species affected parasitoid size. An integrative approach of *A. virlai* performance on different Auchenorrhyncha host insects is provided.

Materials and methods

Origin and maintenance of insect colonies

Cicadellidae and Delphacidae insects were collected from August 2019 to May 2021 during the spring, summer and autumn seasons from two fields (26°48′34.4″S 65°14′28.3″W and 26°48′39″S 65°14′24.2″W) in San Miguel de Tucumán, Argentina, using the sweep–net technique. These sites were not treated with pesticides and were characterized by the presence of grasses and weeds such as *Brachiaria* sp., *Bromus catharticus* Vahl var. *catharticus*, *Cynodon dactylon* (L.), *Paspalum notatum* Flüggé, *Setaria parviflora* (Poir.) and *Sorghum halepense* (L.) Pers. (Poaceae); and *Bidens pilosa* L. and *Eryngium elegans* Cham. et Schlecht (Asteraceae); among others. The collected insects were later transferred to voile bags for identification in the laboratory. Taxonomic identification was based on morphological characters and specific taxonomic keys (Linnavuori 1959; Young 1977; Marino de Remes Lenicov et al. 1999; Dietrich 2005; Zahaniser and Dietrich 2013). Five species of Cicadellidae: *A. dubius*, *A. marginellanus*, *H. similis*, *P. mollicella* and *S. subolivacea*, and one Delphacidae: *M. propinqua*, were obtained from the field. The adults of the corn leafhopper and the planthoppers *D. kuscheli* and *P. maidis* were obtained from a continuous rearing colony from PROIMI-Biotecnología (CONICET), kept under greenhouse conditions (temperature between 20 and 30 °C, natural photoperiod and no humidity control). *Dalbulus maidis* and *P. maidis* were continuously reared on maize plants (landrace sweet white maize "maizón"), whereas for *D. kuscheli*, oat (*Avena sativa* L.) and maize plants ("maizón") were also used as hosts. Greenhouse colonies were maintained for several generations (more than 20) and periodically refreshed with wild insects to avoid inbreeding.

A thelytokous population of *A. virlai* was continuously reared for over 20 generations in *D. maidis* eggs laid in maize plants using the method described by Hill et al. (2019). Females of the corn leafhopper were allowed to oviposit on maize plants over the course of 24 h and the eggs obtained were subsequently offered to newly emerged wasps (age ≤ 24 h) during 24 h.

Host specificity and performance of *Anagrus virlai*

To obtain eggs prior to the tests, all Cicadellidae and Delphacidae species were caged during 24 h inside circular cages (8 cm diameter) that were spliced and fastened through metal clips to maize leaves. These rearing procedures were carried out for three consecutive years, from August 2019 to May 2021, in the laboratories of PROIMI-Biotecnología, Argentina. The number of adults enclosed varied from five to 30 female hoppers to obtain a variable density of host eggs. A total of 3366 *A. dubius* eggs, 84 *A. marginellanus* eggs, 1860 *D. maidis* eggs, 327 *H. similis* eggs, 381 *P. mollicella* eggs and 144 *S. subolivacea* eggs, for Cicadellidae; whereas 1218 *D. kuscheli* eggs, 1238 M. *propinqua* eggs and 1834 *P. maidis* eggs, for Delphacidae, were used in the assays (Table 1).

To estimate the performance of *A. virlai*, we assessed percentages of parasitism (both emerged and non-emerged parasitoids were considered) and wasp emergence in no-choice tests. A maize leaf containing hopper eggs was exposed to a newly emerged wasp in a glass tube (25 cm × 2.5 cm diameter) for 24 h in a controlled environment chamber (25 ± 1 °C, 50 ± 10% RH, and L:D 12:12). This procedure was repeated several times for each hopper species (the total number of exposed eggs and leaves is given in Table 1). A honey supplement placed on a small piece of opaline paper was added to the arena as food for the parasitoids. Leaves were left on the plant for ten to 12 days, and later cut off and transferred to Petri dishes for at least 20 days. Parasitised eggs were then identified by changes in egg coloration (they acquired a reddish coloration due to pupal development) (Jepsen et al. 2007). For unhatched eggs, the presence of undeveloped larvae or fully developed parasitoids that failed to emerge

Table 1 Rates of parasitism and emergence (± SE) recorded for the egg parasitoid *Anagrus virlai* exposed to different hopper species

Family (Subfamily)	Host species	Total exposed eggs (n)[†]	% parasitised eggs[‡]	% emergence[§]
Cicadellidae (Deltocephalinae)	*Amplicephalus dubius*	3366 (71)	49.59 ± 1.95 a	74.86 ± 2.16 a
Amplicephalus marginellanus		84 (12)	50.92 ± 8.03 a	29.65 ± 11.97 bc
Dalbulus maidis		1860 (27)	46.18 ± 2.09 a	79.30 ± 2.64 a
Cicadellidae (Cicadellinae)	*Hortensia similis*	327 (17)	0	–
Plesiommata mollicella		381 (21)	0	–
Scopogonalia subolivacea		144 (17)	0	–
Delphacidae (Delphacinae)	*Delphacodes kuscheli*	1218 (23)	6.35 ± 2.20 b	34 ± 10.22 b
Metadelphax propinqua		1238 (35)	2.54 ± 0.86 c	10 ± 10 bc
Peregrinus maidis		1834 (27)	2.22 ± 0.39 c	5.74 ± 3.34 c

[†] n represents the number of exposed maize leaves carrying host eggs

[‡, §] Different letters in the respective column indicate statistical differences among treatments ($P \leq 0.05$) based on all pairwise multiple comparisons was verified by dissections using a stereoscopic microscope (Zeiss Stemi 2000c).

Effect of host size on the body size and egg load of parasitoids

To determine the influence of host size on parasitism and development success of parasitoids, eggs of all Cicadellidae and Delphacidae species were measured. Eggs were extracted from plants and placed on a concave microscope slide containing physiological saline solution. The formula of Berrigan (1991),$V = \frac{1}{6}\pi W^2 L$ (W = width and L = length), was used to estimate the volume of host eggs. A total of ten *A. dubius*, 15 *A. marginellanus*, 15 *D. maidis*, 15 *H. similis*, 16 *P. mollicella* and 15 *S. subolivacea* eggs; and 15 *D. kuscheli*, 15 M. *propinqua*, and *11 P. maidis* eggs, were measured.

After the emergence of parasitoids from the three most parasitised species (*A. dubius*, *A. marginellanus* and *D. maidis*), egg loads of newly emerged females were recorded and the following morphometric parameters, often used to estimate parasitoid body size (Riddick 2005; Santolamazza Carbone et al. 2009), were measured: total body length, forewing maximum width and length, and hind tibia and gaster lengths. We performed these measurements on 22, three (a small number of wasps emerged from this host was obtained; see Results section) and 20 dissected *A. virlai* females emerged from eggs of *A. dubius*, *A. marginellanus* and *D. maidis*, respectively.

Data analysis

We conducted all statistical analyses and graphics using R software version 4.2.1 (R Core Team 2022). The effect of host species on parasitism and wasp emergence was analysed by fitting generalized linear models (GLM) with a binomial error distribution and a logit link function. For the analysis of emergence, we considered only those species that were successfully parasitised by *A. virlai*. We then performed likelihood ratio tests (LRT) and all pairwise comparisons ($\alpha = 0.05$) using estimated marginal means (EMMs) (Lenth 2023) with Holm-Šidák adjustments.

Volumes of host eggs were tested using a GLM with inverse Gaussian family and mu^{-2} link function. We then conducted a LRT and an all pairwise comparison to compare groups. Comparisons between morphological traits measured on emerged wasps of the three most parasitised species were modelled using a GLM based on the Tweedie family of distributions with a log link function. To contrast differences, we performed a LRT and all pairwise multiple comparisons on least square means using a Holm-Šidák correction method. To determine if there was a relationship between morphometric variables and egg load of emerged parasitoids, we performed Spearman correlation analyses. In addition, we carried out a non-metric multidimensional scaling (NMDS) using Bray–Curtis dissimilarity index and the measured morphometric parameters as variables to visualize the similarity between emerged wasps of the three most parasitised host species. The resulting value of ordination stress (a measure of fit) for NMDS was below the accepted threshold of 0.20 (a stress value of 0.2 or less indicates a good fit) (Dexter et al. 2018). A permutational multivariate analyses of variance (PERMANOVA) with 5000 random starts and 999 permutations was conducted to test the null hypothesis that the centroids and dispersion of the groups as defined by measure space were equivalent for all groups. Finally, we performed a multilevel pairwise comparison using the Holm-Bonferroni method to determine which groups differed from each other. The NMDS and PERMANOVA were carried out using the *metaMDS* and *adonis2* functions (Oksanen et al. 2022), whereas pairwise multilevel comparison using PERMANOVA was performed with the *pairwise.adonis* function (Martinez Arbizu 2020).

Results

Host specificity and performance of *Anagrus virlai*

Rates of parasitism and emergence of *A. virlai* were affected by host species and their taxonomic level ($\chi^2 = 3177.90$, df = 8, $P < 0.001$ and $\chi^2 = 222.59$, df = 5, $P < 0.001$). The three most parasitised species were the Deltocephalinae *A. marginellanus*, *A. dubius* and *D. maidis*, whereas parasitism rates were lower for the Delphacidae *D. kuscheli*, *M. propinqua* and *P. maidis*. The wasps were unable to parasitise the eggs of Cicadellinae *H. similis*, *P. mollicella* and *S. subolivacea* (Table 1). Although *A. marginellanus* was one of the most parasitised species, wasps did not develop successfully in this species and their emergence rate was nearly 2.6 times lower than those recorded in *D. maidis* and *A. dubius*, the most suitable hosts for the development of *A. virlai*. In Delphacidae, despite the low parasitism rate, some parasitoids developed successfully in the eggs of *D. kuscheli*, but their emergence rate was 55.3% lower than those recorded in *A. dubius* and *D. maidis*. Finally, *M. propinqua* and *P. maidis* also appeared to be occasional hosts for *A. virlai*, as evidenced by the lowest rates of parasitism and emergence observed in our tests. The results are summarized in Table 1.

Effect of host size on the body size and egg load of parasitoids

Hopper species had different egg sizes ($\chi^2 = 1132.4$, df = 8, $P < 0.001$). In the case of *H. similis* and *P. mollicella*, females laid eggs in groups (egg masses) of up to 12 eggs, whereas *S. subolivacea* laid them singly. Unlike the other Cicadellinae, *H. similis* had smaller eggs, whereas *S. subolivacea* had the largest eggs of all Cicadellidae tested. The smallest eggs within the Cicadellidae were those laid singly by *D. maidis*. The egg sizes of the two *Amplicephalus* species were similar. On the other hand, all Delphacidae deposited their eggs grouped, usually in the midrib and in close proximity to each other. These species had the smallest eggs of all hopper species measured, with the exception of *D. kuscheli* that oviposited eggs similar in size to *D. maidis* (Fig. 1).

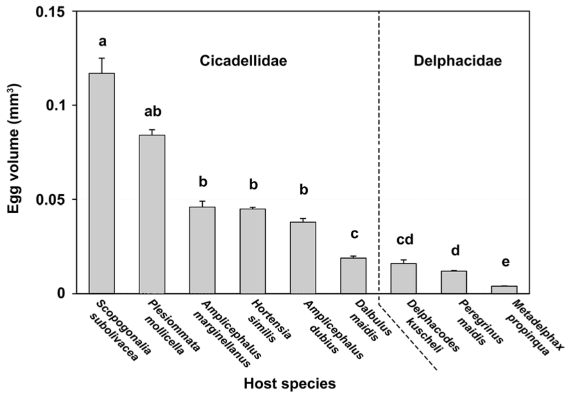

Fig. 1 Mean (+SE) egg volumes of all tested hopper species that were exposed to *Anagrus virlai* females. Bars capped by different letters are significantly different ($P \leq 0.05$)

The wasps emerged from the three most parasitised host species had varying body sizes and egg loads (Table 2). The largest wasps were those emerged from the eggs of *A. dubius*. In addition, the highest egg load was found in wasps reared in this Deltocephalinae. Although *A. marginellanus* laid larger eggs than *D. maidis*, wasps emerged from *A. marginellanus* did not exhibit higher egg loads. In fact, no correlation was found between morphometric variables and egg load for all emerged wasps, except for total body length and hind tibia length in parasitoids reared from *D. maidis* eggs (Table S1). In both cases, length was positively correlated with the egg load (Fig. 2).

The NMDS ordination differentiated between wasps that emerged from the three most parasitised species (PERMANOVA: $R^2 = 0.34$, pseudo-$F_2 = 10.68$, $P = 0.001$; Fig. 3). Parasitoids reared from the eggs of *D. maidis*, which were smaller than the rest of the Deltocephalinae, were clustered separately from those emerged from the eggs of *A. dubius* ($R^2 = 0.35$, pseudo-$F_1 = 21.67$, $P = 0.003$). Wasps emerged from *A. marginellanus* eggs did not segregate from those reared from the eggs of *A. dubius* or *D. maidis* ($R^2 = 0.10$, pseudo-$F_1 = 2.44$, $P = 0.17$; and $R^2 = 0.11$, pseudo-$F_1 = 2.66$, $P = 0.17$).

Table 2 Morphometric measurements (mean ± SE; in mm) of *Anagrus virlai* females emerged from the three most parasitised hopper species, and their egg loads (number of eggs available for oviposition after wasp emergence).

Host species	n	Total length	Forewing length	Forewing width	Hind tibia length	Gaster length	Egg load
Amplicephalus dubius	3	0.751 ± 0.004 a	0.658 ± 0.007 a	0.077 ± 0.001 a	0.217 ± 0.003 a	0.347 ± 0.005 a	48.32 ± 1.33 a
Amplicephalus marginellanus	22	0.711 ± 0.156 b	0.685 ± 0.035 a	0.069 ± 0.004 b	0.225 ± 0.004 ab	0.334 ± 0.217 ab	41.67 ± 1.33 ab
Dalbulus maidis	20	0.710 ± 0.006 b	0.623 ± 0.003 b	0.073 ± 0.001 b	0.210 ± 0.003 b	0.328 ± 0.004 b	43.45 ± 0.93 b

Different letters indicate significant differences ($P \leq 0.05$) between hosts for the same morphometric measurement based on all pairwise multiple comparisons

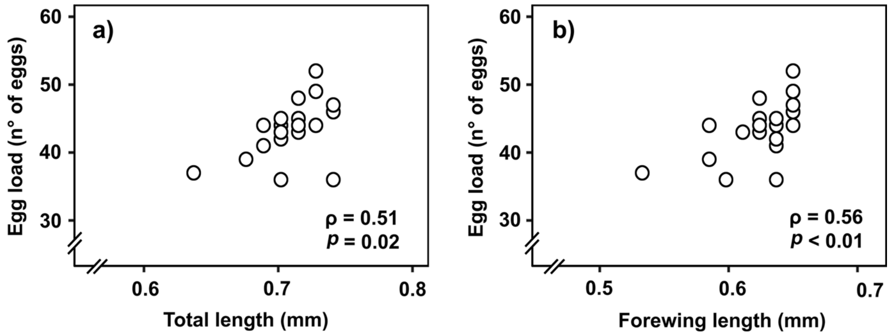

Fig. 2 Relationship between egg load and both total body length (**a**) and forewing length (**b**) of *Anagrus virlai* females emerged from *Dalbulus maidis* eggs. ρ shows the Spearman's rank correlation coefficient and P-value indicates if the correlation coefficient was significantly different from zero ($P \leq 0.05$). n = 20 wasps

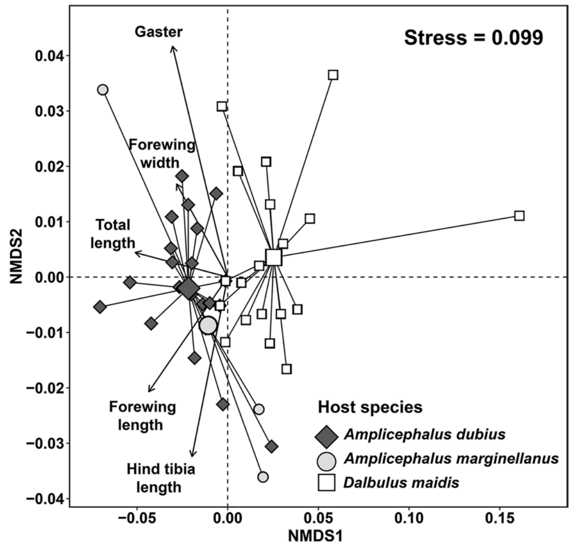

Fig. 3 Bray–Curtis non-metric multidimensional scaling (NMDS) representation of parasitoid females emerged from the three most parasitised species (*Amplicephalus dubius*, *Amplicephalus marginellanus* and *Dalbulus maidis*). Only the first two axes of the NMDS are shown

Discussion

Host specificity of a generalist egg parasitoid that has the potential to control economically important pest species may be a good predictor of its performance in the field, especially in complex agroecosystems where crops and surrounding vegetation are present. From the perspective of conservation biological control, the survival of parasitoids in agroecosystems is not always guaranteed by the provision of food, but also by the presence of alternative hosts and overwintering habitats where they are protected from adverse biotic and abiotic conditions (Gillespie et al. 2016). In our laboratory experiments, *A. virlai* parasitised several species of hoppers and exhibited different degrees of specificity, with its performance varying depending on the hosts. This wasp showed acceptable parasitic potential against *A. dubius*, *A. marginellanus* and *D. maidis*, all species belonging to the subfamily Deltocephalinae. The former two species, as well as the Delphacidae *M. propinqua*, are new factitious host records for *A. virlai*. On the contrary, Cicadellinae sharpshooters that laid larger eggs were not successfully parasitised by this parasitoid. A potential threshold limited by taxonomic, physiological and behavioural characteristics may be present. Our findings suggest that planthoppers may be occasional hosts for *A. virlai*. Thus, alternative hosts and non-crop habitats could alter the population dynamics of this parasitoid, favouring its persistence in the agroecosystem and its role as a biological control agent of Auchenorrhyncha pests in maize.

Although several egg parasitoids are considered generalists, many exhibit some degree of specialization (Bai et al. 1995). Insects in the family Mymaridae, for instance, are opportunistic wasps that parasitise host species, mainly Hemiptera Auchenorrhyncha, that oviposit hidden and endophytic eggs (Huber 2006). However, because it is difficult to observe and capture individuals in the field, the hosts of Mymaridae are mostly unknown, as well as their biological and ecological traits. Regardless, biological control programs have been developed in the past against Cicadellidae and Delphacidae using Mymaridae, including *Anagrus* wasps (Williams III and Martinson 2000; Krugner et al. 2009). Therefore, evaluating potential effects on alternative non-target hosts is critical to knowing their potential efficiency in the field (Mansfield and Mills 2004). Our findings are consistent with previous assumptions that *Anagrus* species have a relatively broad host range but still exhibit host preferences (Williams III and Martinson 2000) that are likely guided by host specificity. Thus, although *A. virlai* shows remarkable plasticity in development in target species and occasional hosts, this wasp manifests a potential host preference for Deltocephalinae eggs. Host preference between Cicadellidae and Delphacidae species has also been noted in other *Anagrus* species. The egg parasitoid *A. incarnatus*, classified as a generalist, appears to have a preference for parasitising Delphacidae eggs (Chantarasa-Ard et al. 1984). For *A. epos*, only Cicadellidae species are known to be hosts (Krugner et al. 2008b). In addition, interspecific competition between *A. virlai* and other *Anagrus* species may have led to a niche differentiation. The egg parasitoid *Anagrus flaveolus* Waterhouse, which co-occurs with *A. virlai*, parasitises three species of Cicadellidae, including *D. maidis* (with a low parasitism rate), and eight Delphacidae, including *D. kuscheli*, *M. propinqua* and *P. maidis* (Triapitsyn 2015), with a parasitism rate of about 40% in the eggs of *D. kuscheli* (Liljesthröm and Virla 2004). Thus, *A. virlai* might actively forage for suitable hosts, but would use other species as alternative hosts in their absence. Nevertheless, this hypothesis should be tested further.

The availability (host presence) and quantity of egg resource may change over time (nutritional content of eggs varies among species, and eggs are only available for parasitism for a short period of time until hatching) affecting the development and survival of the egg parasitoid (Barrett and Schmidt 1991). The adaptability of *A. virlai* is a highly desirable trait when planning biological control strategies through conservation. As previously stated, *Anagrus* species are able to choose between different host species, which in turn are associated with different plant species (Williams III and Martinson 2000; Zanolli and Pavan 2011). The genus *Amplicephalus* has been commonly associated with different grasses and crops, including maize, in different countries of North, Centre and South America (Luft Albarracin et al. 2008; De Oliveira et al. 2013; Perilla-Henao et al. 2016; Pérez López et al. 2017; Quiroga et al. 2020; Silva-Castaño et al. 2020; Almendra Paxtian et al. 2021). *Amplicephalus* has also been documented as vector of phytoplasma strains that infect different host plants (Pérez López et al. 2017) and, specifically in maize, some species may experimentally transmit "Maize Chlorotic Dwarf Virus" (MCDV) (Ammar and Nault 1991). In addition, some *Amplicephalus* species are commonly found on *P. notatum* plants, a common grass in maize agroecosystems (Paradell 1995). *Anagrus virlai* (misidentified as *A. breviphragma*) has also been recorded attacking eggs of *D. kuscheli* in oat in Argentina and *P. maidis* eggs in grasses and cane trash in Guiana (Triapitsyn 1997; Triapitsyn et al. 2019). Consequently, this wasp can use not only alternative host species to develop, but also other host plants where their hosts are available. Moreover, seasonality and availability of maize influence the presence of *D. maidis* eggs, since the corn leafhopper uses only maize and teosintes as host plants (the corn leafhopper does not oviposit eggs in the winter, and adults are the overwintering stage of the life cycle). Therefore, females of *A. virlai* like those of other *Anagrus* species, must exploit other hosts and oviposition sites for overwintering (Wright and James 2007).

The host specificity of an egg parasitoid can be influenced by the size of the host egg (Lytle et al. 2012). Our results showed that parasitoids emerged from larger eggs were larger and had a higher egg load. However, host identity also affected these parameters as females emerged from *A. marginellanus* eggs (the largest host eggs within the Deltocephalini) did not have the largest size and the highest egg load. In addition, only females reared from *D. maidis* eggs showed a positive relationship between egg load and total body length and hind tibia length. In other Mymaridae species, some morphometric variables were positively correlated with egg load: larger females of *Anaphes nitens* Girault (Hymenoptera: Mymaridae) reared from eggs of *Gonipterus scutellatus* Gyllenhal (Coleoptera: Curculionidae) had a higher egg load (Santolamazza Carbone and Cordero Rivera 2003). However, some egg parasitoids such as *Anaphes iole* Girault and *Cosmocomidea annulicornis* (Ogloblin) (Hymenoptera: Mymaridae) may be exceptions to this rule: the lengths of the hind tibia and forewings of these wasps did not correlate with their egg loads (Riddick 2005; Manzano et al. 2022). Although we were unable to measure all morphometric variables in parasitoids emerged from Delphacidae species (parasitism and emergence rates were too low), Hill et al. (2019) found that the wasps emerged from *P. maidis* eggs are smaller than those reared from *D. maidis* eggs.

The relationship between adult size and fitness has received considerable attention in parasitoid behavioural ecology (Petersen and Hardy 1996), and larger females are predicted to carry a higher egg load (Ellers and Jervis 2003). Egg load of pro-ovigenic species (those that mature all or most of their lifetime complement of eggs prior to emergence from the hosts), such as *A. virlai*, has traditionally been used as a predictor of their potential performance in the field (Riddick 2005), although a trade-off between egg load and other life-history traits such as longevity has been long documented (Ellers et al. 2000). *Anagrus virlai* is also an autogenous species that parasitises its hosts from emergence. It does not require a preoviposition period and lays the majority of its eggs on the first day after the emergence (Hill et al. 2020). Therefore, a higher egg load may favour it if many host eggs are found in the field.

The tritrophic interaction between plants, herbivorous insects and their egg parasitoids has received much attention because of its key role in biological control. Although we were only able to test the host specificity of *A. virlai*, our results can be considered in characterizing its ecological host range. Further studies to evaluate the population dynamics of *A. virlai* and its hosts under field conditions may be necessary to better understand its role as a natural enemy of Auchenorrhyncha pests.

Acknowledgements This work was partially supported by PICT-FONCyT nº 01309 and PIP- CONICET nº 0521. Jorge G. Hill and Carolina Manzano want to thank CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina) for their scholarships. We are also grateful to the editor and three anonymous reviewers for their helpful comments and suggestions.

Author contribution JGH reared and managed both hoppers and parasitoids, conducted experiments, analysed data and wrote the manuscript. EGV conceived and designed research, reviewed and edited the manuscript, and secured funding. SLP contributed to Cicadellidae identification and checking and editing this paper. CM contributed to rearing and managing both hoppers and parasitoids, reviewed and edited the manuscript. ELA contributed with experimental design, manuscript corrections and secured funding. All authors have read and approved the manuscript.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose and they declare that there are no conflicts of interest.

Research involving human participants and/or animals No humans and/or animals were used in this work that required informed consent.

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