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Host-Specificity Studies of the Argentine Weevil, *Heilipodus ventralis*, for the Biological Control of Snakeweeds (*Gutierrezia* spp.) in the U.S.

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Abstract

Snakeweeds (*Gutierrezia* spp.) are troublesome native weeds in rangelands of southwestern U.S. and northern Mexico. The plants impede livestock production by competing with forage plants, and their leaves are poisonous to cattle. The genus originated in North America but seven species also are native in Argentina and five in Chile. Explorations for natural enemies in Argentina showed that the root-boring weevil, *Heilipodus ventralis*, has potential for biocontrol. Its host-plant range was investigated in the field and in the laboratory. In the field, more than 4000 plants in 22 different genera of Compositae were examined; three genera were natural host plants: *Grindelia*, *Gutierrezia* and occasionally *Baccharis*. In the laboratory, larvae and adults were tested on 66 different plant species; development from egg to adult was obtained on *Solidago* and *Aster* in addition to the natural hosts. The weevil appears to be restricted to the plant family Compositae, tribe Astereae, to which all the mentioned genera belong. Important native Astereae should be tested in quarantine in the U.S. before deciding whether or not the weevil should be released.

Essais de Spécificité d'Hôte du Charançon Argentin *Heilipodus ventralis* en Vue de la Lutte Contre les Gutierrezies (*Gutierrezia* spp.) aux États-Unis

Les gutierrezies (*Gutierrezia* spp.) sont des plantes nuisibles dans les pâturages du sud-ouest des États-Unis et du nord du Mexique d'ou elles sont originaires. Ces plantes entravent la production du bétail étant donné qu'elles font concurrence aux plantes fourragères et que leurs feuilles sont toxiques pour le bétail. Le genre est originaire de l'Amérique du Nord, mais il existe six espèces indigènes d'Argentine et cinq espèces indigènes du Chili. En Argentine, parmi les ennemis naturels de cette plante qui ont fait l'objet d'études, le charançon rhizophage *Heilipodus ventralis* semble avoir du potentiel comme agent biologique. Les chercheurs ont étudié la gamme de plantes hôtes de cet insecte sur le terrain et en laboratoire. Sur le terrain, plus de 4000 plantes de 22 genres différents de Composées ont été examinées; trois genres étaient des plantes hôtes naturelles: *Grindelia*, *Gutierrezia* et, parfois, *Baccharis*. En laboratoire, des essais ont été effectués avec les larves et les adultes de cet insecte sur 57 espèces de plantes; outre les hôtes naturels, *Solidago* et *Aster* ont favorisé la croissance des insectes depuis la ponte jusqu'au stade adulte. Le charançon semble se limiter aux hôtes de la famille des Composées, de la tribu des Astérées, auxquelles appartiennent tous les genres mentionnés ci-dessus. Il faudrait procéder à des essais en quarantaine de l'insecte sur les Astérées indigènes les plus répardues aux Etats-Unis avant de décider s'il convient d'introduire le charançon.

Introduction

Snakeweeds (*Gutierrezia* spp.; Campanulales: Compositae) are native weeds in rangelands of the southwestern U.S. and northern Mexico. They have increased greatly in density in the last 100 yrs, mostly because of overgrazing. The plants impede livestock production by competing with forage plants and their leaves are poisonous to cattle.

The genus originated in North America where 16 species occur, 10 in the U.S. (Lane *in press*) but 12 native species also occur in South America: seven in Argentina and five in Chile, all perennials (Solbrig 1966; Cabrera 1971).

Control by conventional chemical and mechanical methods is not applied extensively by ranchers because it is relatively expensive. Biological control by the introduction of foreign natural enemies appears to be an economical alternative. However, most previous attempts on biological control of weeds have been directed against introduced weeds, and therefore, there are only a few records of native weeds controlled by exotic organisms. Only one such case resulted from planned introductions. Nonetheless, there are about 25 documented cases of native insects successfully controlled by exotic natural enemies collected on an allied species or genus. The reason for this success may be the lack of host-natural enemy ecological homeostasis in the new association (Pimentel 1963). Thus, the possibility of controlling the native snakeweeds exists because extensive explorations on the Argentine snakeweeds showed that there are at least seven different species of insects with potential for biological control (Cordo and DeLoach, unpubl. data).*

The host range studies of one of these top candidates, the root weevil *Heilipodus ventralis* Kuschel (Coleoptera: Curculionidae), are discussed here.

The genus *Heilipodus*, with 114 neotropical species, was separated from the genus *Heilipus* by Kuschel (1955). Host plants are known for nine species but precise references are given for only four species which develop inside stems and roots of Umbelliferae (*Eryngium* spp.), Solanaceae (*Capsicum pendulum* Willd.), and Compositae (*Vernonia polyanthes* Less.). The remaining five references are records of adults feeding on buds or resting on the foliage of host plants in eight plant families and with little evidence of association with any particular family. In Brazil, the adults of *Heilipodus clavipes* Fabricius and *H. ocellatus* Olivier are mentioned as pests of cacao, but the larval host plant is unknown (Costa Lima 1968).

The genus occurs from Mexico to Argentina but no species occur in the U.S. In Argentina, 14 species are recorded. *H. ventralis* is known from Paraguay (G. Kuschel, pers. comm.) and Argentina (Blackwelder 1957) but no reference in the literature regarding its host plant was found.

Materials and Methods

Field Host Range

The natural host range of *H. ventralis* in Argentina was explored during several trips made in 1981–84, throughout the area of distribution of *Gutierrezia* spp. Since in Patagonia, *Grindelia chiloensis* (Corn.) Cabr. (Campanulales: Compositae) was about equal to *Gutierrezia* spp. as a host, the area of distribution of *Grindelia* spp. was also surveyed. This area included most of the arid and semi-arid regions of the country, from the northwestern and western provinces to Patagonia. At each exploration point, most recognizable shrubby and sub-shrubby composite plants were dug and their roots dissected for immatures; they were transferred to artificial diet (Harley and Wilson 1968, modified by adding an amount of powdered *Grindelia* stems equal to the amount of alphacel) or held in the excised roots, depending on the immature's condition, until they reached the adult stage. Adults emerged from these immatures or collected as tenerals were considered as the only true indication for natural host plants.

*Cordo, H.A., and DeLoach, C.J. Insects and pathogens that attack snakeweeds (*Gutierrezia* spp.) in Argentina. *Ann. Entomol. Soc. Amer.* (in review).

Laboratory Host Range

The potential host range of *H. ventralis* was determined by exposing a series of 66 plants under laboratory conditions to both adults and larvae, separately. The selection criteria and plant species tested were as follows:

Species closely related to *Gutierrezia* and *Grindelia*: Compositae, tribe Vernonieae: *Vernonia fulta* Griseb.; tribe Eupatorieae: *Eupatorium tremulum* H. et A.; tribe Astereae: *Aster novi-belgii* L., *Baccharis darwinii* H. et A., *B. divaricata* Hauman, *B. trimera* (Less.) DC., *Erigeron karvinskianus* DC., *Grindelia buphthalmoides* DC., *G. chiloensis*, *G. pulchella* Dun., *Gutierrezia solbrigii* Cabr., *Solidago chilensis* Meyen; tribe Inuleae: *Inula helenium* L.; tribe Heliantheae: *Dahlia excelsa* Benth., *D. pinnata* Cav., *Helianthus annuus* L., *H. tuberosus* L., *Zinnia elegans* Jacq., *Xanthium cavanillesii* Schouw; tribe Helenieae: *Gaillardia pulchella* var. *picta* (Sweet) Gray, *G. aristata* Pursh, *Hymenoxys robusta* Parker, *Tagetes patula* L., *T. erecta* L.; tribe Anthemideae: *Artemisia absinthium* L., *A. annua* L., *A. drancunculus* L., *A. verlotorum* Lamotte, *Achillea millefolium* L., *A. filipendulina* Lam., *Chrysanthemum carinatum* Schousb., *C. coccineum* Willd., *C. maximum* Ram., *C. parthenium* (L.) Bernh., *C. vulgare* (Lam.) Parsa, *Chrysanthemum* sp.; tribe Senecioneae: *Senecio goldsackii* Ph., *S. cineraria* DC., *S. cruentus* DC., *S. mikanioides* Otto, *S. petasitis* DC.; tribe Cynareae: *Carthamus tinctorius* L., *Centaurea dubia* Suter, *Carduus nutans* L., *Cynara cardunculus* L., *C. scolymus* L.; tribe Mutisieae: *Mutisia retusa* Remy; tribe Cichorieae: *Cichorium intybus* L., *Lactuca sativa* L.

Families, genera, or species attacked by insects of the genus *Heilipodus*: Bromeliaceae: *Ananas comosus* (L.) Merrill, *Bromelia balansae* Mez.; Rosaceae: *Pyrus communis* L.; Vitaceae: *Vitis labruscana* Bailey; Myrtaceae: *Eucalyptus fastigata* Deane & Maiden, *E. kruseana* F.U.M., *Psidium guajava* L.; Umbeliferae: *Eryngium eburneum* Decaisn.; Solanaceae: *Capsicum frutescens* L.

Families, genera, or species attacked by insects of the genus *Heilipus* (*sensu lato*): Moraceae: *Ficus carica* L.; Anonaceae: *Rollinia emarginata* Schlecht.; Lauraceae: *Persea americana* Mill.; Leguminosae: *Glycine max* (L.) Merrill; Aquifoliaceae: *Ilex paraguariensis* Saint Hil.; Malvaceae: *Gossypium hirsutum* L.; Verbenaceae: *Acantholippia seriphioides* (A. Gray) A. Mold., *Aloysia gratissimia* (Gill & Hook.) Troncoso.

Adult testing. Three different types of tests were carried out to determine the ability of *H. ventralis* adults to feed and oviposit on a wide spectrum of plants: a no-choice test of the natural host plants; a multiple-choice test of all 66 test plants; and an oogenesis test. All these tests were done in a 25±3°C cabinet, with fluctuating humidity between 40–70% and 14 h photophase.

The natural host plants were tested for ovipositional preference in a no-choice test to determine if biotypes of the weevil exist. Insects from inside the roots of *G. chiloensis* and *G. solbrigii* were collected as pupae at San Antonio Oeste, Rio Negro Province, 12 November 1982, and as ready-to-emerge adults at Arroyito, Neuquen Province, 7–9 December 1982, respectively. Newly emerged adults from both populations were fed separately with *G. solbrigii*, *G. chiloensis*, and *G. pulchella*, totalling 6 treatments which were repeated 10 times. Each replication consisted of 2 adults (1 male and 1 female) placed in a glass cylinder 12 × 12 cm diam., half-filled with moist peat moss and covered with nylon cloth to confine the insects. The food plant was prepared as a bouquet in a small vial filled with water and buried in the peat moss. For oviposition, 2 or 3 woody stems of *G. pulchella* about 7 mm diam. × 70 mm long, were stuck half-way in the peat moss. Stems of *G. pulchella* were used for all treatments because this plant was locally available, and therefore, the only one able to supply the large number of stems needed. Twice a week the terminal buds and the stems for oviposition were replaced by fresh material and the eggs collected from the renewed stems placed in 1 oz cups with agar gel plus antimicrobials for hatching; the test started 13–20 December 1982 and ended July 1983, when all the adults died.

All test plants were compared in 2 multiple-choice tests of feeding and oviposition. A total of 65 different plants were exposed to a total of 230 adults from diverse origins. Each testing unit consisted of 10 adults (5 males and 5 females, not fed for 24 h) placed in a plastic tray with moist peat moss at the bottom, where pieces of stems for oviposition were introduced, contiguous to terminal buds for feeding. Two stems (2–5 mm diam. × 50 mm long, woody whenever possible) and 2 terminal buds 50 mm long of each plant were placed at opposite locations of the tray, which was covered with a clear polyethylene film. The adults were released in the center of the tray. After the test, the stems were dissected for collection of eggs and the terminal buds were examined for evidence of feeding. The amount of feeding was calculated by measuring the volume of both leaves and stems consumed. In the leaves, the area of the feeding hole was measured with a millimetric grid; that area multiplied by the thickness of the leaf gave the volume consumed. In the stems, the total volume of the partially damaged segment was measured and from that volume the proportion consumed was estimated visually. Using the described methodology, most of the plants were exposed to the attack of 10 adults, 12–14 times. Two different populations of *H. ventralis* were tested with slight variation in the methods as follows:

Test A. Insects were collected as adults on *Grindelia chiloensis* and *Gutierrezia solbrigii* in several eastern sites of Chubut and Rio Negro Provinces in Patagonia, 13–16 January 1983. Estimated age at beginning of test was 1–2 months. Fifteen testing units were set: 5 containing the 28 chosen test plants plus the natural host plants; 5 with the 28 chosen test plants without the natural host plants; and 5 with the natural host plants only. In this way, every plant was equally exposed to the attack of 100 adults total. Duration of the test was 72 h.

Test B. Insects were collected as larvae inside the roots of *G. chiloensis*, near Chelforo, Rio Negro in northern Patagonia, 21 February 1982. They were reared on artificial diet until emergence of adults on September 1982 and fed on *G. chiloensis* until their use, about one month later. Four pairs of testing units were set at different times, according to adult availability. Each pair consisted of 1 tray (35 × 25 × 8 cm) containing the chosen test plants (about 10–15) plus the natural host plants, and another tray with the chosen test plants only. Examination for eggs and feeding was done 48 h after beginning the test.

An oogenesis test was conducted to determine if potentially suitable host plants (as found in previous tests) in the tribe Astereae, like *Aster* and *Solidago*, were appropriate for maturation of oocytes when newly emerged adults fed exclusively on these plants. Other plant species were also tested for comparison. *Gutierrezia* was not included because sufficient plants were not available at the time. It is important to remark that since stems for oviposition used for all the test plants were of *G. pulchella*, this test was intended to determine the nutritional suitability of the tested plants, rather than their total potentiality.

Adults used for the oogenesis test were collected as larvae inside the roots of *G. solbrigii* and *G. chiloensis* at San Antonio Oeste, Rio Negro Province, 15 September 1983 and reared on artificial diet. Each test plant was exposed to 2 newly emerged adults (1 male and 1 female), using the same technique described for the natural host preference test, and repeated 10 times.

Larval testing. This test was conducted using plants of the Compositae because previous tests suggested that the best chances to detect potential host plants were among members of that family. Larvae were obtained from eggs laid in the laboratory by insects collected as adults on *G. solbrigii* and *G. chiloensis* in Chubut and Rio Negro, 13–16 January 1983. One neonate larva was placed in each of 3 holes in the stems of each test plant. The holes were made with a 2 mm drill in the crown or in the stem up to 5–8 cm above the crown. Ten replications of each test plant were made, i.e. each plant species was exposed to 30 larvae of *H. ventralis.* After the larvae were inserted, the hole was sealed with teflon tape and an adhesive plastic tape covering it for protection. When the larvae were placed in the crown or below (because stems were too thin), the hole was plugged with solid paraffin and then sealed with melted paraffin. Plants used were growing in pots inside an open insectary, except for *C. tinctorius, H. annuus,* and *C. intybus* which were growing in the ground. One month after the beginning of the test, the first replication of each test plant was dissected for evidence of larval survival. If the 3 larvae were found dead, then the second replication was examined and so on, until the first living larva was found; at this point, the surviving larva was transferred to a new plant. This operation was repeated at the second, third, fourth, and seventh month to record larval mortality. The test started in February 1983 (summer) and continued until all surviving adults had emerged 10 months later in December (spring). During the winter months, the insectary sides were closed with clear polyethylene and slightly heated; the temperature for that period was mean minimum 11°C and mean maximum 25°C.

Results and Discussion

Adults of *H. ventralis* are brownish, mottled with white, about 11 mm long by 4 mm wide. They fed mostly on the tender stem tissues at the tip of the *Grindelia* spp. plants, but on *Gutierrezia* spp. (where the terminal stems are very thin and not succulent as in *Grindelia*) they fed mostly on the sap by clipping off buds and leaves. Laboratory potted plants were killed by this feeding, but no evidence of similar heavy damage was observed in the field. Females oviposited in the summer. A female bored a hole in the crown with her rostrum, in which she laid a single egg. Females produced about 100 eggs during their lifetime. Larvae tunneled in the crown and taproot, where usually several were found together. Larvae pupated in roots in early spring. In late spring, adults emerged by making a hole through the pupation cell with their mandibles. There was only one generation/yr.

Field Host Range

Among the 4076 composite plants examined in the field, which included 7 tribes, 22 genera and 45 species, 12 species were found as larval host plants of *H. ventralis* (Table 1). These species are in the genera *Grindelia*, *Gutierrezia*, and *Baccharis*, all in the tribe Astereae and all shrubby or sub-shrubby plants, except for *B. pingraea* DC. which is a perennial herb. The number of insects found and the proportion of plants damaged at each site surveyed were definitely greater for *Grindelia* spp. and *Gutierrezia* spp. than for *Baccharis* spp. Adult feeding was easily detected on the tips of *Grindelia* spp., whereas it was unnoticed on *Gutierrezia* spp. and *Baccharis* spp. *Solidago* was surveyed only once, in spite of the large distribution of *S. chilensis* in the country,

Table 1. List of Compositae dissected in the field to determine the natural host range of *Heilipodus ventralis* Kuschel in Argentina.

Plants dissected	*H. ventralis*			
	No. sites surveyed	No. plants dissected	No. sites where found	No. insects found[1]
Tribe Vernonieae				
Vernonia nitidula Less.	1	5	0	0
Tribe Eupatorieae				
Eupatorium patens Don (H. et A.)	1	8	0	0
Tribe Astereae				
Baccharis articulata Pers.	3	45	2	+
B. boliviensis Cabr.	2	30	0	0
B. crispa Spreng.	2	63	2	+
B. darwinii H. et A.	13	145	1	+
B. divaricata Hauman	1	30	1	+
B. pingraea DC.	3	62	2	+
B. salicifolia Persoon	2	10	0	0
B. trimera (Less.) DC.	1	5	0	0
B. ulicina H. et A.	4	35	0	0
Baccharis spp. (X 2)	5	41	3	+
Grindelia buphthalmoides DC.	1	20	0	0
G. cabrerae Ariza	1	6	0	0
G. chiloensis (Corn.) Cabr.	19	610	17	+++
G. pulchella Dun.	28	729	13	+++
G. tehuelches Cabr.	6	101	5	++
Gutierrezia gilliesii Gris.	9	266	4	++
G. mandonii Solbr.	3	170	0	0
G. solbrigii Cabr.	17	592	16	+++
G. spathulata Kurtz	4	265	3	+++
Solidago chilensis Meyen	1	20	0	0
Heterothalamus sp.	1	40	0	0
Tribe Heliantheae				
Flourensia sp.	3	20	0	0
Helianthus sp.	1	25	0	0
Parthenium sp.	1	15	0	0
Thelesperma megapotamica OK.	1	10	0	0
Zinnia peruviana L.	1	10	0	0
Tribe Helenieae				
Gaillardia megapotamica (Spreng.) Baker in Martius	1	10	0	0
Helenium alternifolium Cabr.	1	10	0	0
Schkuhria pinnata OK.	1	33	0	0
Thymophylla belenidium Cabr.	1	10	0	0
Tribe Senecioneae				
Senecio filaginoides DC.	9	151	0	0
S. goldsackii Ph.	2	40	0	0
S. hyeronymi Gris.	1	50	0	0
S. schreiteri Cabr.	2	150	0	0
S. subulatus Don.	1	10	0	0
S. viridis Phil.	1	50	0	0
Senecio sp.	6	74	0	0

Table 1. Continued.

Plants dissected	*H. ventralis*			
	No. sites surveyed	No. plants dissected	No. sites where found	No. insects found[1]
Tribe Mutisieae				
Aphyllocladus spartioides Weld.	1	15	0	0
Brachyclados hycioides Don.	1	15	0	0
Chuquiraga avellanedae Lor.	1	30	0	0
Hyalis argentea Don. var. *latisquama* Cabr.	1	30	0	0
Trichocline plicata H. et A.	1	10	0	0
T. reptans Rob.	1	10	0	0

[1]+ : less than 10
++ : 10 to 50
+++ : more than 100

because it occurs only in more humid areas where *H. ventralis* is not present. Although the genus *Aster* has about 14 species in Argentina, no species of Aster were found at the sites surveyed.

Laboratory Testing

Adult testing. A test was conducted to determine if reproduction differences between two weevil populations from Patagonia, one from *Gutierrezia solbrigii* and one from *Grindelia chiloensis*, might indicate different biotypes of the weevil on different host plant genera. Survival, preoviposition period, and total eggs/female were not different, therefore providing no evidence for the existence of biotypes.

When field-collected adults were offered 66 plant species in 14 different families, in a multiple-choice test, weevils showed a marked preference to feed and oviposit on the composites, particularly those in the tribe Astereae (Table 2). In fact, they laid all the eggs on members of that tribe, except for 3 eggs laid on *Artemisia annua*. Of the 99 eggs laid, 89 were laid on plants previously determined as natural hosts. Therefore, feeding or oviposition on plants other than the field hosts were relevant only on *Aster*, *Solidago*, and *Artemisia* and consequently, further testing was necessary for these plants. No consistent differences were seen between Test A where the adults were collected from the field from both *Grindelia* and *Gutierrezia* and Test B where the adults were reared from larvae collected in the field only in *Grindelia*.

When newly emerged, immature adults were fed with *Aster*, *Solidago*, and *Artemisia* (*A. verlotorum* was tested because *A. annua* was not available) as a sole source of food, only *Aster* proved to be nutritionally adequate to induce oocyte maturation (Table 3). Feeding and fertile eggs were produced on every plant of the test, but these results are meaningful only when the test plants are compared with the control of *G. chiloensis*. A clear-cut difference was seen between *G. chiloensis*, *G. buphthalmoides*, and *A. novi-belgii* and the rest of the plants. Feeding, number of eggs laid, and survival were larger in the first group, than in the second group. Also, in the first group the number of eggs laid were proportional to the amount of food consumed, and no eggs were laid before beginning of feeding. In the second group, the number of fertile eggs/female varied from 1 to 3, showing no relationship with the amount of food consumed. For

Table 2. Feeding and ovipositional preferences of *Heilipodus ventralis* Kuschel adults on plants of different families in two multiple choice tests[1]

Test plants	Total		
	Feeding (mm^3)	No. eggs	No. testing units (10 adults/unit)
Anonaceae			
Rollinia emarginata Schlecht.	2.4	0	12
Leguminosae			
Glycine max (L.) Merrill	6.5	0	10
Aquifoliaceae			
Ilex paraguarensis Saint Hil.	2	0	12
Vitaceae			
Vitis labruscana Bailey	1	0	12
Myrtaceae			
Psidium guajaba L.	1.5	0	14
Solanaceae			
Capsicum frutenscens L.	7.7	0	14
Compositae			
Tribe Vernonieae			
Vernonia fulta Griseb.	5	0	14
Tribe Astereae			
Aster novi-belgii L.	212	3	14
Baccharis darwinii H. et A.	15	0	13
B. divaricata Hauman	300.7	2	14
B. trimera (Less.) DC.	47.4	7	16
Erigeron karvinskianus DC.	6.3	0	14
Grindelia buphthalmoides DC.	1486	4	13
G. chiloensis Cabr.	3073.5	14	14
G. pulchella Dun.	1043	33	14
Gutierrezia solbrigii Cabr.	704	29	14
Solidago chilensis Baker	518.5	4	14
Tribe Heliantheae			
Dahlia excelsa Benth.	4	0	14
Helianthus annuus L.	2.2	0	14
H. tuberosus L.	0.7	0	14
Tribe Helenieae			
Gaillardia aristata Pursh.	3.4	0	14
G. pulchella var. *picta* (Sweet) Gray	40	0	14
Tagetes patula L.	11.5	0	14
Tribe Anthemidae			
Artemisia absinthium L.	15	0	14
A. annua L.	57.5	3	12
A. dracunculus L.	13.3	0	14
A. verlotorum Lamotte	5.4	0	14
Chrysanthemum carinatum Schousb.	4	0	4
C. coccineum Willd.	8.6	0	14

Table 2. Continued.

Test plants	Total		
	Feeding (mm^3)	No. eggs	No. testing units (10 adults/unit)
C. parthenium (L.) Bernh.	50	0	4
Tribe Senecioneae			
Senecio cruentus (Mass.) DC.	4	0	4
S. mikanioides Otto	0.4	0	2
Tribe Cynareae			
Carduus nutans L.	6	0	12
Carthamus tinctorius L.	15.8	0	14
Cynara cardunculus L.	11	0	14
Tribe Mutisiae			
Mutisia retusa Remy	1.4	0	10
Tribe Cichorieae			
Cichorium intybus L.	2.2	0	14

[1] The plants showing neither feeding nor eggs are not included in the table. These are: *Ananas comosus* (L.) Merrill, *Bromelia balansae* Mez., *Ficus carica* L., *Persea americana* Mill., *Pyrus communis* L., *Gossypium hirsutum* L., *Eucalyptus fastigata* Deane and Maiden, *E. kruseana* F.U.M., *Eryngium eburneum* Decaisn., *Acantholippia seriphioides* (A. Gray) A. Mold., *Aloysia gratissima* (Gill & Hook.) Troncoso, *Eupatorium tremulum* H. et A., *Inula helenium* L., *Dahlia pinnata* Cav., *Zinnia elegans* Jacq., *Xanthium cavanillesii* Schoum., *Hymenoxys robusta* Parker, *Tagetes erecta* L., *Achillea millefolium* L., *A. filipendulina* Lam., *Chrysanthemum* sp., *C. maximum* Ram., *C. vulgare* (L.) Bernh., *Senecio goldsackii* Ph., *S. cineraria* DC., *S. petasitis* DC., *Cynara scolymus* L., *Lactuca sativa* L.

example, adults that consumed 44.5 mm^3 of *Solidago* laid about equal numbers of fertile eggs/female as did adults placed on *B. darwinii* that did not feed; adults fed on *Artemisia* and *Lactuca* laid 4 and 18 fertile eggs, respectively, before feeding started. Therefore, females were able to lay fertile eggs before any food was consumed. Many of the eggs laid in the second group of plants in Table 3 were laid before females began feeding, and thus are not associated with nutritive quality of the food plant.

Larval testing. Further testing of larvae on different Compositae showed that larval development occurred only among members of the tribe Astereae; adults were produced on the natural host plants plus *Aster* and *Solidago* (Table 4). Mortality during the first instar was high for all the plants, but lesser in the Astereae (72.6%) than in the remaining plants (95.0%), where no larvae reached the fourth instar.

Conclusions

It can be safely assumed that the host range of *H. ventralis* is restricted to the plant family Compositae, tribe Astereae. Extensive field explorations in most of the weevil's distribution area showed that its natural host plants are species of *Grindelia*, *Gutierrezia*, and occasionally *Baccharis*. No explorations were done in Paraguay where the insect also occurs, but the preference of *H. ventralis* for arid situations in Argentina suggests that probably the insect populations in the subtropical climate of Paraguay would be low.

Although adult feeding preferences for *Grindelia*, then *Gutierrezia*, and last *Baccharis* were detected in the field and observed in the laboratory, we found no evidence for the existence of sibling species. Two populations tested, occurring on different host plants and from different locations, showed about equal reproductive parameters. Previous observations not reported here also proved that insects of *Grindelia* and *Gutierrezia* from different sites interbred freely. Laboratory studies to determine the potential host range indicated that the genera *Aster* and *Solidago* could serve as host plants if certain ecological conditions are met. These two genera were not surveyed much in Argentina for two reasons: first, they usually do not coexist with the normal host plants because they prefer more humid habitats and second, most Argentine species of both genera are perennial herbs in contrast to the sub-shrubby and shrubby form of the normal host plants. Therefore, there is little chance that *Aster* and *Solidago* are natural hosts of *H. ventralis* in Argentina.

Table 3. Oviposition, feeding and survival of *Heilipodus ventralis* Kuschel adults during their entire life when fed exclusively on certain Compositae[1]

	Feeding (mm^3)	Number of eggs laid per female				Female survival (days)
				Laid before beginning of feeding		
Test plants	Total/adult	Total	Fertile	Total	Fertile	
Tribe Astereae						
Grindelia chiloensis Cabr.	1157.5 *a*	51.1 *a*	38.7 *a*	0	0	86.7 *a*
G. buphthalmoides DC.	984.6 *b*	38.4 *b*	20.5 *b*	0	0	83.7 *a*
Aster novi-belgii L.	252.2 *c*	14.0 *c*	8.5 *c*	0	0	81.3 *a*
Solidago chilensis Baker	44.5 *d*	2.4 *d*	1.5 *d*	0	0	52.7 *bc*
Baccharis trimera (Less.) DC.	7.8 *d*	3.9 *d*	1.8 *d*	1	0	53.6 *bc*
B. darwinii H. et A.	0 *d*	3.3 *d*	1.4 *d*	3.3	1.4	39.4 *de*
Tribe Heliantheae						
Helianthus tuberosus L.	12.8 *d*	4.4 *d*	3.0 *d*	0	0	50.9 *bc*
Tribe Anthemideae						
Artemisia verlotorum Lamotte	21.3 *d*	2.9 *d*	1.0 *d*	1.4	0.4	32.0 *e*
Tribe Cynareae						
Centaurea dubia Cabr.	19.2 *d*	4.5 *d*	2.9 *d*	0	0	57.5 *b*
Tribe Cichorieae						
Latuca sativa L.	5.8 *d*	4.5 *d*	1.8 *d*	4.1	1.8	46.5 *cd*

[1] Numbers are means of 10 replications. Same letter means non-statistical difference at 1% level (Duncan's test).

In regard to both the natural and potential host range of *H. ventralis*, a distinction should be made between adult and larval host range. Adult host range seems narrower and restricted to *Grindelia*, *Gutierrezia*, and to a minor extent *Aster*, the 'perfectus' host plants that are able to sustain the development and maturation of larvae and adults. Regarding larval host range, the results of the oogenesis and larval survival tests suggest that species in the genera *Baccharis* and *Solidago* could be considered as 'imperfectus' host plants, because they are nutritionally adequate for larval development but not for adult oogenesis. Therefore, they probably would be occasional host plants as the paucity of *H. ventralis* found on *Baccharis* spp. seems to indicate.

Table 4. Survival of 30 larvae of *Heilipodus ventralis* Kuschel placed in crowns or stems of each species of certain Compositae.

	No. of larvae found dead in instar					
Test plants	I	II	III	IV	V-VIII	Adults emerged
Tribe Vernonieae						
Vernonia fulta Griseb.	30	0	0	0	0	0
Tribe Astereae						
Aster novi-belgii L.	24	1	4	0	0	1
Baccharis darwinii H. et A.	30	0	0	0	0	0
Erigeron karvinskianus DC.	28	1	1	0	0	0
Grindelia chiloensis Cabr.	12	4	4	3	0	7
G. pulchella Dun.	20	0	0	8	0	2
Guterrezia solbrigii Cabr.	20	0	5	2	0	3
Solidago chilensis Baker	20	4	2	2	0	2
Tribe Heliantheae						
Dahlia sp.	30	0	0	0	0	0
Helianthus annuus L.	29	1	0	0	0	0
H. tuberosus L.	28	1	1	0	0	0
Xanthium cavanillesii Schoum.	30	0	0	0	0	0
Zinnia elegans Jacq.	29	1	0	0	0	0
Tribe Helenieae						
Gaillardia pulchella var. *picta* (Sweet) Gray	28	1	1	0	0	0
Tagetes patula L.	27	2	1	0	0	0
Tribe Anthemideae						
Achillea filipendulina Lam.	29	0	1	0	0	0
Artemisia verlotorum Lamotte	24	3	3	0	0	0
Chrysanthemum maximum Ram.	29	1	0	0	0	0
Tribe Senecioneae						
Senecio cineraria DC.	29	1	0	0	0	0
Tribe Cynareae						
Carthamus tinctorius L.	30	0	0	0	0	0
Centaurea dubia Carb.	23	2	5	0	0	0
Cynara cardunculus L.	30	0	0	0	0	0
Tribe Mutisiae						
Mutisia retusa Remy	30	0	0	0	0	0
Tribe Cichorieae						
Cichorium intybus L.	29	1	0	0	0	0

The tribe Astereae is better represented in the northern than in the southern hemisphere. The genera *Grindelia, Gutierrezia, Aster*, and *Baccharis* have several to many species native in North America, and the risks of a foreign insect attacking them must be assessed before any introductions are made. For this reason it is recommended that important native Astereae should be tested in quarantine in the U.S. before deciding whether or not the weevil should be released.

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