International Journal of Pest Management
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713797655

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To cite this Article Fenoglio, M. S. and Salvo, A.'*Liriomyza commelinae* (Diptera: Agromyzidae): an alternative host for parasitoids of the leafminer pest *Liriomyza huidobrensis*', International Journal of Pest Management, 55: 4, 299 — 305
To link to this Article: DOI: 10.1080/09670870902890561
URL: http://dx.doi.org/10.1080/09670870902890561

International Journal of Pest Management
Vol. 55, No. 4, October–December 2009, 299–305

Liriomyza commelinae (Diptera: Agromyzidae): an alternative host for parasitoids of the leafminer pest *Liriomyza huidobrensis*

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(*Received 22 February 2008; final version received 12 March 2009*)

The potential of *Liriomyza commelinae* (Frost) (Diptera: Agromyzidae) as an alternative host for parasitoids of the pest leafminer *Liriomyza huidobrensis* (Blanchard) was investigated. We particularly focussed on the specific composition of the parasitoid complex and its impact on *L. commelinae*, frequency of associations, dependency of parasitism on host density and additive effects of species richness on total parasitism. Mined leaves of *Commelina erecta* (Commelinaceae) were collected from different localities of Córdoba province (Argentina) from 1991 to 1994, and also from different sites of Córdoba city. In total, 25 species of parasitoids (Hymenoptera) were associated with *L. commelinae*, of which 13 were shared with *L. huidobrensis*. *Chrysocharis flacilla* and *Diglyphus websteri* (Eulophidae) were the most abundant parasitoid species on *L. commelinae*, the former being the most frequently associated with the leafminer. Total parasitism, averaging 50%, did not depend on parasitoid species richness. No significant relationship was found between parasitism caused by the main species and host abundance. The potential for using the system *C. erecta*–*L. commelinae* in the conservation biological control of *L. huidobrensis* is discussed.

Keywords: parasitism; Hymenoptera; natural vegetation; open rearing system; Commelina erecta

1. Introduction

Leafminers are insects whose larvae feed within the leaf lamina. The punctures in leaves made by adult females for oviposition or feeding, and by larval activity, inflict damage which can severely reduce yields and/or kill the plants (Spencer 1973). Many leafminer species are serious pests of different crops around the world (Parrella and Robb 1985; Dempewolf 2004). *Liriomyza huidobrensis* (Blanchard) (Diptera: Agromyzidae), first described in Argentina (Blanchard 1954), is currently found as a pest on several ornamental, horticultural and cultivated plant species throughout the New and Old World (Weintraub and Horowitz 1995; Dempewolf 2004). This extremely polyphagous species has been recorded on 39 different crops in central Argentina (Valladares et al. 1999), reaching high levels of infestation on many of them (Salvo and Valladares 1995; Valladares and Salvo 1999). Its management commonly involves several applications of insecticide (Larrain 2004), without consideration being given to potential for pesticide resistance development (Weintraub and Horowitz 1995) and the known harmful effects of these insecticides on natural enemies (Prijono et al. 2004; Hidrayani et al. 2005).

Hymenopteran parasitoids, mainly braconids and eulophids, are the most important source of mortality for *Liriomyza* leafminers (Parrella 1987; Hespenheide 1991). One of the biological control strategies appropriate for *Liriomyza* spp. is the introduction of natural enemies from the area of origin of the pest or from related leafminers from other areas (Murphy and La Salle 1999). Given that *L. huidobrensis* supports a large and rich parasitioid community in the region of this study (Valladares and Salvo 1999), the implementation of a classical biological control programme for this species would not be justified, unless a biocontrol agent with specific traits (e.g. pesticide resistance) were to be introduced. Thus, augmentative and conservative strategies of biological control to increase parasitism would be more appropriate methods to regulate this species (Murphy and La Salle 1999), particularly in early stages of the pest cycle.

In conservation biological control, the habitat is modified in order to increase parasitoid populations in relation to that of the pest. Increasing plant species diversity in and around the crop field, or promoting the growth of natural vegetation, can be beneficial to parasitoids by providing food resources and refuges (Gurr et al. 1998; Stephens et al. 1998; Lavandero et al. 2006). Although some plant species can act as reservoirs of the leafmining pest (Smith and Hardman 1986; Schuster et al. 1991), other species can support specialist leafminers which are not harmful to crops, and can act as alternative hosts for parasitoids. Those plant species can be useful in the implementation of a 'parasitoid open rearing system' (Parkman

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ISSN 0967-0874 print/ISSN 1366-5863 online

DOI: 10.1080/09670870902890561
http://www.informaworld.com

et al. 1989) which consists of favouring the presence of plants hosting an innocuous leafminer species in the pest habitat in order to increase its parasitoid populations.

Although there are examples of successful open rearing systems to control aphids (Hansen 1983; Yano 2006), white flies (Stacey 1977), and leafminers (Van der Linden 1992), and this is seen to be a low-cost, non-polluting strategy, it is still rarely explored. To achieve an open rearing system, it is necessary to know which parasitoid species are associated with non-harmful leafminers and to have accurate information about the interactions occurring in the system. Thus, short-term apparent competition effects might be considered since an increase in alternative hosts could lead to a decrease in target species parasitism (Holt and Lawton 1994; Langer and Hance 2004). The study of insect–plant food webs in different habitats, including specific details of interactions between Agromyzidae, their host plants and their parasitoids in the central region of the country, has made an open rearing system for leafminer parasitoids a theoretically possible proposal (Valladares and Salvo 1999).

Liriomyza commelinae (Frost) (Diptera: Agromyzidae) is a specialist herbivore on plants of the genus *Commelina* (Commelinaceae) (Valladares 1984), and particularly in the study region on *Commelina erecta*. Larvae of *L. commelinae* construct white linear mines and pupate within the leaf (Smith 1987). Parasitoids are the main biotic mortality factor affecting *L. commelinae* (Smith 1987) and several of the parasitic species associated with this leafminer were also found to attack *L. huidobrensis* (Salvo 1996). The system formed by the plant *C. erecta*, the leafminer *L. commelinae* and their parasitoids could be useful in the implementation of an open rearing system of parasitoids of *L. huidobrensis* in horticultural and ornamental crops, given the verified degree of specialisation of *L. commelinae*. In the USA, *L. commelinae* feeding on *C. diffusa* Burm have been reported to have a high abundance of chalcidoid parasitoids (Genung 1981). Several of these parasitioid species are shared with *Liriomyza trifolii* (Burgess), a serious pest of cultivated and ornamental plants in tropical and subtropical regions, and thus the presence of *C. diffusa* could enhance biological control of this pest (Parkman et al. 1989).

The aim of this study was to analyse the potential of *L. commelinae* as an alternative host of parasitoids of the pest leafminer *L. huidobrensis*. We examined the specific composition of the parasitoid complex and its impact on *L. commelinae*, with special emphasis on the interactions between parasitoid species shared with the pest insect. We also analysed different factors related to the function of parasitoids as regulators: frequency and impact of associations between *L. commelinae* and their parasitoids, dependency of parasitism caused by main species on host density and additive effects of different parasitoid species on total parasitism. Finally, we discuss the potential for using the *C. erecta*–*L. commelinae* system for conservation biological control of *L. huidobrensis*.

2. Materials and methods

The *C. erecta*–*L. commelinae* system was studied from 1991 to 1994 as part of the thesis project of A.S. (Salvo 1996), collecting leaves mined by this leafminer in 12 localities of Córdoba province representing both natural and urban habitats. In addition, during January and February of 2005 and of 2006, *L. commelinae* was sampled in 18 sites located in different neighbourhoods of Córdoba city. In each site, from 1380 to 3200 linear metres of pavement were checked in order to find a plant or plant group of *C. erecta*, each separated by more than 2 m (hereafter referred to as a 'patch'). This distance was arbitrarily selected, due to a lack of studies on the dispersal ability of this species, and thus it might be ecologically irrelevant. However, only the frequency of association between the host and parasitoid species was examined on this patch scale.

In each sampling site, all mined leaves found were collected from every plant patch, placed in plastic bags, transported to the laboratory, and kept until flies and parasitoids emerged. Adults of both leafminers and parasitoids were stored in glass vials plugged with cotton-wool; once emergence had ceased they were counted and identified (Salvo and Valladares 2004). Voucher specimens of all parasitoid species and *L. commelinae* were deposited in the Cátedra de Entomología, Universidad Nacional de Córdoba, Argentina.

The total list of species associated with *L. commelinae* was determined from data obtained from all samples (periods 1991–1994 and 2005–2006). Parasitoid species shared with *L. huidobrensis* were determined by comparison with Salvo (1996) and Salvo and Valladares (1995). As no significant differences were found in the abundance of parasitoids of *L. commelinae* between the 2 years of sampling (Manova, Wilks' Lambda = 0.236, $P = 0.286$), variable estimation and subsequent statistical analyses were performed by pooling data taken in 2005 and 2006. The following variables were calculated:

- abundance of the leafminer (total adults, i.e. flies plus parasitoids);
- parasitoid species richness;
- proportion of each guild richness in the total of parasitoid species. The guilds considered were: larval–pupal (i.e. species that oviposit in larvae and emerge from host pupae), larval (i.e. species that oviposit in and emerge from larvae), and pupal (i.e. species that oviposit in and emerge from pupae);

- total parasitism percentage (i.e. sum of parasitoids divided by total adults multiplied by 100); and
- relative parasitism percentage caused by parasitoid species and guilds.

Parasitic species were assigned to one of five host-range categories proposed by Salvo and Valladares (2004): (1) parasitoids associated with a single host species (henceforth referred to as 'specialists'); (2) parasitoids attacking two to four host species; (3) species associated with five to eight host species; (4) those with nine to 16 host species; and (5) parasitoids associated to 17 or more host species (henceforth called 'generalists').

The frequency of associations between the leafminer and its parasitoids was analysed as a percentage: number of cases in which the association was registered divided by total number of cases. Frequency was calculated considering the total number of sampled sites ($N = 18$) and the total number of mined patches of *C. erecta* ($N = 1022$).

Linear regression analyses were performed using Infostat (version 1.1) (Infostat, 2002) to evaluate the relationship between the following variables: percentage of total parasitism and leafminer abundance versus the number of parasitic species; and, total parasitism and those occasioned by the dominant parasitic species shared with *L. huidobrensis* versus leafminer abundance. Possible differences between parasitism caused by larval–pupal versus larval plus pupal guilds were analysed by paired *t*-test. Larval and pupal guilds were pooled for data analyses given the low number of species in each. Given the low abundance of parasitoids (<10 individuals) registered in two sampling sites, we decided not to include these in statistical analyses of species richness and parasitism percentages.

Data were transformed to the log (species richness) or arc-sine square root (parasitism) to achieve normal distributions. In all cases the significance level was 0.05.

3. Results

A total of 12,920 adults were obtained from all samples (1991–1994 and 2005, 2006), of which approximately 52% were parasitoids. Twenty-five parasitoid species belonging to four families of Hymenoptera (Table 1) were associated with *L. commelinae*, and three parasitoid guilds were recorded: larval–pupal (12 species), larval (9 species), and pupal (one species) (Table 1). Among parasitoids of leafminers, obligate hyperparasitism is very rare (Askew 1975). To our knowledge, there are no records of hyperparasitoids associated with *L. commelinae* and *L. huidobrensis*. However, given the methodology employed, occurrences of hyper-, super- and multiparasitism were not determined in this study. In relation to their host ranges, 10 parasitoid species were generalist and one specialist (Salvo and Valladares 2004) (Table 1). Thirteen parasitoid species were shared by *L. commelinae* and *L. huidobrensis* (Table 1).

From a total of 1698 patches of *C. erecta* analysed (data 2005–2006), 1022 were mined by *L. commelinae*. Of a total of 10,805 adults reared in the laboratory, 52% were parasitoids. *Chrysocharis flacilla* and *Diglyphus websteri* (Chalcidoidea: Eulophidae) were the most abundant parasitoid species. The former was the most constant in its association with *L. commelinae*, being recorded in all 18 sites evaluated and in almost 40% of sampled patches of *C. erecta* (Table 1).

Species diversity of *L. commelinae* parasitoids per sampling site varied between 7 and 17 (mean $= 11.88 \pm 0.66$, $n = 16$) and was significantly correlated with host abundance ($F_{1,14} = 6.50$, $P = 0.02$, $R^2 = 0.32$) (Figure 1). Total parasitism percentages per site fluctuated between 37.86 and 71.33%, with an average of $52.75 \pm 2.39\%$ ($n = 16$) and they were independent of leafminer abundance ($F_{1,14} = 0.20$, $P = 0.65$). The pooled parasitism percentages of *L. commelinae* caused by larval–pupal species were higher ($68.13 \pm 3.79\%$) than those caused by larval and pupal species ($31.31 \pm 3.69\%$) ($t = -4.93$, $P = 0.0002$, $n = 16$) (Figure 2).

Total parasitism observed in *L. commelinae* did not depend on parasitoid species richness ($F_{1,14} = 0.33$, $P = 0.57$) (Figure 3). Relative percentage of parasitism caused by each parasitoid species are shown in Table 1. Species with high impact on the leafminer (relative parasitism over 10%) were *C. flacilla, D. websteri, C. vonones, Chrysocharis* sp. A, *Chrysonotomyia* sp. C and *Agrostocynips enneatoma*. No significant relationship was found between parasitism percentages and host abundance for any of the species analysed (*C. flacilla:* $F_{1,14} = 0.04$, $P = 0.84$; *D. websteri:* $F_{1,14} = 2.91$, $P = 0.11$; *C. vonones:* $F_{1,14} = 0.23$, $P = 0.64$; *Chrysocharis* sp. A: $F_{1,14} = 1.1$, $P = 0.31$; *Chrysonotomyia* sp. C: $F_{1,14} = 0.17$, $P = 0.68$; *A. enneatoma:* $F_{1,14} = 0.56$, $P = 0.46$).

4. Discussion

The number of parasitoid species associated with *L. commelinae* in this study was similar to the average richness (19 parasitoid species) reported for most common agromyzid species in the central region of Argentina (Salvo and Valladares 1999), but considerably higher than that recorded for *L. commelinae* in Jamaica (nine species) (Smith 1987). Parasitism of *L. commelinae* reached high levels, averaging 50%, a figure similar to that reported by Smith (1987). Contrary to observations in other parasitoid–host systems (Hawkins 1993; Towner 2002), an increase in the number of parasitoid species did not produce higher parasitism percentages.

Table 1. Hymenopteran parasitoid species of *Liriomyza commelinae*, biology: host range, relative parasitism and frequency of association with its host.

Superfamily Family Parasitoid Species	Species shared with *L. huidobrenis*[1]	Parasitoid guild	Host range interval (no. species)	% Relative parasitism (mean ± SE) (n = 18)	Frequency of association (%) Patch (n = 1022)	Site (n = 18)
Chalcidoidea Eulophidae						
Chrysocharis caribea (Boucek)	x	L–P En	9–16	7.22 ± 1.52	14.87	77.78
C. flacilla (Walker)	x	L–P En	17–36	22.47 ± 2.77	28.47	100.00
C. vonones (Walker)	x	L–P En	17–36	11.75 ± 1.91	23.68	94.44
Chrysocharis Forster sp. A		L–P ?	?	11.14 ± 1.38	23.58	94.44
Chrysocharis sp. B		L–P ?	?	0.22 ± 0.20	0.20	11.11
Chrysonotomyia Ashmead sp. A	x	L Ec	17–36	2.58 ± 0.63	8.51	72.22
Chrysonotomyia sp. B		L Ec	?	0.86 ± 0.78	0.59	22.22
Chrysonotomyia sp. C		L Ec	2–4	10.58 ± 2.47	20.94	88.89
Chrysonotomyia sp. D		L Ec	?	0.07 ± 0.04	0.39	16.67
Proacrias thysanoides (De Santis)	x	L En	17–36	0.01 ± 0.01	0.10	5.56
P. xenodice (Walter)	x	L En	17–36	0.01 ± 0.01	0.10	5.56
Diglyphus websteri (Crawford)	x	L Ec	17–36	12.80 ± 2.73	16.73	88.89
Elachertini sp. A		L ?	5–8	2.13 ± 0.92	3.52	61.11
Elachertini sp. B		L ?	5–8	0.59 ± 0.40	1.08	27.78
Eulophinae sp.		? ?	?	0.46 ± 0.36	0.29	22.22
Tetrastichinae sp.		? ?	?	–	–	–
Pteromalidae						
Herbertia ca. brasiliensis Ashmead		P En	1	0.93 ± 0.48	0.88	27.78
Halticoptera helioponi (De Santis)	x	L–P En	17–36	0.88 ± 0.26	2.25	55.56
Thinodytes Graham sp. A		L–P ?	9–16	2.03 ± 0.50	6.85	77.78
Thinodytes Graham sp. B	x	L–P ?	5–8	–	–	–
Ichneumonoidea Braconidae						
Phaedrotoma luteoclypealis (Van Achterberg & Salvo)	x	L–P En	9–16	1.78 ± 0.67	1.57	55.56
P. scabriventris (Nixon)	x	L–P En	17–36	–	–	–
*P. mesoclypealis (Van Achterberg & Salvo)**		L–P En	17–36	–	–	–
Cynipodea Figitidae						
Agrostocynips enneatoma (Diaz)	x	L–P En	17–36	11.49 ± 2.30	18.00	88.89
Eucoilidae sp.		L–P En	?	–	–	–

The latter two measures were calculated from 2005, 2006 data (see text). Parasitoid guilds L, larval; P, pupal; L–P, larval–pupal; En, Endoparasitoid; Ec, Ectoparasitoid; ?, unknown. Host rage intervals were defined according to Salvo and Valladares (2004).
[1]*Sources:* Salvo (1996), Salvo and Valladares (1995).

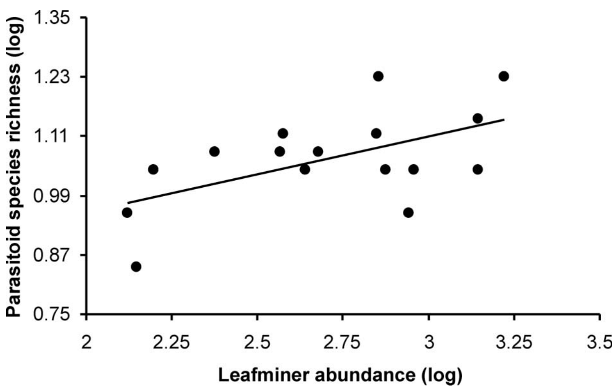

Figure 1. Relationship between *Liriomyza commelinae* abundance and parasitoid species richness ($y = 0.65 + 0.15x$, $R^2 = 0.32$, $P = 0.02$).

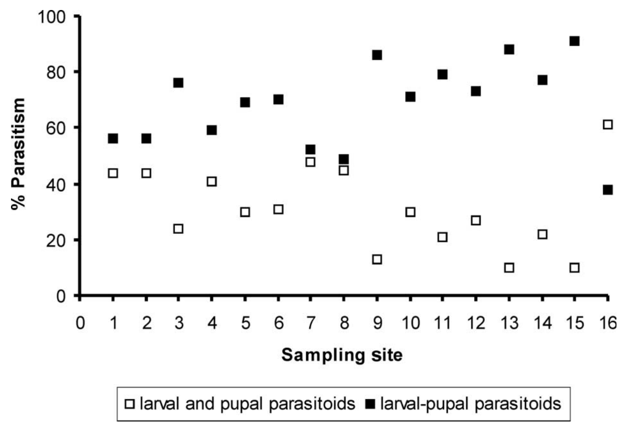

Figure 2. Parasitism of *Liriomyza commelinae* caused by parasitoid guilds in each sampling site.

The prevalence of larval–pupal parasitoids in parasitic complexes of the leafminer found in this study matches results found in other similar systems (Sanchez and Redolfi 1985; Salvo and Valladares 1995). However, this is not the prevalence expected for internal plant-feeding insects, for which a dominance of larval parasitoid species is predicted (Hawkins 1994).

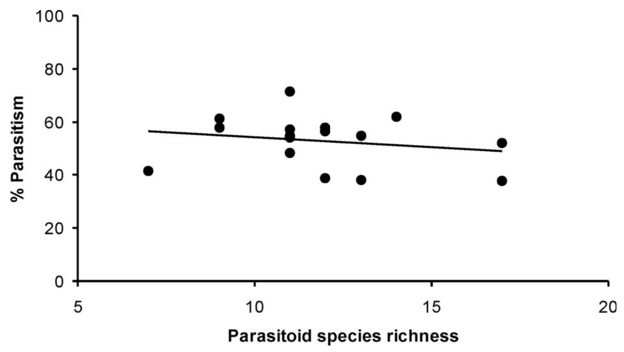

Figure 3. Parasitoid species richness and total parasitism on *Liriomyza commelinae*.

Associations between *L. commelinae* and parasitoid species such as *C. flacilla, C. vonones* and *Chrysocharis* sp. A were very constant at both levels studied: sample site (>90%) and *C. erecta* patch (>20%). There is thus a high probability of finding these parasitoid species in association with *L. commelinae*, at both regional and local scales.

Chrysocharis flacilla caused the highest mortality rate to *L. commelinae*, but other species such as *D. websteri, C. vonones* and *A. enneatoma* were also important. No relationship was detected between host abundance and the parasitism of the main species of parasitoids.

The importance of *L. commelinae* as an alternative host for parasitoid species of *L. huidobrensis* has been broadly demonstrated in this study. Both leafminer species share at least 13 parasitoid species (Table 1) (Salvo 1996; Salvo et al. 2005), several of which (e.g. *C. flacilla, D. websteri*, and *A. enneatoma*) cause a great impact on the pest species. In addition to causing high rates of parasitism of *L. commelinae*, they have been reported as efficient mortality agents of *L. huidobrensis*, which was found feeding on several horticultural crops in Argentina (Salvo and Valladares 1995; Videla et al. 2006). *Diglyphus begini*, a congeneric species of *D. websteri*, has been repeatedly used for inoculative and inundative releases in greenhouses against *L. trifolii* and other *Liriomyza* species (Heinz and Parrella 1990; Cure and Cantor 2003). Both *D. begini* and *D. websteri* are generalist species attacking leafminers with the potential for orienting their searching behaviour towards more abundant host species (Murdoch 1969).

As with *D. websteri*, other generalist parasitoid species in the study region were very frequently associated with *L. commelinae*, while the single specialist occurred in less than one third of sampled sites. This result strongly suggests that the system composed by *C. erecta–L. commelinae* could act as a reservoir of generalist parasitoids, a fact that would improve the biological control of *L. huidobrensis*.

Phaedrotoma scabriventris (Braconidae) and *C. flacilla* caused the highest parasitism rates for *L. huidobrensis* in the study region (Valladares and Salvo 1999; Salvo et al. 2005). Although the former was not observed in association with *L. commelinae* in this study, there are preliminary results from field experiments in cultivated habitats that record this association (Fenoglio, unpublished data).

Our results reveal that *L. commelinae* shares a high number of parasitoids with *L. huidobrensis*, the main leafminer pest in the region, which suggests that it could be a useful host for the implementation of a parasitoid open rearing system through the sowing of *C. erecta* in crop fields. From our data, we cannot assume that parasitoids reared on *C. erecta* would move to *L. huidobrensis* on crop plants. However, it is expected that generalist species, which are the majority of leafminer parasitoids (Hawkins 1994), would tend to congregate where a particular host is abundant, i.e. show 'switching behaviour' between elements of their diet (Murdoch 1969). The fact that higher-order mobile generalists respond rapidly in time and space by converging on areas of increasing prey abundance has been recently demonstrated for parasitoids (Eveleigh et al. 2007).

There are some requirements for achieving an effective open rearing system of leafminer parasitoids: the alternative leafminer host should not be detrimental to crops, both host plant and leafminer should be easy to breed in high numbers, and the host plant should not be harmful to other crops (van der Linden 1992). *Liriomyza commelinae* is a monophagous species that regionally feeds only on *C. erecta* plants, which usually grow in dry and sandy soils (Sérsic et al. 2006) and it reproduces both sexually and asexually, so there are minimal requirements for laboratory rearing. Among horticultural crops we have found no records mentioning *C. erecta* as a problem weed, even though populations of this species have increased in recent years in soybean and corn crops due to its tolerance to glyphosate (Papa 2004). The possibility that *C. erecta* may become a problem weed in horticultural crops should not be ignored, and studies should be conducted in order to determine the dispersal potential of this species and its ability to compete with vegetable crops, before promoting its use in parasitoid open rearing systems.

The results of this study provide preliminary support for the use of the system made up of *C. erecta*, *L. commelinae* and its parasitoids in the conservation biological control of *L. huidobrensis*, although further experimental studies are necessary to confirm the potential of this system.

Acknowledgments

We would like to thank Graciela Valladares for helpful comments on the manuscript and Marisela Perez, Enrique Frana and Luis Auyeros for field assistance. Special thanks to Joss Heywood for reviewing the manuscript translation. The manuscript benefited from the comments of three anonymous reviewers. This work was supported by

Secretaría de Ciencia y Técnica, Universidad Nacional de Córdoba. Both authors belong to the Consejo Nacional de Investigaciones Científicas y Técnicas.

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