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Host Specificity of the Argentine Root-Boring Weevil, *Heilipodus ventralis* (Coleoptera: Curculionidae), a Potential Biocontrol Agent for Snakeweeds (*Gutierrezia:* Asteraceae) in Western North American Rangelands—U.S. Quarantine Tests

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Native snakeweeds, especially *Gutierrezia sarothrae* (Pursh) Britton and Rusby and *Gutierrezia microcephala* (DC.) A. Gray, are among the most widespread and damaging weeds of rangelands in the western United States and northern Mexico. The genus long ago spread to southern South America, where further speciation occurred. We have found several species of insects in Argentina that damage other species of snakeweeds there and are possible candidates for biological control in North America. The first of these, the root-boring weevil, *Heilipodus ventralis* (Hustache), was tested in Argentina and then sent to the USDA-ARS Insect Quarantine Facility at Temple, Texas, for host specificity testing on North American plants. We tested *H. ventralis* on 40 species of the family Asteraceae, in 19 tests of five types, using 686 adults and 365 larvae. Host specificity increased from adult feeding, to ovipositional selection, to larval development. At Temple, adults fed mostly on 6 species of the closely related genera *Grindelia, Gutierrezia,* and *Gymnosperma,* but with substantial feeding on four other genera of the two preferred subtribes Solidagininae and Machaerantherinae and on *Baccharis* in the tribe Baccharidinae, with lesser feeding on the subtribe Asterinae, all in the tribe Astereae, and on 1 species in the tribe Anthemideae. Females oviposited primarily on the same 6 species but very little on plants outside the 2 preferred subtribes. Larvae developed only on 9 of the 29 U.S. plant species tested, 6 within the two preferred subtribes and on *Brickellia* and *Aster* in other tribes. Only 5 species of three genera appear to be potential true hosts of *H. ventralis* in North America, on which all stages of the life cycle, adult feeding, oviposition, and larval development, can take place; these are *Gymnosperma glutinosum* (Spreng.) Less., *Gutierrezia grandis* Blake, *Gut. microcephala, Gut. sarothrae,* and *Grindelia lanceolata* Nutt. None of these genera contain species of economic or notable ecological value; the few rare species appear to be protected by habitat isolation from attack by *H. ventralis. H. ventralis,* therefore, appears sufficiently host specific for field release in North America. This is the first introduced biocontrol agent to be approved for release in a continental area to control a native weed. © 1999 Academic Press

***Key Words: Heilipodus ventralis; Gutierrezia;* snakeweed; broomweed; *Grindelia;* weeds; rangeland weeds; biological control weeds.**

INTRODUCTION

Native species of snakeweeds, the most important of which are *Gutierrezia sarothrae* (Pursh) Britton and Rusby and *Gut. microcephala* (DC.) A. Gray (family Asteraceae), have increased enormously in density during the past 150 years and today are among the most widespread and damaging weeds of western rangelands. Platt (1958) reported that snakeweeds infested 142 million acres in the United States. These small, perennial subshrubs seriously compete with forage plants (Ueckert, 1979; Osman, 1982; McDaniel *et al.*, 1982; McDaniel, 1990a) and are potentially poisonous to livestock (Flores-Rodriquez *et al.*, 1989). Annual direct losses in Texas are estimated at $16.9 million (McGinty and Welch, 1987) and are probably at least three times that throughout the infested area. Snakeweeds are perhaps the most damaging weeds of rangelands in New Mexico (Huddleston and Pieper, 1990).

The genus *Gutierrezia* originated in semiarid southwestern North America, where all 16 species that occur are native, including 10 perennial (snakeweeds) and 6 nonpoisonous annual species (broomweeds). *Gutierrezia sarothrae* occurs from central Mexico to southern Canada and from the central Great Plains to the Pacific; *Gut. microcephala* occurs in the southern half of that area (Lane, 1985). Another 12 species are native in

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semiarid northern Argentina and Chile; these species are all higher polyploids of the North American species (Solbrig, 1966).

Research on the ecology, damage caused, and control of snakeweeds was reported in a recent symposium (Huddleston and Pieper, 1990). Effective herbicides are available for snakeweed control (McDaniel, 1990b), but the uncertain cyclic development of weed problems coupled with low economic return per unit area from rangelands in these semiarid southwestern areas (McDaniel, 1990b; Torell *et al.*, 1990) discourage most ranchers from using either herbicidal or mechanical controls (McGinty and Welch, 1987). Biological control of invading exotic weeds has been highly successful in rangelands and natural areas (Kelleher and Hulme, 1984; Hoffmann, 1991; DeLoach, 1991, 1997; Julien, 1992; Nechols *et al.*, 1995; Rees *et al.*, 1996), and the philosophy and methodology has been well developed over many years (Huffaker, 1957; Zwölfer and Harris, 1971; Goeden, 1983; Harley and Forno, 1992; Peschken and McClay, 1995).

More than 338 species of insects are known to attack snakeweeds and broomweeds in North America (Foster *et al.*, 1981; Richman and Thompson, 1999) and some of these damage snakeweeds severely (Falkenhagen, 1978; Richman and Huddleston, 1981; Thompson and Richman, 1990), but damage is sporadic. Since the combined effect of the native natural enemies does not provide satisfactory control, and conventional controls are too expensive, we have developed a rationale and strategy for biological control using insects from different species of snakeweeds native to southern South America (DeLoach, 1981, 1995). In a 15-year survey, Cordo and DeLoach (1992) found 79 species of insects, a mite, and a pathogen attacking snakeweeds throughout their range in Argentina; several are promising candidates for introduction.

The first candidate insect chosen for research was the weevil, *Heilipodus ventralis* (Hustache) (Tribe Hylobiini), whose larvae bore in the lower stems and roots. Hustache (1938) described *Heilipus ventralis* and *H. mendozensis* from Argentina. Kuschel (1955) revised the generic relationships, placed *ventralis* in a new genus, *Heilipodus*, and assigned *mendozensis* to varietal status. Wibmer and O'Brien (1986) treated *mendozensis* as a junior synonym and recorded *H. ventralis* from Argentina and Paraguay. They listed 85 species of *Heilipodus* from South America and O'Brien and Wibmer (1982) listed 36 species from Central America and Mexico; none are known from the United States. However, one species of *Heilipus*, *H. squamosus* (Le Conte), occurs in the southeastern United States where it is a pest of avocado (*Persea americana* Mill.) in Florida (Wolfenbarger, 1948).

Cordo (1985) examined 4076 plants of 45 species in seven tribes of Asteraceae in the field in Argentina and found larvae of *H. ventralis* in the roots of only 12 species, all in the tribe Astereae. The greatest rate of infestation was in 2 species of *Gutierrezia* (*Gut. solbrigii* Cabrera and *Gut. spathulata* Kurtz) and in 2 species of the closely related genus *Grindelia* (*Grin. chiloensis* (Corn.) Cabrera and *Grin. pulchella* Dun.). Lesser numbers of larvae were found in *Grin. tehuelches* Cabrera and *Gut. gilliesii* Gris, and a few larvae were found in 6 species of *Baccharis*.

Cordo (1985) also tested adult feeding, ovipositional selection, and larval survival of *H. ventralis* in the laboratory, using 49 species of Argentine plants in 11 tribes of Asteraceae and 17 species in 13 families reported to be hosts of other species of *Heilipodus* or *Heilipus*. In the tribe Astereae, adult feeding in a multiple-choice test averaged 704 to 3074 mm^2 per 10 adults during the 3-day test on the four species of *Gutierrezia* and *Grindelia*, 15 to 301 mm^2 on *Baccharis* (3 spp.), 212 mm^2 on *Aster* (1 sp.), and 518 mm^2 on *Solidago* (1 sp.). Feeding did not exceed 58 mm^2 on any of the 10 species of Helenieae or 16 mm^2 on the 11 species of Vernonieae, Heliantheae, Anthemidae, Senecioneae, Mutisiae, or Cichorieae tested. Of the 99 eggs laid, 29 were on *Gutierrezia* (1 sp. tested), 51 on *Grindelia* (3 spp. tested), 9 on *Baccharis* (3 spp.), 4 on *Solidago* (1 sp.), 3 on *Aster* (1 sp.) (all tribe Astereae), and 3 on *Artemisia* (tribe Anthemidae). In the no-choice larval test (30 larvae tested in each of 24 plant species in 9 tribes of Asteraceae), adults were reared only from 5 species of the tribe Astereae, 9 from *Grindelia* (2 spp.), 3 from *Gut. solbrigii*, 2 from *Solidago* (1 sp.), and 1 from *Aster* (1 sp.) (Cordo, 1985). The life and seasonal history, distribution, and behavior of *H. ventralis* were reported by Cordo (1987) and Cordo *et al.* (1999).

In November 1978, a petition to resolve the few conflicts of interest in the proposed biological control program against snakeweeds in North America was submitted to the Technical Advisory Group for the Introduction of Biological Control Agents of Weeds (TAGIBCAW) [whose function was described by Coulson (1992)] of the USDA's Animal and Plant Health Inspection Service (APHIS). A favorable response was received and the testing began in Argentina the next year. A permit to introduce *H. ventralis* into quarantine was issued by APHIS Plant Protection and Quarantine (PPQ) on May 11, 1981. The first shipments were received in quarantine at Temple, Texas on December 31, 1981, and host-range experiments began in early 1982.

The present paper reports our tests of the host range of *H. ventralis* on species of North American plants. The tests were conducted in the insect quarantine facility of this laboratory at Temple, Texas, using weevils collected in the field in Argentina by H. A. Cordo, R. Ferrer, and others at the ARS Biological Control Laboratory at Hurlingham. These data provide the informa-

tion needed, together with that already reported by Cordo (1985, 1987; Cordo *et al.*, 1999), to demonstrate that *H. ventralis* is safe to release in the field in North America.

METHODS AND MATERIALS

The methods used in our tests are similar to those previously developed by Cordo (1985, 1987) in Argentina, especially for maintaining colonies of adults in the laboratory, obtaining eggs from females, and placing eggs in host-plant stems for larval development.

Test Plants

The plant species to be tested were selected according to the phylogenetic system of Harris and Zwölfer (1968) and Wapshere (1974), with most emphasis on species in the subtribes of the Argentine natural hosts (Solidagininae and Machaerantherinae) and lesser emphasis on tribes of Asteraceae more distantly related. Plants used in the tests were obtained from fields where they grew naturally near the laboratory at Temple or from western Texas, New Mexico, or Arizona, depending on the species. *Chrysanthemum* plants were a commercial variety obtained from a local nursery and *Helianthus tuberosus* plants were grown from tubers. All plants were grown for 3 to 24 months before testing in pots in a mixture of one part local topsoil, one part sand, and one part peat moss. The plant culture was maintained out-of-doors in a slat house (50% shade), watered as needed, and fertilized each 1 to 2 months. The plants were moved into a heated greenhouse during the winter. The potted plants used in some tests were 20 to 60 cm tall; the cut branches used in other tests consisted of the terminal 15 to 25 cm, with foliage, cut from plants growing in pots in the laboratory garden or in the field. Potted plants or branches used were in healthy condition and of approximately equal foliage volume between species in a given test.

The tribal classification of the test plants follows that of Bremer (1994). Within the subtribe Solidagininae of the tribe Astereae, he constructed several species groups: a *Gutierrezia* group with *Gutierrezia* and *Gymnosperma*, an *Ericameria* group with *Ericameria* and *Chrysothamnus*, a *Grindelia* group with *Grindelia* and *Isocoma*, and with *Solidago* and *Machaeranthera* in separate groups. However, within the tribe Astereae, we follow Nesom (1994), in which he redefined the subtribes and moved (our test plants) *Machaeranthera*, *Grindelia*, and *Isocoma* to the newly created subtribe Machaerantherinae from the Solidagininae. He also changed the previous *Ericameria austrotexana* to *Xylothamia palmeri* (Nesom *et al.*, 1990), *Isocoma wrightii* to *I. pluriflora* (Nesom, 1991), and *Senecio longilobus* to *S. douglasii* var. *longilobus* (Johnston, 1990). Scientific and common names and taxonomic arrangement of all test plants are given in Table 1.

Cages

Four types of cages were used for testing adults. The multiple-choice adult tests (Tests 1 to 6) used three types of cages. The first type (pots) was an aluminum-screen-covered cage, 1.2 × 1.5 × 0.5 m high. Twenty 20-cm-diam (8-liter) pots (each with a different test plant species) were suspended through holes in the cage floor in a 4 × 5 grid, 30 cm between each plant; 1 to 2 cm of peat moss was placed on top of the soil in each pot so that the top of the peat moss was level with the plywood of the cage floor (Fig. 1A). The second type (vials) was similar except that cut branches of the test plants were placed in vials of water inserted through small holes in the cage floor; these were also arranged in a 4 × 5 grid, 30 cm between plants. A small pile of peat moss, ca. 15 cm diam × 5 cm high, surrounded each plant (Fig. 1B). In the third type (pans) cut branches of 20 test plants were inserted through a wire grid (to hold them in place) into wet peat moss ca. 5 cm deep in an enamel pan 23 × 38 × 8 cm deep. The pan was placed in a wooden sleeve cage 45 × 60 × 52 cm high with a glass top and screened ventilation holes in the sides and across the back. The plants in this cage were ca. 6 to 8 cm apart (Fig. 1C).

In the no-choice test (Test 7), stems of cut branches of test plants were inserted through a small hole in the lid of a 1-liter fruit jar filled with water, and were covered with a 7.5-cm-diam × 30-cm-high clear plastic tube with a nylon gauze top.

Source of Insects

The insects used in Adult Tests 1 to 6 were reared from larvae collected from roots of the host plants in Argentina. These roots were dug up, placed in large plastic bags, and returned to the laboratory at Hurlingham, where they were dissected. The medium-size or large larvae were placed individually in 28-ml cups of antifungal artificial diet for rearing to larger larvae, pupae, or adults for shipment to the United States. Sometimes, the larvae were left inside the roots and stored at 10 to 15°C to delay development for 1 to 3 months until they were needed at Temple. We used the diet of Harley and Willson (1968), as modified by Cordo *et al.* (1999). It contained 53 g alphacel, 12 g sucrose, 12 g corn starch, 12 g glucose, 3.6 g Weston salt mix, 24 g casein, 0.48 g cholesterol, 0.48 g linoleic acid, 1.2 g lecithin, 15 ml antimicrobial mix (20.0 g sorbic acid, 15.0 g methyl *p*-hydroxybenzoate, 170.0 ml ethanol (95%)), 7 ml vitamin mix (Vanderzant modification vitamins mix for insects; NBC Biochemicals, Cleveland, OH), 3 ml formol, 25 g agar, and 1000 ml water, modified by adding 158 g of dried, ground stems of *Grin.*

TABLE 1

Feeding by Adult *Heilipodus ventralis* on Foliage of 40 Species of Asteraceae: Multiple-Choice Tests

Test plant: tribe, subtribe, genus, and species (common name)	Amount of feeding (mm^2) per 10 weevils per 10 days[a,b] (means ± SE)							
	Test 1 (n = 6)	Test 2 (n = 6)	Tests 1 and 2 (n = 12)	Test 3 (n = 4)	Test 4 (n = 4)	Tests 3 and 4 (n = 8)	Test 5 (n = 4)	Test 6 (n = 4)
Tribe Vernonieae								
Vernonia baldwinii Torr. (Baldwin ironweed)							12.5 ± 6.8c	2.2 ± 2.2f
Tribe Eupatorieae								
Brickellia laciniata A. Gray (splitleaf brickellbush)							0.0 ± 0.0c	0.0 ± 0.0f
Tribe Astereae								
Subtribe Asterinae								
Aster ericoides L. (heath aster)							0.0 ± 0.0c	
A. praealtus Poir. (tall aster)								**40.5 ± 19.1bcde**
Subtribe Baccharidinae								
Baccharis brachyphylla A. Gray	0.0 ± 0.0d	0.1 ± 0.1f	0.0 ± 0.0i					
B. halimifolia L. (groundsel bush)	3.1 ± 1.1d	11.4 ± 4.2def	7.3 ± 2.4fghi	1.2 ± 1.1gh	11.7 ± 6.9cde	6.4 ± 3.8f		
B. neglecta Britt. (narrowleaf baccharis)	5.8 ± 7.1d	15.4 ± 4.0def	10.6 ± 2.8efghi	18.5 ± 2.9efgh	12.4 ± 4.7cde	15.4 ± 2.8def		27.6 ± 15.5def
B. pteronioides DC. (yerba de pasmo)				13.1 ± 7.7fgh	10.7 ± 4.3cde	11.9 ± 4.1ef		
B. salicifolia (R & P) Persoon (seepwillow)	**44.7 ± 13.5a**	**86.1 ± 18.7a**	**65.4 ± 12.6a**	**76.4 ± 28.9ab**	**124.8 ± 40.9a**	**100.6 ± 24.9ab**	9.0 ± 4.3c	**36.8 ± 11.8cde**
B. sarothroides A. Gray (desert broom)	11.5 ± 2.5cd	**19.4 ± 7.5de**	**15.4 ± 3.9defg**	22.8 ± 5.8efgh	9.3 ± 2.2cde	16.1 ± 3.9def		
Subtribe Solidagininae								
Chrysothamnus nauseosus (Pall.) Britt. (rabbitbrush)	**24.7 ± 7.1bc**	**43.9 ± 3.4bc**	**34.3 ± 4.7bc**					12.4 ± 7.6ef
Xylothamia palmeri (A. Gray) Nesom (false broomweed)	2.0 ± 1.0d	12.4 ± 6.7def	7.2 ± 3.6fghi	**35.6 ± 11.2cdef**	**53.6 ± 24.1bc**	**44.6 ± 12.7cd**		
Gutierrezia grandis Blake	10.3 ± 3.5d	**31.0 ± 10.5cd**	**20.6 ± 6.1cdef**	**58.3 ± 20.8bc**	**138.3 ± 55.5a**	**98.3 ± 31.3ab**		
Gut. microcephala (DC.) A. Gray (threadleaf snakeweed)	0.9 ± 0.4d	**31.0 ± 17.7cd**	**15.9 ± 9.6efgh**	**53.6 ± 11.1bcd**	**113.6 ± 19.4a**	**83.6 ± 15.3ab**		**72.8 ± 8.3b**
Gut. sarothrae (Pursh) Britt. & Rusby (broom snakeweed)	2.2 ± 1.0d	**26.2 ± 11.7cd**	14.2 ± 6.7efghi	**45.6 ± 11.3bcde**	**140.2 ± 45.0a**	**92.9 ± 28.0ab**	**78.3 ± 36.7b**	**199.9 ± 35.0a**
Gymnosperma glutinosum (Spreng.) Less. (tatalencho)	**33.1 ± 13.8ab**	**71.1 ± 21.2ab**	**52.1 ± 13.4ab**	**100.4 ± 28.8a**	**181.2 ± 66.6a**	**140.8 ± 36.9a**		
Solidago altissima L. (tall goldenrod)	1.0 ± 0.5d	1.0 ± 0.6ef	11.0 ± 0.4hi	10.7 ± 6.2fgh	0.0 ± 0.0e	28.6 ± 18.7f	9.0 ± 5.2c	15.2 ± 7.7ef
Subtribe Machaerantherinae								
Grindelia lanceolata Nutt. (gulf gumweed)	**34.7 ± 11.3ab**	**26.0 ± 7.5cd**	**30.3 ± 6.6cd**	11.6 ± 5.1fgh	**44.5 ± 21.8bcd**	28.1 ± 12.1def	**239.2 ± 24.4a**	
Grindelia squarrosa (Pursh) Dun. (curly-cup gumweed)							21.6 ± 3.3c	**57.6 ± 22.4bcd**
Isocoma coronopifolia (A. Gray) Rydb. (common goldenweed)	6.5 ± 2.9d	**44.8 ± 9.2bc**	**25.7 ± 7.4cde**	**54.8 ± 12.3bcd**	**91.2 ± 34.9ab**	**73.0 ± 18.5bc**		
I. tenuisecta Greene (burroweed)				**25.0 ± 8.6defg**	36.4 ± 8.9bcde	**30.7 ± 6.1cde**		
I. pluriflora (T. & G.) Greene (jimmyweed)								**71.9 ± 29.9bc**
Machaeranthera pinnatifida (Hook.) Shinners (cutleaf goldenweed)							15.1 ± 5.7c	**34.0 ± 10.2cde**
Tribe Heliantheae								
Subtribe Ambrosiinae								
Ambrosia deltoidea (Torr.) Payne (triangle-leaf bursage)				10.9 ± 5.9fgh	17.4 ± 9.1cde	14.2 ± 5.2def	0.6 ± 0.6c	
A. psilostachya DC. (western ragweed)							9.5 ± 9.5c	
Parthenium argentatum A. Gray (guayule)	0.4 ± 0.4d	1.2 ± 0.6ef	0.8 ± 0.4hi	1.0 ± 0.4gh	8.3 ± 3.6cde	4.7 ± 2.2f		
P. incanum H.B.K. (mariola)	0.0 ± 0.0d	0.2 ± 0.2f	0.1 ± 0.1i	0.3 ± 0.3gh	1.0 ± 1.0e	0.6 ± 0.5f		0.3 ± 0.3f
Subtribe Helianthinae								
Helianthus ciliaris DC. (blueweed sunflower)	1.6 ± 0.7d	3.7 ± 2.5ef	2.6 ± 1.3ghi	1.9 ± 1.0gh	1.0 ± 1.0e	1.5 ± 0.7f		16.5 ± 9.3ef
H. tuberosus L. (Jerusalem artichoke)							0.2 ± 0.2c	
Ratibida tagetes (James) (prairie coneflower) Barnh.	0.0 ± 0.0d	0.5 ± 0.2ef	0.2 ± 0.1i	0.2 ± 0.2h	0.0 ± 0.0e	0.1 ± 0.1f		
Viguiera dentata (Cav.) Spreng (sunflower goldeneye)							3.4 ± 2.2c	0.0 ± 0.0f
V. stenoloba Blake (skeleton goldeneye)							0.0 ± 0.0c	0.2 ± 0.2f

TABLE 1—*Continued*

Test plant: tribe, subtribe, genus, and species (common name)	Amount of feeding (mm^2) per 10 weevils per 10 days[a,b] (means ± SE)							
	Test 1 (n = 6)	Test 2 (n = 6)	Tests 1 and 2 (n = 12)	Test 3 (n = 4)	Test 4 (n = 4)	Tests 3 and 4 (n = 8)	Test 5 (n = 4)	Test 6 (n = 4)
Tribe Helenieae								
Subtribe Gaillardiinae								
Baileya multiradiata Harv. & Gray (desert baileya)							0.0 ± 0.0c	
Psilostrophe tagetina (Nutt.) Green (paperflower)							1.1 ± 1.1c	0.0 ± 0.0f
Tribe Anthemideae								
Subtribe Achilleinae								
Achillea millefolium L. (yarrow)							0.0 ± 0.0c	
Subtribe Artemisiinae								
Artemisia filifolia Torr. (sand sagebrush)	0.0 ± 0.0d	0.2 ± 0.2f	0.1 ± 0.1i	0.0 ± 0.0h	3.1 ± 2.8de	1.5 ± 1.4f		
A. frigida Willd. (fringed sagebrush)							0.1 + 0.1c	0.0 + 0.0f
A. tridentata Nutt. (big sagebrush)	0.0 ± 0.0d	0.8 ± 05ef	0.4 ± 0.2hi					
Subtribe Chrysantheminae								
Chrysanthemum x morifolium Ramat. (florist's chrysanthemum)							**57.6 ± 32.5b**	**38.7 ± 15.0bcde**
Tribe Senecioneae								
Senecio douglasii DC. var. *longilobus* (Benth.) Benson (threadleaf groundsel)							0.8 ± 0.8c	2.3 ± 1.3f
$P > F$ (0.05)	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001

[a] Means followed by the same letter within the same column are not significantly different [$P < 0.05$; Fisher's protected LSD (SAS Institute, 1990)]; n, number of cages in test (replications). Values for each test plant are pooled across the three cage types and two weevil sources for Tests 1 to 4, which are equal in Tests 1 and 2 but unequal in Tests 3 and 4. Tests 5 and 6 included only one cage type (pots) and only one weevil source (*Grindelia*) (see Table 2 for experimental design). Analyses of pooled Tests 1 through 4 (17 common test plants) and Tests 5 and 6 (13 common test plants) are given in Fig. 2. Main effects with P values for the different test combinations are given in Tables 3 and 7.

[b] Values in bold type indicate values statistically greater than zero ($P < 0.05$).

pulchella Dun. and 260 ml more water. The diet was poured into 28-ml clear plastic cups with cardboard caps (creamers). The larvae pupated in the diet, after which the pupae were placed in fresh creamers with slightly damp tissue paper in the bottom for emergence of the adults.

In these shipments, the adults collected as larvae on *Grin. chiloensis* and *Gut. solbrigii* were kept separate and fed on fresh bouquets of their respective host plants after they emerged in Argentina, during shipment, and in quarantine at Temple. Bags of foilage of the two host plants were included in the shipment, held at 5°C in quarantine, and used to feed the adults before the tests began.

Upon arrival at Temple, the packages were immediately opened in the quarantine high-security room, the insects counted, and the packing materials autoclaved. The adult weevils were held in clear plastic boxes (12 × 20 × 30 cm) with ventilation in each end and with moist peat moss in the bottom. Fresh bouquets of their respective host plants were placed in each box and changed every 3 to 4 days. The weevil cultures were held in the quarantine laboratory at a temperature of 25 ± 1°C and a 14-h photoperiod.

Adult tests. Six multiple-choice tests measured feeding and oviposition simultaneously in the same cages and using the same weevils. Adults used in Tests 1 to 4 were collected on May 28, 1983, as larvae from roots of *Grin. chiloensis* or *Gut. solbrigii* at San Antonio Oeste, Río Negro Province, and reared on artificial diet. The 173 adults that emerged September 15 to 28 were shipped by air freight October 5, and arrived at Temple October 9; 144 of these were used in Test 1. At the end of Test 1, the survivors were returned to their respective *Gutierrezia* or *Grindelia* cultures. A week later, 126 weevils, which included some weevils used in Test 1 and some that had not been tested, were taken from these culture cages and used in Test 2. The 120 adults that emerged in Argentina from October 5 to 28 were shipped November 1 and arrived on November 3; 84 of these were used in Test 3. After Test 3, the survivors were returned to their respective cultures; 2 days later, 84 weevils, which included some weevils from Test 3 and some that had not been tested, were taken from their culture cages and used in Test 4.

The adults used in Tests 5 and 6 were reared from larvae collected February 15 to 21, 1985, in roots of *Grin. chiloensis* only, growing in the field near Cutral-Có, Neuquén Province, Argentina. They were dissected from the roots, reared on artificial diet, and shipped in the same manner as the 1983 shipments. On September 23, 1985, 120 large larvae and 240 pupae still in

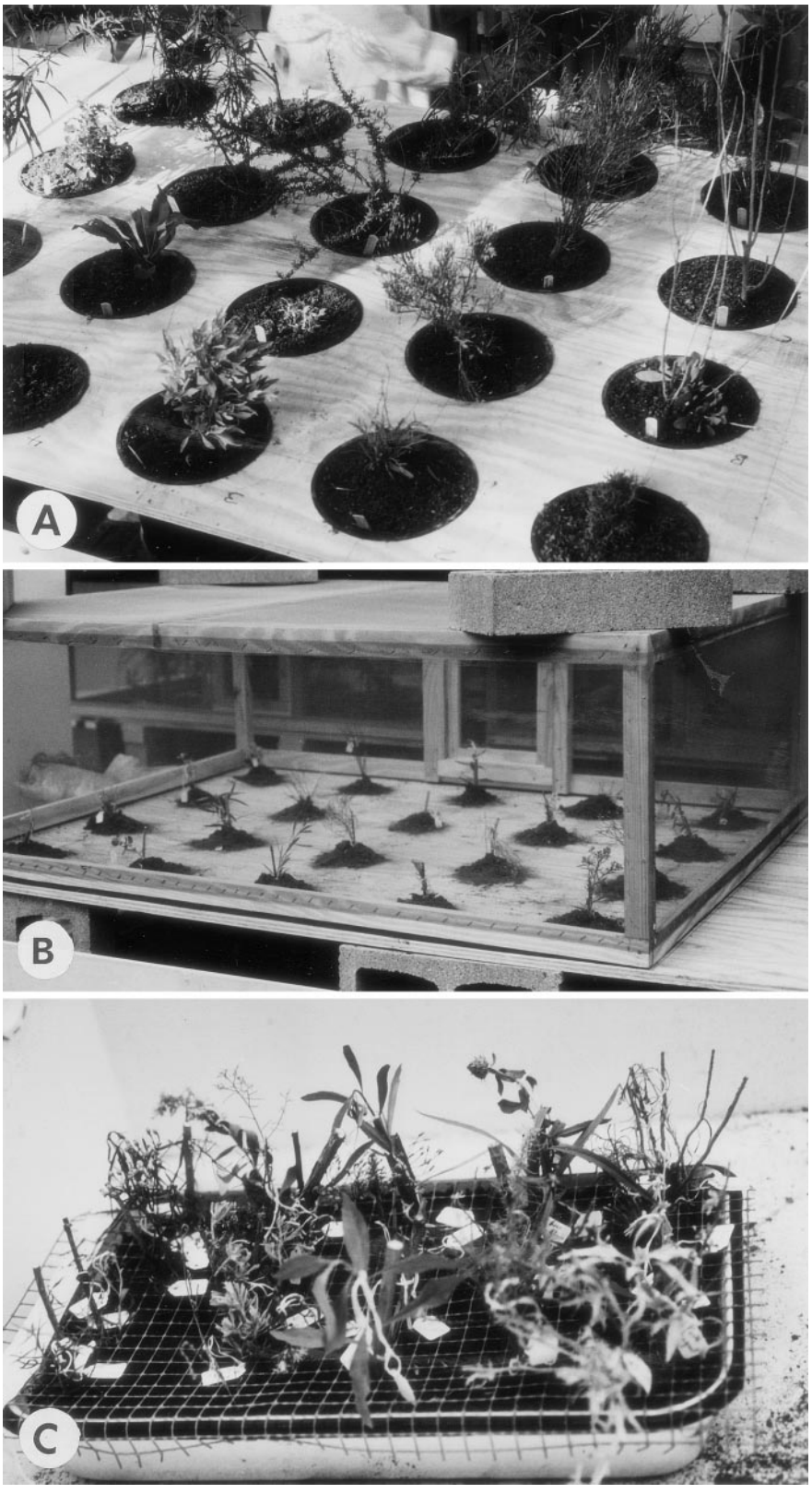

FIG. 1. Cages used for multiple-choice, host-range testing of adult *Heilipodus ventralis:* (A) pots, (B) vials, and (C) pan.

their individual cups of artificial diet were shipped to Temple and arrived September 26. When the adults emerged from the diet cups, they were placed on fresh bouquets of *Gut. sarothrae* and *Gut. microcephala* collected from the laboratory garden at Temple. We placed 96 of these adults in Test 5 as they became available: five pairs in each of the four cages October 4, three pairs October 7, and one pair each October 8, 9, 10, and 12. The survivors were returned to the culture cages at the end of the test; 13 days later, 88 weevils, which included some previously tested and some not, were taken from the culture and used in Test 6.

One no-choice test of adult oviposition and survival (Test 7) used 64 of the 108 adults sent from Hurlingham that arrived at Temple February 20, 1982. These were collected as adults in the field at Puerto Pirámides, Chubut Province, Argentina, from *Grin. chiloensis* and *Gut. spathulata*.

Larval tests. Eggs for use in the larval tests were obtained at Temple by placing adults in an "oviposition bucket." This was a 20-liter black plastic bucket half-filled with moist peat moss. Bouquets of *Gut. sarothrae* and *Gut. microcephala* were placed in the center, surrounded by a circle of 5-mm-diam cut stems of these plants, stuck halfway into the peat moss, into which the females oviposited. The stems were dissected and the eggs removed periodically. Larvae were designated as small, medium, or large, since precise identification of each of the eight instars was uncertain (Cordo *et al.*, 1999).

Five no-choice tests of larval development were conducted. The first test used eggs obtained from the first shipment of adults, received from Hurlingham February 20, 1982. This was the same shipment used in the adult no-choice test described above. These adults laid eggs in the laboratory, from which 91 eggs or neonate larvae were placed in stems as they became available from March 11 to April 21.

Larval Test 2 used 48 eggs obtained from the adult multiple-choice Test 1; these were placed in stems of 19 test plant species from November 3, 1983, to January 3, 1984, as they became available.

Larval Test 3 used eggs obtained in the laboratory at Hurlingham from adults collected in the field from *Gut. solbrigii* growing near Arroyito, Neuquén Province, February 7 to 10, 1984. These eggs were surface sterilized in 1% Clorox for 1 min; 127 eggs were shipped to Temple March 7 and arrived March 10. This test used 32 eggs, which were placed in stems of 16 test plant species from March 17 to 23.

Larval Test 4 used eggs laid by adults collected from *Gut. solbrigii* growing near San Antonio Oeste, Río Negro, January 16 to 20, 1985, and held on bouquets of *Grin. pulchella* and *Grin. chiloensis*. On February 8, 400 adults were shipped to Temple, arriving on February 11. They were provided with bouquets of *Gut. sarothrae* and *Gut. microcephala* for feeding and for oviposition. This test used 94 eggs, placed in stems of 17 test plant species from February 23 to 28, 1995.

Larval Test 5 used 100 eggs laid in adult multiple-choice feeding and oviposition Test 6, placed in stems of 19 test plant species from December 9, 1985, to January 6, 1986.

Experimental Design and Testing Procedure

Adult tests. One no-choice (Test 7) and six multiple-choice tests (Tests 1 to 6) were conducted to compare feeding and oviposition on various species of test plants. The no-choice test compared two Argentine and two North American plant species, using 64 weevils collected as adults from *Grin. chiloensis* and *Gut. spathulata* in Argentina. Two adults (1 female and 1 male) were placed on cut branches of each test plant using clear plastic tube cages. The stems were examined for feeding and eggs and were replaced with fresh stems weekly from February 22 to March 25. The few plants of *Gut. spathulata* received in the shipment were used by March 1 and were replaced by *Grin. chiloensis* from March 2 to 25. This test was conducted in the quarantine laboratory at 25 ± 1°C, in front of a window for natural lighting, but with supplementary fluorescent lighting to provide a 14:10 light–dark photoperiod.

The six multiple-choice tests of feeding and oviposition, using 622 adults and 40 test-plant species, were conducted in cages in the quarantine greenhouse, at natural photoperiod. Temperature was held below 32°C during the summer and above 15°C during the winter. Tests 1 to 4 compared weevil responses in three types of cages (pots, vials, and pans), with both potted plants and cut branches, and compared weevils collected from either *Gut. solbrigii* or *Grin. chiloensis* in Argentina (Table 2). Tests 1 and 2 were similar and Tests 3 and 4 were similar; 23 different test-plant species were compared in Tests 1 to 4, with 17 of them common in all four tests. In Tests 5 and 6, we used only potted plants in the large cages to simulate more natural conditions. In Tests 5 and 6, we compared 27 test-plant species, 13 of them common to both tests and 10 common to Tests 1 through 4. The treatments using weevils from *Gutierrezia* (vials and pans in Tests 3 and 4 and all treatments in Tests 5 and 6) were omitted because only weevils from *Gut. chiloensis* were available from Argentina at the time of these tests.

Each cage contained 20 different test-plant species, arranged randomly in each cage, and all cages in each test contained the same plant species and began with the same number of weevils. Weevils were introduced into the cage by placing one pair (one male and one female) in the space between each row and column of plants in the cage. As much as possible, we selected plants that were free of damage by other insects, and

TABLE 2

Experimental Design of Multiple-Choice Adult Feeding and Oviposition Tests of *Heilipodus ventralis*

	Type cage and weevil source[a]								
	Weevils ex. *Gutierrezia*			Weevils ex. *Grindelia*			No. weevils		
Test no.	Pots	Vials	Pan	Pots	Vials	Pan	Per cage	Total	Date test started (days tested)
1	1	1	1	1	1	1	24	144	Oct. 14, 1983 (10)
2	1	1	1	1	1	1	21	126	Oct. 31, 1983 (10)
3	1			1	1	1	21	84	Nov. 10, 1983 (11)
4	1			1	1	1	21	84	Nov. 23, 1983 (11)
5				4			24	96	Oct. 4, 1985 (27)
6				4			22	88	Nov. 13, 1985 (19)
Total								622	(88)

[a] Number of cages in each treatment. Source of weevils collected in Argentina. Each cage contained 1 each of 20 different test-plant species. Adult feeding data from these tests is presented in Tables 1 and 3, ovipositional data in Tables 5 and 6, and responses to Test No., weevil source, and cage type in Table 7.

any damaged leaves were removed before the plant was put in the test.

At the end of each test, the amount of feeding on leaves, stems, and flowers was measured under a dissecting microscope using a 1-mm^2 grid placed over the feeding scars. On some plants, *H. ventralis* adults fed by cutting the petiole, causing the leaf to fall from the plant. Since we could not measure the amount of feeding, we assumed that each fallen leaf equaled 1 mm^2 of leaf feeding. Fallen leaves were collected two or three times during the test and added to the measurement made at the end of the test.

The cage and the plants were searched carefully at the end of the tests for living and dead weevils, and the peat moss was sifted to find burrowing adults. Oviposition was measured at the end of each test by peeling off the outer bark of the stems with forceps under the dissecting microscope, exposing the oviposition punctures. The eggs were then counted, removed, and held to observe fertility and for use in subsequent larval host-range tests.

Larval tests. Larval development was measured in five no-choice tests using 365 eggs or neonate larvae and 31 test-plant species. One egg soon ready to hatch (head capsule visible through the chorion) or one newly emerged larva (hatched within the past 4 to 12 h), was placed with a small brush into a hole (one hole per stem) ca. 2 to 3 cm above the soil surface in the stems of healthy, potted plants. The holes were ca. 1.5 mm diam × 2–3 mm deep, made with a 1.5-mm-diam drill turned between the fingers. After the egg was inserted, the hole was covered by Teflon tape wrapped around the stem to prevent the larva from escaping. A maximum of three eggs was placed in each plant and only one or two eggs in smaller plants. In general, stems at least 4 mm in diam were selected. The plants were maintained in the quarantine greenhouse for 7 to 14 months until the larvae should have completed their development. The stems were then dissected under a microscope, the length and diameter of the feeding tunnels were measured, and the size and condition of any larvae were recorded. Living larvae were placed in cups of artificial diet for rearing to the adult stage.

Larval Test 1 compared larval development in seven plant species, including the Argentine known host, *Grin. chiloensis.* From March 11 to April 22, 1982, 91 neonate larvae or eggs were placed in stems of healthy potted plants. Plants containing 18 larvae were dissected May 26 to observe the progress of development; all living larvae were transferred to a fresh plant of the same species so they could continue their development. The final examination of all plants was made 12 to 14 months after the test began.

In larval tests 2 to 5, neonates or eggs were placed in various of the 29 test-plant species, 48 eggs on 19 plant species in Test 2, 32 eggs on 16 plants in Test 3, 94 eggs on 17 plants in Test 4, and 100 eggs on 19 plant species in Test 5.

Statistical Analysis

Data from the laboratory tests were subjected to analysis of variance using the ANOVA procedure in SAS (SAS Institute, 1990). Feeding and oviposition data were transformed for analysis by the formula $\log_e(X + 1)$ and larval development data by the formula $\sqrt{X + 1}$. However, for clarity of inspection, the untransformed data are presented in the tables. The multiple comparison of means shown in the tables are based on analysis of the transformed data; therefore, some significant intervals may appear nonsignificant, and vice versa, when viewing the untransformed data in the tables. The experimental unit in all tests was one plant. Means were compared with Fisher's protected LSD test, $P < 0.05$. In larval Tests 2 to 5, each plant

contained one to three larvae; treatments (test-plant species) with fewer than two plants were not included in the analysis of larval development.

RESULTS AND DISCUSSION

We measured adult feeding and ovipositional host selection simultaneously and in the same cages using 622 weevils on 40 species of North American Asteraceae in six multiple-choice tests in the quarantine greenhouse. One no-choice test compared adult survival and feeding by 64 weevils on cut branches of the two major Argentine host plants with two major U.S. snakeweed species in the quarantine laboratory. Larval survival and development was tested in five separate tests, using 365 neonate larvae or eggs just before hatching on 30 potted test plant species, in the quarantine greenhouse.

Adult Feeding Host Specificity

Multiple-choice tests. A comparison of means in the six multiple-choice tests revealed a strong concentration of feeding on test plants in the tribe Astereae. Adults fed mostly on seven species of the genera *Grindelia, Gutierrezia, Gymnosperma,* and *Baccharis.* They fed less on species of *Isocoma, Chrysothamnus,* and *Xylothamia,* in the subtribes Solidagininae, Machaerantherinae, and Baccaharidinae, and even less on other species of the subtribe Asterinae, all in the tribe Astereae. The weevils also fed moderately on *Chrysanthemum* in the tribe Anthemideae. These also were the species most closely related to the Argentine natural hosts, *Grindelia* spp., *Gutierrezia* spp., and, to a lesser degree, *Baccharis* spp. Feeding on plants in other tribes generally was not different from zero (Table 1).

Feeding responses to all test plant species could not be analyzed across all tests because Tests 1 and 2, Tests 3 and 4, Test 5, and Test 6 all contained different plant species. An ANOVA in which only the 17 test-plant species common to Tests 1 through 4 were included revealed highly significant differences in feeding between plant species (Table 3). When each test was analyzed separately (cage type and weevil source pooled), differences between means for feeding on many of the plant species were significantly different in all the tests; however, the preference for several plant species varied somewhat between tests (Table 1). The differences between tests probably was caused by slight differences in plant condition or physiology that we could not detect or control.

When Tests 1 and 2 and Tests 3 and 4 (each pair of tests containing the same test plant species) were pooled for analysis, the results were more consistent but still varied somewhat between the two pairs of tests (Table 1). In Tests 1 and 2, adults fed significantly more on *B. salicifolia* and *Gym. glutinosum* and next most on *Chryso. nauseosus, Grin. lanceolata, I. coronopifolia, Gut. grandis, B. sarothroides, Gut. microcephala,* and *Gut. sarothrae* in that order. In Tests 3 and 4, adults fed significantly more on *Gym. glutinosum, B. salicifolia, Gut. grandis, Gut. sarothrae,* and *Gut. microcephala* (with *I. coronopifolia* intermediate) than on any of the other 14 test-plant species. All of these favored test plants, except the *Baccharis* species, were in the tribes

TABLE 3

Analysis of Variance for Different Effects on the Amount of Feeding (mm^2) per Adult Weevil per Day[a]

Source of variation	Pooled Tests 1–4 (17 plant species in common)					Pooled Tests 1 and 2 (20 plant species in common)[c,d] $P < F$	Pooled Tests 3 and 4 (20 plant species in common)[b,c,d] $P < F$
	Degrees of freedom	Sum of squares	Mean square	F value	$P < F$[d]		
Overall							
Model	101	13.68	0.1355	2.77	0.0001***	0.0001***	0.0001***
Error	238	11.66	0.0490				
Corrected total	339	23.34					
Model effects							
Plant species	16	8.679	0.542	11.08	0.0001***	0.0001***	0.0001***
Cage type	2	0.294	0.147	3.00	0.0514*	0.459	0.149
Source host of weevil	1	0.238	0.238	4.86	0.0284*	0.184	
Plant × cage	32	1.187	0.037	0.76	0.826	0.493	0.914
Plant × source host of weevil	16	0.647	0.040	0.83	0.656	0.340	
Cage × source host of weevil	2	0.163	0.082	1.67	0.191	0.492	
Plant × cage × source host of weevil	32	0.607	0.019	0.39	0.999	0.999	

[a] See Table 2 for experimental design.
[b] Tests 3 and 4 had only one weevil source; effects of source could not be compared and are omitted here.
[c] For brevity, degrees of freedom, sum of squares, mean square, and F are omitted here.
[d] Significant ($P < 0.05$); ***very highly significant ($P < 0.0001$).

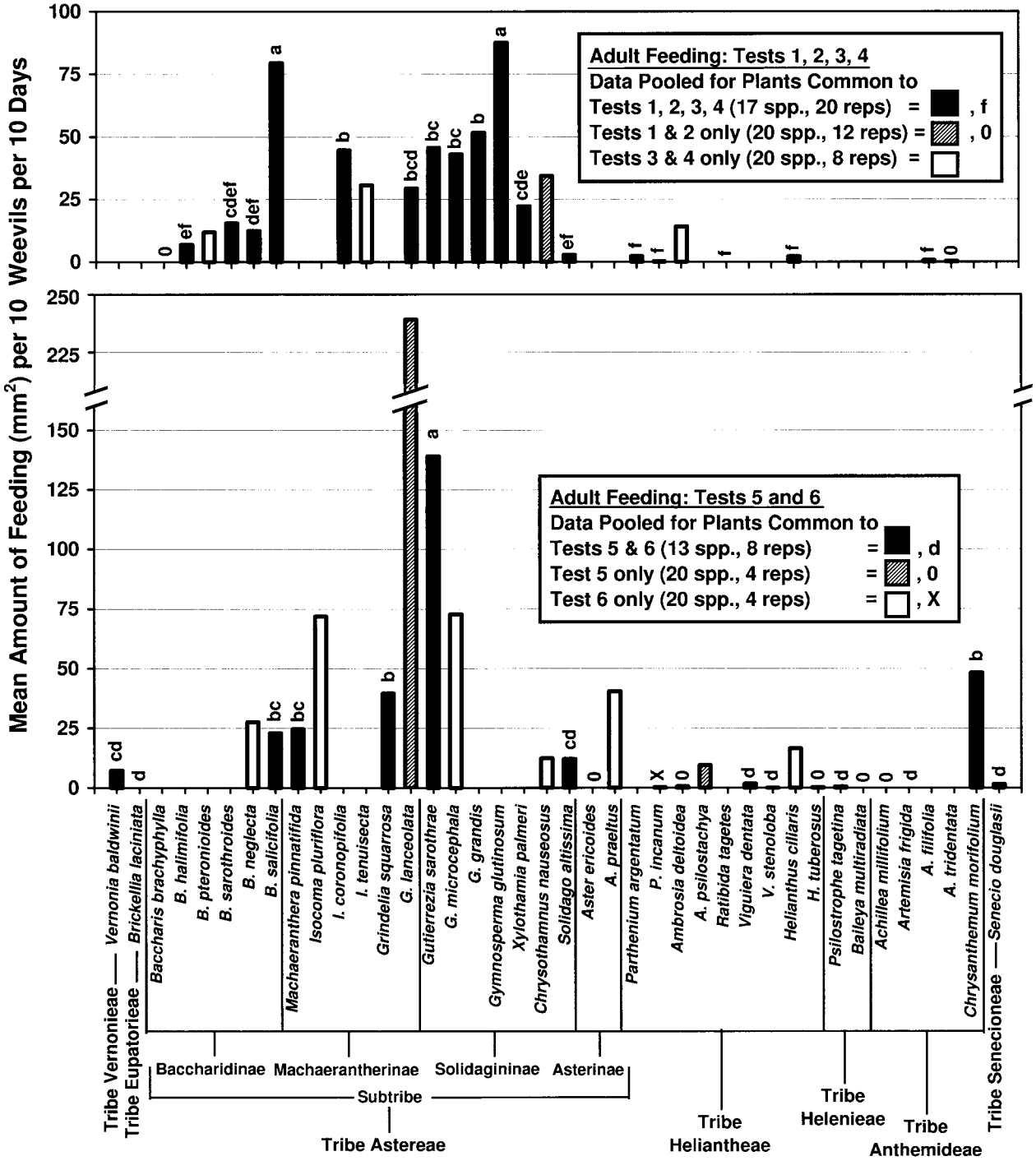

FIG. 2. Feeding by adult *H. ventralis* in multiple-choice Tests 1–6. Plants were tested for statistical differences only if included in all four pooled Tests 1–4 or in pooled Tests 5 and 6. Plants followed by the same letter are not statistically different ($P < 0.05$) according to Fisher's protected LSD test. 0 and X represent zero and near zero feeding for their respective tests; f (in Tests 1–4) and d (in Tests 5 and 6) indicate statistical differences for low or zero values included in the pooled analyses. (Data from Table 1.)

Solidagininae and Machaerantherinae. Feeding on the other seven species of plants in the other tribes was not different from zero. When the data for Tests 1 and 4 were pooled for the 17 common test-plant species (Fig. 2), adults fed significantly more on *Gym. glutinosum* and *B. salicifolia;* the next most favored plants were the three species of *Gutierrezia, I. coronopifolia,* and *Grin. lanceolata.* Similar amounts of feeding occurred on *I. tenuisectas* in pooled Tests 1 and 2 and on *Chryso. nauseosus* in pooled Tests 3 and 4 (Fig. 2).

The objective of Tests 5 and 6 was to compare several plant species more distantly related to the major host-

plant group while retaining a few species common to Tests 1 to 4 for comparison. When the data from Tests 5 and 6 were analyzed separately (Table 1), the weevils fed primarily on species of *Grindelia* and *Gutierrezia,* but preference varied between the tests for these and the other plant species. The weevils also fed substantially on *Chrysan.* × *morifolium* and *M. pinnatifida* in Test 5 and on *I. pluriflora, A. praealtus,* and *Chrysan.* × *morifolium* in Test 6 (Table 1). When the data from Tests 5 and 6 were pooled for the 13 common test-plant species (Fig. 2), feeding was significantly greater on *Gut. sarothrae* and next most on *Chrysan.* × *morifolium, Grin. squarrosa, M. pinnatifida,* and *B. salicifolia. Grindelia lanceolata* also should be included as a favored plant in the pooled results, even though it was not included in Test 6; feeding in Test 5 was so great that it still would equal *Gut. sarothrae* if averaged between the two tests.

Adult Survival

No-choice test. In the no-choice test that compared adult survival and oviposition on the Argentine host plants with those on North American species of *Gutierrezia* (Test 7), survival over the 1-month period of the test was ca. 50% greater on the Argentine *Grin. chiloensis* plants than on the others (Table 4). Although the larval host of the weevils found in Argentina had little effect on survival, females survived slightly longer than males except on the Argentine *Gut. spathulata.*

Ovipositional Host Specificity

No-choice test. In the above adult survival test, the 32 females tested laid a total of 177 eggs during the 1-month test. They laid more eggs on *Gut. sarothrae* and *Grin. chiloensis* than on the other test plants (Table 4). Females laid an average 36% more eggs per plant on the two North American plant species than on the two South American plant species, and those collected as adults from *Gutierrezia* in Argentina laid 15% more eggs on all test-plant species than those collected from *Grindelia.* These results were not significant because of the small numbers of weevils tested and the substantial variation between weevils in the same treatment, although the difference between the totals for the four test-plant species approached significance. Nevertheless, we could see nothing to indicate that the

TABLE 4

Test 7—Oviposition and Survival of Adult *Heilipodus ventralis* on North American vs South American Plants: No-Choice Test[a]—1982

Test plant	Weevil source (No. plants used)		Mean survival (days) Female	Mean survival (days) Male	No. eggs laid Total	No. eggs laid Per plant (means ± SE)
			Argentine test plants			
Grindelia chiloensis	*Grin. chilonesis*	(5)	30	27	42	8.4 ± 3.3
	Gut. spathulata	(3)	32	22	18	6.0 ± 4.2
	Mean or total		31	25	60	7.2
Gutierrezia spathulata[b]	*Grin. chiloensis*	(5)	20	20	14	2.8 ± 1.4
	Gut. spathulata	(3)	26	26	4	1.3 ± 0.9
	Mean or total		21	21	18	2.0
			North American test plants			
Gutierrezia sarothrae	*Grin. chiloensis*	(5)	23	19	54	10.8 ± 2.8
	Gut. spathulata	(3)	23	15	25	8.3 ± 5.8
	Mean or total		23	18	79	9.6
Gutierrezia microcephala	*Grin. chiloensis*	(5)	17	14	4	0.8 ± 0.6
	Gut. spathulata	(3)	24	17	16	5.3 ± 3.5
	Mean or total		20	15	20	3.1
			Overall test plant means			
Gut. sarothrae		(8)			79	9.9 ± 2.6
Gut. microcephala		(8)			20	2.5 ± 1.5
Grin. chiloensis		(8)			60	7.5 ± 2.4
Gut. spathulata[b]		(8)			18	2.2 ± 0.9
			Overall weevil source means			
Ex. *Grin. chiloensis*		(20)			114	5.7 ± 1.4
Ex. *Gut. spathulata*		(12)			63	5.25 ± 1.9

[a] One pair of young adults (one male and one female) placed on cut stems of each plant species. Five replications (plants) on each test plant species used weevils collected as adults from *Grindelia chiloensis* in Argentina and three replications used weevils collected from *Gutierrezia spathulata* in Argentina.

[b] Provided with branches of *Gut. spathulata* Feb. 22 to March 1, then with *Grin. chiloensis* March 2 to 25.

North American *Gut. sarothrae* was not accepted at least as well as the natural hosts from Argentina, and the source of the weevils in Argentina appeared to make little difference.

Multiple-choice tests. In the six multiple-choice tests, the 311 females tested (3941 female exposure days) laid a total of 351 eggs. Ovipositional host preference (Fig. 3) was centered more strongly on *Gutierrezia* and the genera most closely related to it than was true for adult feeding preference (Fig. 2). The most favored plants were the two *Grindelia* species, the three *Gutierrezia* species, and *Gym. glutinosum,* with lesser oviposition on *I. coronopifolia, X. palmeri, M. pinnatifida, Chryso. nauseous,* and *S. altissima,* all in the tribes Solidagininae and Machaerantherinae. Only slight oviposition occurred on 5 species and none on 20 species of the other tribes tested (Fig. 3).

As with the feeding tests, oviposition could not be analyzed across all tests because of differences in plant species in some tests. When each test was analyzed separately (Table 5), many significant ($P < 0.05$) differences were seen among the test plants in all the tests. Preferences for different plants varied between tests, but varied less than had feeding preference.

When Tests 1 and 2 and Tests 3 and 4 (each pair of tests containing the same test-plant species) were pooled for analysis (Table 5), ovipositional preference was identical for the first five plant species, with significantly more oviposition on *Grin. lanceolata* and *Gut. grandis* and next most on *Gym. glutinosum, Gut. microcephala, I. coronopifolia,* and *X. palmeri* but still varied somewhat between the other species.

When the data for Tests 1 to 4 were pooled for the 17 common plant species (Fig. 3), females laid more eggs on *Grin. lanceolata* and *Gut. grandis* and next most on *Gym. glutinosum, Gut. microcephala, I. coronopifolia, X. palmeri,* and *Gut. sarothrae.* Similar numbers of eggs were laid on *Chryso. nauseosus* (included only in Tests 1 and 2). Females laid only a few eggs on two species of *Baccharis* and none on *Chrysan.* × *morifolium,* even though adults fed moderately heavily on these plants. An ANOVA revealed highly significant differences ($P < 0.0001$) in oviposition on the different plant species (Table 6).

In Tests 5 and 6, females oviposited only on 10 of the 27 plant species presented, but 3 of the species received only 0.1 or 0.2 eggs per 10 females per 10 days during the tests. When the data from Tests 5 and 6 were analyzed separately (Table 5), females oviposited most on species of *Grindelia* and *Gutierrezia,* but preference varied between the tests for the other species. When Tests 5 and 6 were pooled for the 13 common plant species (Fig. 3), females oviposited significantly more on *Grin. squarrosa, Gut. sarothrae,* and *M. pinnatifida,* and next most on *S. altissima.* Females laid the greatest number of eggs of either test on *Grin. lanceolata* (included only in Test 5) and also oviposited substantially on *Gut. microcephala* and *I. pluriflora* (included only in Test 6) (Fig. 3).

Differences within cage type, weevil source, and test number. The ANOVAs performed (Tables 3 and 6) revealed significant differences in both adult feeding and oviposition between cage type (pots, vials, or pans) and larval host of the weevils when collected in Argentina (*Grin. chiloensis* or *Gut. solbrigii*); Tests 1 through 4 were pooled for these analyses.

When the means for adult feeding were compared (Table 7), weevils fed more on the potted plants in large cages than on cut branches in pans in small cages; feeding on cut branches in vials in large cages was intermediate; those differences were almost significant ($P < 0.0514$, Table 3). Weevils collected as larvae from *Grindelia* fed significantly more ($P < 0.0284$, Table 3) than those collected from *Gutierrezia* in Argentina (Table 7).

When the means for oviposition were compared (Table 7), females laid significantly more eggs in stems of potted plants in the large cages than in cut branches in either vials in large cages or in pans in small cages. Also, females collected as larvae from *Grindelia* oviposited significantly more than those collected from *Gutierrezia* in Argentina (Tables 6 and 7). Significant differences ($P < 0.0001$) also were seen in the interaction of plant species × cage type (Table 6), which was not seen in feeding preference. Oviposition on potted plants of *Grin. lanceolata* was 7.1 times, and on *Gut. grandis, Gym. glutinosum,* and *Gut. microcephala* 2.6 times, that on cut branches in vials and 2 to 4 times that in cut branches in pans; these were the most favored plants, on which most of the eggs were laid (Table 5). In contrast, on *I. coronopifolia,* females laid 3.6 times as many eggs on branches in vials as on potted plants. On the other six plant species, fewer eggs were laid, and the differences were smaller, with cut branches in vials or pots slightly preferred. Therefore, both the difference in orientation of the response on *I. coronopifolia* and the difference in magnitude of the response between the most and least preferred plant species contributed to the interaction. We can only speculate that plant physiology was less favorable to ovipositing females in cut branches when compared with growing, potted plants.

Differences in the source host of the weevils (whether collected as larvae from *Grindelia* or *Gutierrezia* in Argentina) were significant for both feeding (Table 3) and oviposition (Table 6). A comparison of means (Table 7) showed that weevils from *Grindelia* both fed and oviposited more than those from *Gutierrezia.* However, the ANOVAs revealed no evidence that this influenced host preference (i.e., weevil source × plant species interaction was not significant) (Tables 3 and 6).

We also observed substantial differences between the

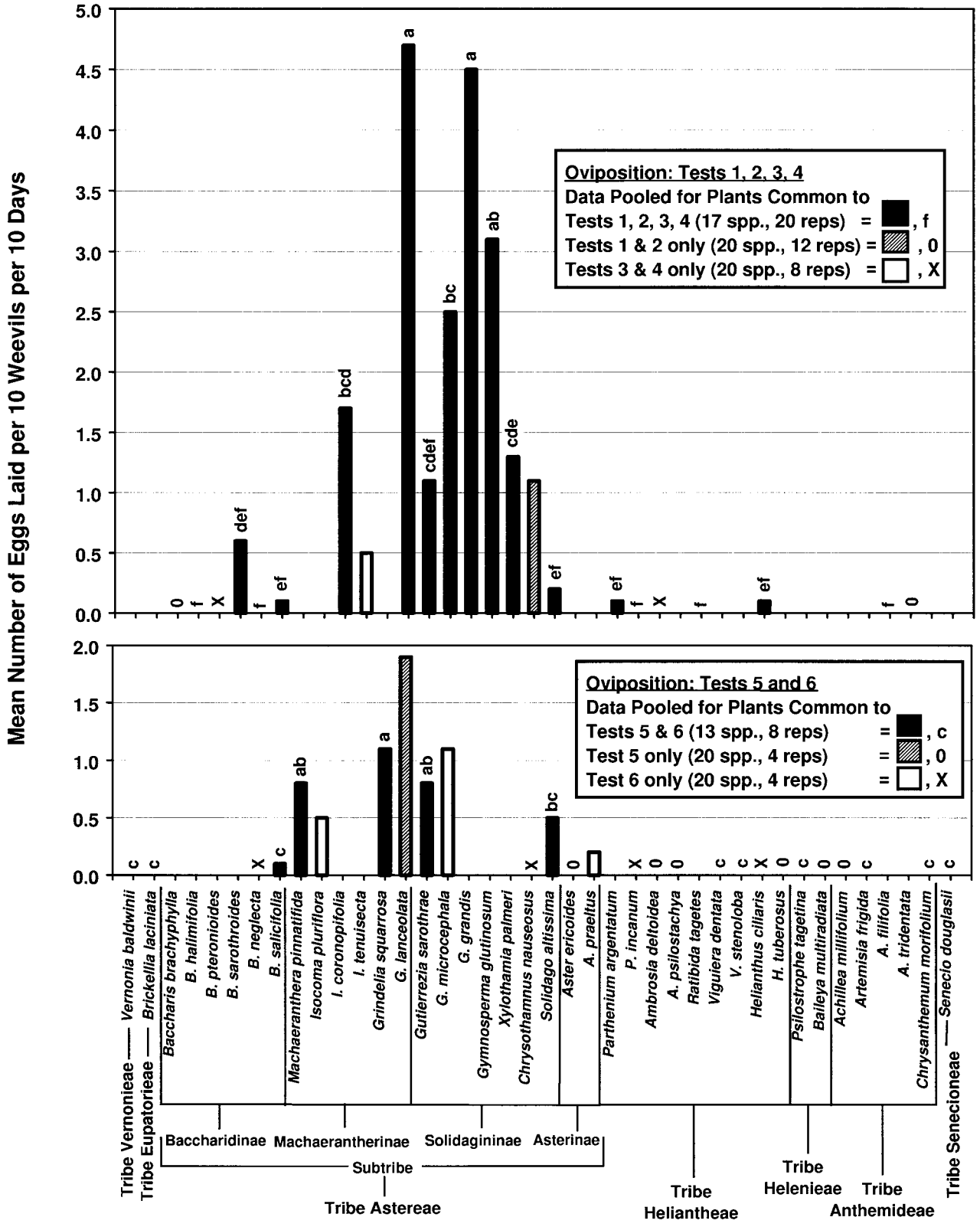

FIG. 3. Oviposition by female *H. ventralis* in multiple-choice Tests 1–6. Plants were tested for statistical differences only if included in all four pooled Tests 1–4 or in pooled Tests 5 and 6. Plants followed by the same letter are not statistically different ($P < 0.05$) according to Fisher's protected LSD test. 0 and X represent zero and near zero oviposition for their respective tests; f (in Tests 1–4) and c (in Tests 5 and 6) indicate statistical differences for low and zero values included in the pooled analyses. (Data from Table 5.)

TABLE 5

Oviposition by Adult *Heilipodus ventralis* in Stems of 40 Species of Asteraceae: Multiple-Choice Tests

Test plant (tribe, subtribe, genus, and species)	No. of eggs laid by 10 females per 10 days (means ± SE)[a,b]							
	Test 1 (n = 6)	Test 2 (n = 6)	Tests 1 and 2 (n = 12)	Test 3 (n = 4)	Test 4 (n = 4)	Tests 3 and 4 (n = 8)	Test 5 (n = 4)	Test 6 (n = 4)
Tribe Vernonieae								
Vernonia baldwinii							0.0 ± 0.0d	0.0 ± 0.0d
Tribe Eupatorieae								
Brickellia laciniata							0.0 ± 0.0d	0.0 ± 0.0d
Tribe Astereae								
Subtribe Asterinae								
Aster ericoides							0.0 ± 0.0d	
A. praealtus								0.2 ± 0.1cd
Subtribe Baccharidinae								
Baccharis brachyphylla	0.0 ± 0.0d	0.0 ± 0.0e	0.0 ± 0.0e					
B. halimifolia	0.0 ± 0.0d	0.0 ± 0.0e	0.0 ± 0.0e	0.0 ± 0.0e	0.0 ± 0.0c	0.0 ± 0.0c		
B. neglecta	0.0 ± 0.0d	0.0 ± 0.0e	0.0 ± 0.0e	0.0 ± 0.0e	0.0 ± 0.0c	0.0 ± 0.0c		0.0 ± 0.0d
B. pteronioides				0.0 ± 0.0e	0.0 ± 0.0c	0.0 ± 0.0c		
B. salicifolia	0.0 ± 0.0d	0.4 ± 0.2e	0.2 ± 0.0de	0.0 ± 0.0e	0.0 ± 0.0c	0.0 ± 0.0c	0.2 ± 0.1cd	0.1 ± 0.1d
B. sarothroides	0.6 ± 0.6cd	0.4 ± 0.2de	0.5 ± 0.3cde	0.0 ± 0.0e	1.7 ± 1.1c	0.8 ± 0.6c		
Subtribe Solidagininae								
Chrysothamnus nauseosus	**1.7 ± 0.5abc**	0.6 ± 0.2cde	**1.1 ± 0.3bcd**				0.0 ± 0.0d	0.1 ± 0.1d
Xylothamia palmeri	0.6 ± 0.3cd	**1.8 ± 0.6bcd**	**1.2 ± 0.4bcd**	0.5 ± 0.3de	2.2 ± 0.9c	1.4 ± 0.5c		
Gutierrezia grandis	**1.7 ± 1.1bc**	**4.6 ± 1.9a**	**3.1 ± 1.1a**	**5.3 ± 0.9a**	**7.8 ± 4.9ab**	**6.5 ± 2.4a**		
Gut. microcephala	**2.5 ± 1.3ab**	1.1 ± 0.5bcde	**1.8 ± 0.7b**	**3.3 ± 1.3b**	3.9 ± 2.3bc	3.6 ± 1.2abc		**1.1 ± 0.6ab**
Gut. sarothrae	0.6 ± 0.3cd	0.7 ± 0.4bcde	0.6 ± 0.2cde	1.0 ± 0.6de	2.8 ± 1.7bc	1.9 ± 0.9bc	**1.0 ± 0.3b**	0.6 ± 0.4bcd
Gymnosperma glutinosum	**1.7 ± 0.6bc**	**2.4 ± 0.9b**	**2.0 ± 0.5b**	**5.6 ± 1.3a**	3.9 ± 1.1bc	**4.7 ± 0.9ab**		
Solidago altissima	0.0 ± 0.0d	0.4 ± 0.2e	0.2 ± 0.1de	0.3 ± 0.3e	0.0 ± 0.0c	0.1 ± 0.1c	0.2 ± 0.1cd	0.7 ± 0.3abcd
Subtribe Machaerantherinae								
Grindelia lanceolata	**3.2 ± 1.3a**	**2.4 ± 1.8bc**	**3.1 ± 1.1a**	**2.5 ± 0.3bc**	**11.7 ± 5.5a**	**7.1 ± 3.1a**	**1.9 ± 0.7a**	
Grindelia squarrosa							**0.7 ± 0.4bc**	**1.4 ± 0.7a**
Isocoma coronopifolia	1.1 ± 0.5bcd	1.7 ± 0.8bcde	**1.4 ± 0.5bc**	**1.8 ± 0.5cd**	2.8 ± 2.8bc	2.3 ± 1.3abc		
I. tenuisecta				1.0 ± 0.4de	0.0 ± 0.0c	0.5 ± 0.3c		
I. pluriflora								0.5 ± 0.3d
Machaeranthera pinnatifida							0.6 ± 0.5bcd	**1.0 ± 0.6abc**
Tribe Heliantheae								
Subtribe Ambrosiinae								
Ambrosia deltoidea				0.0 ± 0.0e	0.0 ± 0.0c	0.0 ± 0.0c	0.0 ± 0.0d	
A. psilostachya							0.0 ± 0.0d	
Parthenium argentatum	0.4 ± 0.4cd	0.0 ± 0.0e	0.2 ± 0.2de	0.0 ± 0.0e	0.0 ± 0.0c	0.0 ± 0.0c		
P. incanum	0.0 ± 0.0d	0.0 ± 0.0e	0.0 ± 0.0e	0.0 ± 0.0e	0.0 ± 0.0c	0.0 ± 0.0c		0.0 ± 0.0d
Subtribe Helianthinae								
Helianthus ciliaris	0.3 ± 0.2cd	0.2 ± 0.2e	0.2 ± 0.1de	0.0 ± 0.0e	0.0 ± 0.0c	0.0 ± 0.0c		0.0 ± 0.0d
H. tuberosus							0.0 ± 0.0d	
Ratibida tagetes	0.0 ± 0.0d	0.0 ± 0.0e	0.0 ± 0.0e	0.0 ± 0.0e	0.0 ± 0.0c	0.0 ± 0.0c		
Viguiera dentata							0.0 ± 0.0d	0.0 ± 0.0d
V. stenoloba								0.0 ± 0.0d
Tribe Helenieae								
Subtribe Gaillardiinae								
Baileya multiradiata							0.0 ± 0.0d	
Psilostrophe tagetina							0.0 ± 0.0d	0.0 ± 0.0d
Tribe Anthemideae								
Subtribe Achilleinae								
Achillea millefolium							0.0 ± 0.0d	
Subtribe Artemisiinae								
Artemesia filifolia	0.0 ± 0.0d	0.0 ± 0.0e	0.0 ± 0.0e	0.0 ± 0.0e	0.0 ± 0.0c	0.0 ± 0.0c		

TABLE 5—*Continued*

Test plant (tribe, subtribe, genus, and species)	No. of eggs laid by 10 females per 10 days (means ± SE)[a,b]							
	Test 1 (n = 6)	Test 2 (n = 6)	Tests 1 and 2 (n = 12)	Test 3 (n = 4)	Test 4 (n = 4)	Tests 3 and 4 (n = 8)	Test 5 (n = 4)	Test 6 (n = 4)
A. frigida							0.0 ± 0.0d	0.0 ± 0.0d
A. tridentata	0.0 ± 0.0d	0.0 ± 0.0e	0.0 ± 0.0e					
Subtribe Chrysantheminae								
Chrysanthemum × *morifolium*							0.0 ± 0.0d	0.0 ± 0.0d
Tribe Senecioneae								
Senecio douglasii var. *longilobus*							0.0 ± 0.0d	0.0 ± 0.0d
$P > F$ (0.05)	0.0001	0.0001	0.0001	0.0001	0.0021	0.0001	0.0001	0.0066

[a] Means followed by the same letter within the same column are not significantly different [$P < 0.05$; Fisher's protected LSD (SAS Institute, 1990)]. Values for each test plant are pooled across the three cage types and two weevil sources for Tests 1 to 4, which are all equal in Tests 1 and 2 but unequal in Tests 3 and 4. Tests 5 and 6 included only one cage type (pots) and only one weevil source (*Grindelia*) (see Table 2 for experimental design). Analyses of pooled Tests 1 through 4 (17 common test plants) and Tests 5 and 6 (13 common test plants) are given in Fig. 3. Main effects with P values for the different test combinations are given in Tables 6 and 7.

[b] Values in bold type indicate values statistically greater than zero ($P < 0.05$).

six tests in the overall amount of both feeding and oviposition (Table 7). The smaller amount of feeding in the first test (Tests 1, 3, and 5) of each of the three test pairs may have been because we used young, recently eclosed weevils that may not have been sufficiently mature for normal feeding until several days into the tests. However, oviposition did not follow this pattern. The lower apparent performance in Tests 5 and 6 compared to Tests 3 and 4 was at least in part because of the much longer duration of the tests which reduced the numbers of eggs laid per day in the analysis. We did not make midtest counts and so we cannot confirm this hypothesis. The plants in Tests 5 and 6 probably did not deteriorate over time because all plants in these tests were growing in pots. The cage × plant interaction in oviposition could have been caused by the decline of plant condition in the vial and pan cages (which used cut stems) vs the pot cages (which used potted plants).

Larval Development

Larval Test 1 compared development of 91 neonate larvae on seven test-plant species, using different numbers of larvae per species. When stems of four plant

TABLE 6

Analysis of Variance for Different Effects on the Number of Eggs Laid per Female Weevil per Day[a]

Pooled Tests 1–4 (17 plant species in common)						Pooled Tests 1 and 2 (20 plant species in common)[c,d] $P < F$	Pooled Tests 3 and 4 (20 plant species in common)[b,c,d] $P < F$
Source of variation	Degrees of freedom	Sum of squares	Mean square	F value	$P < F$[d]		
			Overall				
Model	101	0.1361	0.0013	3.32	0.0001***	0.0001***	0.0001***
Error	238	0.0968	0.0004				
Corrected total	339	0.2329					
			Model effects				
Plant species	16	0.0496	0.0031	7.63	0.0001***	0.0001***	0.0001***
Cage type	2	0.008	0.004	9.84	0.0001***	0.0171*	0.0933
Source host of weevil	1	0.0027	0.0027	6.74	0.0100**	0.0017**	
Plant × cage	32	0.0370	0.0016	2.84	0.0001***	0.0002***	0.2282
Plant × source host of weevil	16	0.0068	0.0004	1.04	0.4102	0.1056	
Cage × source host of weevil	2	0.0002	0.0001	0.22	0.7980	0.6472	
Plant × cage × source host of weevil	32	0.0068	0.0002	0.57	0.9691	0.5309	

[a] See Table 2 for experimental design.

[b] Tests 3 and 4 had only one weevil source; source effects could not be compared and are omitted here.

[c] For brevity, degrees of freedom, sum of squares, mean square, and F are omitted here.

[d] * Significant ($P < 0.05$); ** highly significant ($P < 0.01$); *** very highly significant ($P < 0.0001$).

TABLE 7

Effects of Test Number, Cage Type, and Weevil Source on Feeding and Oviposition by Adult *Heilipodus ventralis*[a]

	Feeding (mm^2 per 10 weevils per 10 days) (data from Table 2)					
Test No. (all plants)[b]	1	2	3	4	5	6
	9.1 ± 1.7 (120)	21.3 ± 2.9 (120)	27.1 ± 3.9 (80)	49.9 ± 8.3 (80)	22.9 ± 6.5 (80)	31.4 ± 5.8 (80)
	Tests 1–4 (17 plants in common)					
Cage type	Pots		Vials		Pans	
	32.8 ± 5.2 (136)a		23.5 ± 3.8 (102)ab		20.4 ± 2.9 (102)b	
Weevil source	*Grindelia*		*Gutierrezia*			
	28.5 ± 3.4 (204)a		23.1 ± 3.8 (136)b			
	Oviposition (eggs per 10 ♀♀/per 10 days) (data from Table 5)					
Test no (all plants)[b]	1	2	3	4	5	6
	0.74 ± 0.15 (120)	0.83 ± 0.18 (120)	1.06 ± 0.22 (80)	1.83 ± 0.51 (80)	0.24 ± 0.07 (80)	0.29 ± 0.07 (80)
	Tests 1–4 (17 plants in common)					
Cage type	Pots		Vials		Pans	
	1.8 + 0.3 (136)a		0.8 ± 0.2 (102)b		0.8 ± 0.2 (102)b	
Weevil Source	*Grindelia*		*Gutierrezia*			
	1.4 ± 0.2 (204)a		0.9 ± 0.2 (136)b			

[a] Means followed by the same letter within the same row are not significantly different ($P < 0.05$; Fisher's protected LSD test) (SAS Institute, 1990). Before analysis, data were transformed by the factor $\log_e (X + 1)$, but the untransformed data are presented here. All data are expressed as means ± SE (n). n, Number of plants tested (see Table 2).

[b] Overall means of individual tests cannot be directly compared due to differences in plant species, cage types, and weevil sources between tests.

species containing 18 larvae were dissected after ca. 1 month, 12 of the larvae had fed and produced short tunnels, but 6 of these had already died (Table 8). The living larvae were transferred to fresh plants of the same species to continue their development. At the final examination 12 to 13 months after the test was initiated, 5 of the neonates had developed to the adult and 1 to the pupal stage (37.5% of the original 16 neonates) in *Gut. sarothrae*, 5 had reached the adult, 1 the pupal stage, 3 were large larvae (24.4% of the neonates) in *Gut. microcephala*, and 2 were large larvae in *Grin. chiloensis* (25% of the neonates) (Table 8).

Larval Tests 2 to 5 compared development of 274 neonates in 29 test-plant species with from 16 to 19 plant species in each test. From 6 to 24 larvae were used on the plant species most closely related to the natural host (Table 9, Fig. 4). Larvae had reached significantly greatest average development at the time of dissection on *Gym. glutinosum*, *Gut. grandis*, and *Grin. lanceolata*. Lesser development occurred on *Br. laciniata*, *Chryso. nauseosus*, *Gut. sarothrae*, *Gut. microcephala*, *A. praealtus*, and *M. pinnatifida* but this was not significantly different from zero. Only slight or no development occurred on the other 23 plant species tested. No larvae developed in species of other genera on which feeding and oviposition had occurred.

Discussion of Host Range

Our tests indicate that the only potential true host plants for *Heilipodus ventralis* in North America are five species in three genera of the tribe Astereae (family Asteraceae): *Gym. Glutinosum*, *Gut. grandis*, *Gut. microcephala*, *Gut. sarothrae* (subtribe Solidagininae), and *Grind. lanceolata* (subtribe Machaerantherinae). If released in the field, *H. ventralis* may attack and develop primarily in *Gutierrezia* since only those species are abundant and widespread. We regard the only true host-plant species of a phytophagous insect as being those on which the insect can complete its development and maintain or increase its population in successive generations. Active host selection by *H. ventralis* was determined most importantly by the ovipositing females, which was further limited by the suitability of the plant for larval development. Since the larvae develop internally in the stems, crowns, and

TABLE 8

Larval Development of *Heilipodus ventralis* in Stems of Seven Plant Species (Larval Test 1)

		Found when dissected									
		Stems dissected 5/26/82[a]				Stems dissected 4/28/83–5/2/83[a]					
				Stage reached				Stage reached			
Test plant	No. larvae tested	Avg tunnel length (cm)	No development	Sm	Med[b]	Avg tunnel length (cm)	No development	Lg	P	A	% larvae reaching at least Lg
Baccharis neglecta	9	0.7	4	1d	1a	0	3				0
Grindelia chiloensis	8	3.9			3d	13.5	3	2			25
Gutierrezia sarothrae	16	2.3	1		2d, 2a	6.7	5		1	5	37.5
Gut. microcephala	41	2.5	1		3a	7.4	27	4	1	5	24.4
Gym. glutinosum	1					0	1				0
X. palmeri	1					0	1				0
I. coronopifolia	15					0	15				0

[a] Sm, small; Med, medium; Lg, large larvae; P, pupa; A, adult; a, alive; d, dead.
[b] All living larvae transferred to a fresh plant; one of those from *Gut. sarothrae* was among the five that produced adults; three of those from *Gut. microcephala* were among those that produced a large larva and two adults.

roots, they have no mechanism of host selection other than survival or death. Thus, feeding by adults on *Chrysanthemum* and some other plants was unimportant because females did not oviposit on these plants. Oviposition on *Baccharis, Xylothamia, Chrysothamnus,* and some other plants was unimportant because larvae did not develop in these plants. Larval development in *Brickellia* was unimportant because females did not oviposit on this plant.

In our tests, host specificity of *H. ventralis* increased through the stages of adult feeding, ovipositional selection, and larval development. Adults fed on a rather broad range of test plants, which encompassed 24 species in 14 genera of all four tribes of Astereae plus Heliantheae, Vernoninae, and Anthemideae among the 40 species of Astereaceae that we tested. However, most of the feeding was on 11 species of *Grindelia, Gymnosperma, Gutierrezia, Isocoma, Xylothamia,* and *Chrysothamnus* of the two subtribes Solidagininae and Machaerantherinae and on *Baccharis* (subtribe Baccharidinae) all in the tribe Astereae, plus *Chrysanthemum* in the tribe Anthemideae. We did not know precisely how much the adult weevils ate when they cut leaves from the plants, which was nearly always the case when they fed on *Gutierrezia* spp. We conservatively assumed that they ate 1 mm^2 per leaf but we could as well have assumed more, perhaps 2 mm^2 per leaf; this would have greatly increased the apparent relative adult feeding preference for *Gutierrezia* in our tests but would not have influenced the amount we report on the other plant species. Oviposition was concentrated more on the species of Solidagininae and Machaerantherinae plus a small amount on one species of *Baccharis.* Females always laid the most eggs on species of the three genera, *Grindelia, Gutierrezia,* and *Gymnosperma.* Very little or no oviposition occurred on any other test plants in other subtribes or tribes and no eggs were laid on *Chrysanthemum,* which was a potential adult feeding host. Larval development was concentrated even more on the preferred genera, *Gutierrezia, Gymnosperma,* and *Grindelia.*

The moderate larval development on *Chrysothamnus* and *Machaeranthera* suggest that they might be occasional hosts and the small amount on *Aster* that it might rarely be a host. None of those genera contain species that are economically beneficial or of notable benefit in the natural environment, but all contain some weedy species. The host preference shown by *H. ventralis* in our tests and by the studies in Argentina (Cordo, 1985) suggests a close taxonomic relationship between *Gutierrezia* and *Grindelia* more similar to that proposed by Lane (1985) than to that proposed by Nesom (1994). Results in Argentina, from both field surveys of potential host plants and of laboratory host-range tests, confirm our host-range measurements.

We experienced considerable difficulty in conducting the larval tests. A lower percentage of larvae completed their development and pupated in the better hosts than we expected. We attributed this mostly to the unnatural holding conditions during the 12-month or more life cycle of the insect inside the plant stems. These desert plants are difficult to transplant from the field and are difficult to maintain in good condition in pots for the more than 1 year as required for the tests in the quarantine greenhouse. However, in the first test (Table 8) we obtained good results, with 24 to 38% of the neonates reaching at least large larvae, and 10 adults and two pupae were recovered; number of eggs laid per female also was substantially greater in this test. We cannot explain why development did not proceed as

TABLE 9

Larval Development of *Heilipodus ventralis* in 29 Species of Asteraceae

			Found when dissected					
					No. reaching stage:			
Test plant	Included in larval test no.	No. larvae tested	Mean tunnel length (mm) (range) n[a]	No. larvae missing	Small larvae (dead)	Med. larvae or larger (alive)[b]	Mean stage completed (±SE) (n)[c]	% alive when dissected
Tribe Eupatoriaeae								
Brickellia laciniata	5	11	35.9 (0–197) 11	2	7	2FG	0.89 ± 0.89 (3)abc	18.2
Tribe Astereae								
Subtribe Baccharidinae								
Baccharis biglovii	4	2	39.0 (33–45) 2		2		0.00 ± 0.00 (1)	0.0
B. brachyphylla	2	2	0	2			0.00 ± 0.00 (1)	0.0
B. pilularis	4	2	14.5 (12–17) 2	1	1		0.00 ± 0.00 (1)	0.0
B. halimifolia	2, 3, 4	13	15.6 (1–48) 8	8	5		0.00 ± 0.00 (5)c	0.0
B. sarothroides	2, 4	6	0	3	3		0.00 ± 0.00 (2)	0.0
B. neglecta	2, 3, 4, 5	13	4.0 (1–12) 8	4	9		0.00 ± 0.00 (6)c	0.0
B. salicifolia	2, 4, 5	18	5.7 (1–11) 15	3	15		0.00 ± 0.00 (7)c	0.0
Subtribe Machaerantherineae								
Grindelia squarrosa	5	2	13.5 (2–25) 2		2		0.00 ± 0.00 (1)	0.0
Gr. lanceolata	2, 3, 4, 5	10	66.0 (10–115) 7	5	3	1-FG, 1A	1.20 ± 0.80 (5)ab	20.0
Isocoma coronopifolia	2, 3, 4, 5	13	12.2 (1–32) 6	6	7		0.00 ± 0.00 (5)c	0.0
I. pluriflora	5	7	12.2 (1–32) 6	4	3		0.00 ± 0.00 (3)c	0.0
Machaeranthera pinnatifida	5	6	45.3 (1–213) 5	2	3	1-FG	0.67 ± 0.00 (1)	16.7
Subtribe Solidagininae								
Gymnosperma glutinosum	2, 3, 4	6	51.6 (2–140) 5	1	2	1-Med, 2-FG	1.75 ± 1.03 (4)a	50.0
Gutierrezia sarothrae	2, 3, 4, 5	16	20.9 (1–105) 13	4	9	2-Sm, 1A	0.40 ± 0.28 (7)bc	18.75
Gut. microcephala	2, 3, 4, 5	23	37.4 (1–125) 12	5	13	3-Sm, 2-Med	0.30 ± 0.16 (8)bc	21.7
Gut. grandis	2, 3, 4	8	72.8 (50–94) 5	3	2	1-Med, 2-FG	1.40 ± 0.75 (5)a	37.5
Chrysothamnus nauseosus	2, 3, 4, 5	22	28.9 (1–133) 17	3	16	2-Sm, 1-FG	0.33 ± 0.25 (8)bc	13.6
Xylothamia palmeri	2, 3	6	0	4	2		0.00 ± 0.00 (2)	0.0
Solidago altissima	2, 3, 5	7	18.3 (1–50) 5	5	2		0.00 ± 0.00 (5)c	0.0
Subtribe Asterinae								
Aster preaealtus	5	5	45.3 (1–78) 5	3	1	1-Med	0.22 ± 0.22 (3)bc	20.0
Tribe Heliantheae								
Subtribe Ambrosiinae								
Parthenium argentatum	2, 3, 4	12	0	7	5		0.00 ± 0.00 (4)c	0.0
P. incanum	2, 3, 4, 5	15	1.0 (1–1) 3	9	6		0.00 ± 0.00 (6)c	0.0
Subtribe Helianthinae								
Viguiera stenoloba	5	4	1.0 (1–1) 3		4		0.00 ± 0.00 (2)	0.0
Helianthus ciliaris	2, 3, 4, 5	16	19.7 (3–59) 6	10	6		0.00 ± 0.00 (7)c	0.0
Tribe Anthemideae								
Artemisia filifolia	2, 3, 4, 5	20	3.9 (1–11) 11	5	15		0.00 ± 0.00 (8)c	0.0
A. tridentata	2, 3	3	0	3			0.00 ± 0.00 (2)	0.0
Chrysanthemum × morifolium	5	2	26.1 (1–51) 2	1	1		0.00 ± 0.00 (2)	0.0
Tribe Senecioneae								
Senecio douglasii var. *longilobus*	5	4	2.5 (1–5) 4		4		0.00 ± 0.00 (2)	0.0

[a] Data from stems with no tunnels are included.

[b] Sm, small; Med, medium; FG, full-grown larvae or prepupa; A, adult.

[c] *n*, Number of plants tested (plants had from 1 to 3 larvae each); missing larvae assumed to have not developed beyond the first instar. Stage completed equals stage found when dissected less 1: first instars dead or alive, 0; small larva, 1; medium larva, 2; large larva, 3; full-grown larva, 4; pupa, 5; adult, 6. Calculation of mean stage completed is based on the mean of the average stage reached by all of the 1 to 3 larvae found on each plant when dissected (not shown), not on the simple mean of all larvae and adults found. For example, mean stage completed on *Gut. grandis* of 1.40 signifies that the average larva found had completed the small larval stage (scored 1) and was 0.4 of the way toward the medium stage; this value included the 2 dead first instar larvae (scored 0), the 1 medium larva (scored 2), and the 2 full-grown larvae (scored 4) found at dissection. Values followed by the same letter are not significantly different ($P < 0.05$) according to Fisher's protected LSD test; plants were tested for statistical differences only if *n* (number of plants tested) was greater than 2.

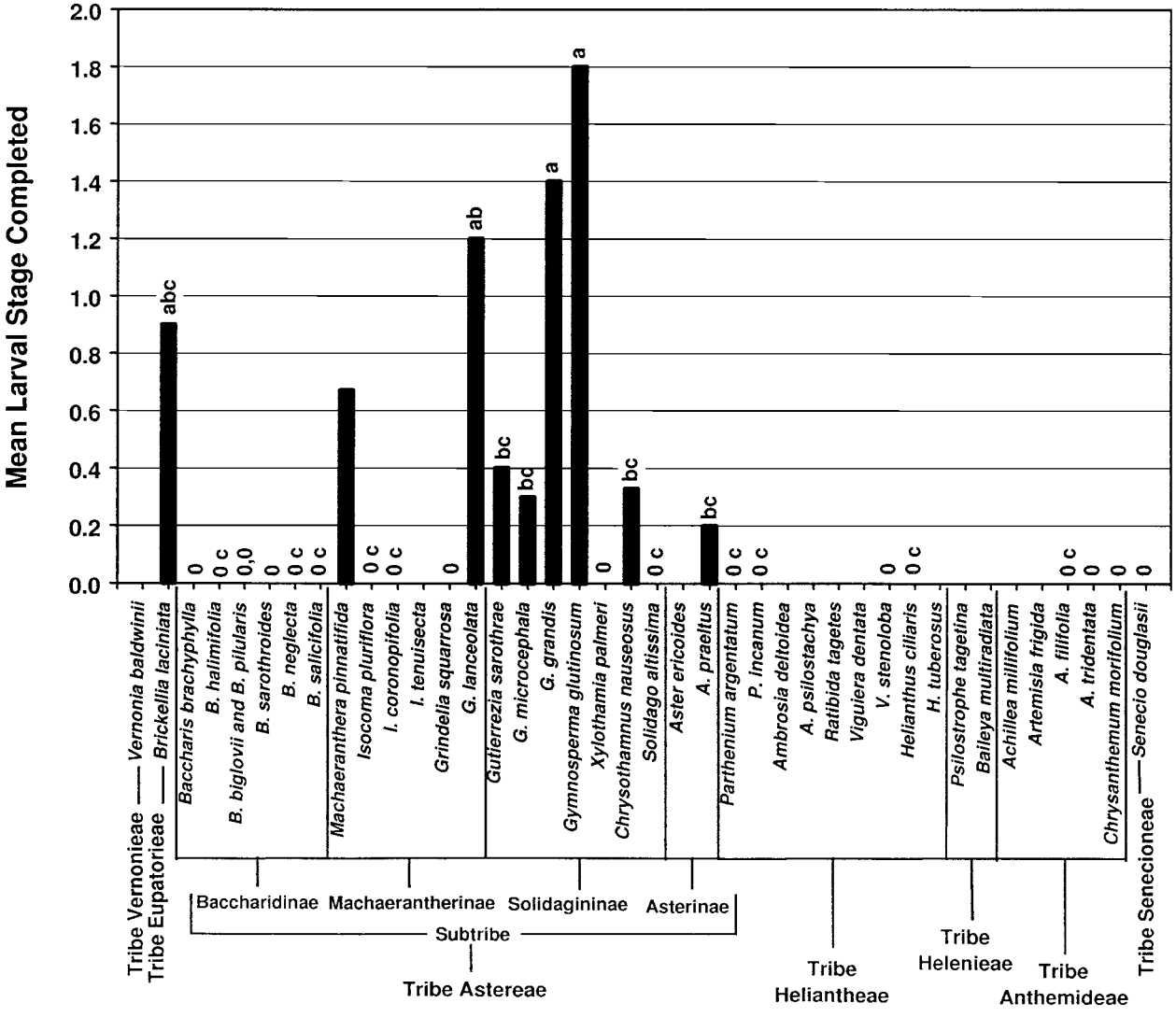

FIG. 4. Developmental state attained by larvae in stems of 29 species of potted test plants when examined after 12 to 14 months. Plants tested for statistical differences only if *n* (number of plants tested) was greater than 2; 0, no development; plants with no symbol were not tested but are listed for alignment of the graph with the feeding and oviposition tests. Plants followed by the same letter are not statistically different ($P < 0.05$) according to Fisher's protected LSD test. (Data from Table 9.)

well in the later tests. However, both plants and insects used in the later tests were collected from different locations in Argentina and our test plants also were collected from different sites in the United States. Also, this was the only test we conducted in which part of the weevils were collected from *Gut. spathulata* in Argentina. Adult no-choice Test 7 and Larval Test 1 were the only tests using weevils collected at Puerto Pirámides, Argentina; also, Larval Test 1 used eggs from these field-collected adults, whereas Larval Tests 2 and 5 and Adult Tests 1 to 6 all used weevils reared from field-collected larvae that were reared on antifungal artificial diet at Hurlingham. This raises questions about whether the nutrition or holding conditions of field-collected larvae may have affected the performance of the reared adults and of the eggs and larvae reared from them. Perhaps if neonate larvae were obtained from field-collected adults in Argentina, especially those from Puerto Pirámides, a greater number might complete their development in the North American snakeweeds. However, Larval Tests 3 and 4 also used eggs obtained from field-collected adults (from Arroyito, Neuquén and San Antonio Oeste, Río Negro) and these did not perform better than those reared from field-collected larvae used in Larval Tests 2 and 5. However, Cordo (1985) and Cordo *et al.* (1999) could not detect biotypic differences in host preference between weevils reared from *Grindelia* or those reared from *Gutierrezia* (collected at San Antonio Oeste and at Arroyito) in Argentina. When released in North America, *H. ventra-*

lis may establish with varying success on biotypes of host plants growing in different areas.

GENERAL DISCUSSION

The "Endemoclassical" Approach for Controlling Native Weeds

The classical approach to biological control of weeds has been used since the control of prickly pear cactus in Ceylon (Sri Lanka) in 1865. Since then it has been applied with great success against many weeds in many areas of the world, including North America (Goeden, 1978; Schroeder, 1983; Kelleher and Hulme, 1984; Funasaki *et al.*, 1988; Hoffman, 1991; Julien, 1992; Nechols *et al.*, 1995). This approach involves searching for, testing, and releasing foreign control agents (historically, mostly insects) to control exotic invading weeds (Huffaker, 1957; Harley and Forno, 1992).

Several species of woody, native plants have increased enormously in density in southwestern rangelands to become damaging weeds of major importance during the past 150 years; these include snakeweeds, mesquites (*Prosopis* spp.), creosotebush (*Larrea* sp.), huisache (*Acacia* spp.), and others (Humphrey, 1958; Buffington and Herbel, 1965). The major causative factors in the increases in population density of these weeds are probably related to the grazing livestock industry (especially overgrazing of rangelands), to the 30% increase in atmospheric carbon dioxide (which favors snakeweeds and other shrubs over warm-season grasses) (Johnson *et al.*, 1993), to periodic droughts, and to the near elimination of rangeland fires (Humphrey, 1958; Buffington and Herbel, 1965). These factors have area-wide effects, and biological control, which also has area-wide effects, could be the method of choice for control of some of them (DeLoach, 1978, 1981, 1995). Although poor management may be one of the major causes of the problem, experience has shown that improved management does not eliminate the problem and damaging weed populations persist (Jameson, 1970).

Exotic plants become weedy primarily because they are introduced without the guilds of natural enemies that keep their populations in balance within their area of native distribution. Native plants become weedy primarily because of human-produced changes in the environment. Both types of weeds can be controlled effectively and safely by the introduction of exotic natural enemies of the weed, following the established methodologies, protocols, and safeguards of biological control (DeLoach, 1995). However, native weeds always have been considered more difficult to control with introduced control agents and to involve more conflicts of interest between the beneficial and harmful values of the weed, and therefore have been little considered for biological control. At this laboratory, we are using an "endemoclassical approach" of using foreign control agents to suppress out-of-control native weeds (DeLoach, 1978, 1981, 1995). This is the first such project anywhere in the world to target native weeds in a continental area for biological control by the introduction of foreign insects.

This concept has developed gradually over the past 35 years. Hoy (1961) observed that the accidentally introduced mealybug (*Eriococcus orariensis* Hoy) had given good control of manuka weed (*Leptospermum scoparium* J.R. and G. Forster), a native small tree in New Zealand, that had become a serious weed. Simmonds and Bennett (1966) made a planned introduction of the moth *Cactoblastis cactorum* (Bergroth) from Argentina into the Caribbean island of Nevis, which controlled prickly pear cactus, which was native there. Finally, Goeden *et al.* (1967) introduced the scale *Dactylopius opuntiae* (Cockerell) into Santa Cruz Island off the coast of California, which provided excellent control of prickly pear, which was native there. All these cases were on islands, where past experience indicates that biocontrol may be easier. Such an approach in a continental area raises concerns not only about whether it would be successful but also about whether it would be safe in the natural ecosystem.

Pimentel (1963) proposed that the use of control agents from foreign areas that have never evolved with the target pest (new associations) in some cases might be excellent control agents, because they would not have evolved the homeostatic mechanisms that allow coevolved host–predator systems to coexist. This concept is key to controlling native weeds. Control agents for native weeds usually can be found only on related plant species (same genus) overseas because the weedy species itself usually does not occur outside North America. These are, by definition, "new associates." Hokkanen and Pimentel (1984) discussed several highly successful past projects on biocontrol of introduced weeds, including several projects on prickly pear cacti that illustrate the effectiveness of the concept. Several other unplanned (and unwanted) cases have demonstrated the validity of the theory of Pimentel (1963) and the efficacy of the approach, such as the "control" of the native American elm and the American chestnut in the United States and of grapes in Europe by the accidental introduction of foreign insects and pathogens through uncontrolled commerce (DeLoach, 1995). Although these are beneficial plants, the mechanism of control is the same as with weeds.

The question of safety is of much greater concern than is that of efficacy. In the beginning of our project, leading biocontrol scientists questioned whether a great reduction in density of a species in the native plant community might not have a reverberating effect throughout the food chains of many interdependent

animals and plants, with possible severe and unknown consequences in the entire biosphere. These concerns were based largely on the Clementsian theory of climax plant communities (Clements, 1920) in which each species is stable in time and space. These concerns were reviewed and effectively contested by Johnson (1985) who pointed out that the Gleasonian concept of a resilient plant community (Gleason, 1926) is overwhelmingly accepted by plant ecologists as much more closely describing the real world than is the Clementsian theory. Johnson (1985) also pointed out that the structure of North American plant communities has changed drastically during the past few thousand years and is continuing to change today, but that the essential "goods and services" of the ecosystem remain approximately constant. This does not imply that the control of a given weed might not reduce the abundance of particular animal species strongly dependent on it. Each case proposed for biological control should be examined carefully from this point of view.

Another concern in recent years is the possibility of attack by the introduced control agents on nonharmful species closely related to the target weed (Miller and Aplet, 1993; Louda *et al.*, 1997). Substantial feeding has in fact been observed in a few cases, but careful investigation has revealed no reduction in density or distribution of the native species (Turner *et al.*, 1987; Funasaki *et al.*, 1988; DeLoach, 1997; McFadyen, 1998). Some of the cases of nontarget attack by introduced biological control agents occurred because the control insects reached high population levels on the target weeds as control reached its peak; the excess insects then spilled over onto and fed on nearby plants that normally would not be hosts. Once this peak passed, both weed and control agent population declined, and nontarget attacks ceased. This form of nontarget damage sometimes can be expected with a very effective control agent but, historically, this has not resulted in permanent damage to nontarget plants. The evidence gathered by Harris (1988) indicates that a reduced level of attack would occur on rare species because of the density-dependent nature of natural enemies. The small risk of biological control, carefully considered and carefully applied, would appear to be much less than the great damage caused to both the native plant communities and to agriculture by these recently abundant weeds.

Native western rangeland plants that logically would be targeted for biological control would be only the species that have increased enormously in density and today are "out-of-control" weeds. These present-day weeds (including snakeweeds), were not overabundant until after the introduction of European livestock. The degree of control expected by biological methods would seem extremely unlikely to reduce weed abundance below the "natural" levels of pre-European settlement times. Even if we regard the state of "pre-European settlement" as the standard by which ecosystem health is measured, and that biological control might reduce the present overabundant weeds to that level, this degree of control should be considered advantageous and not dangerous to ecosystem health.

The experience in biological control of weeds since the 1960s indicates that host range of the introduced control agents can be determined with a high degree of reliability; no case of unexpected attack on nontarget plants (except of the temporary type described above), or of a change in host range after release, has been reported (Julien, 1992). The major aim of the very extensive host-range testing done both in Argentina (Cordo, 1985) and in the present study was to evaluate this risk for snakeweed control.

Application of the Endemoclassical Approach in Control of Snakeweeds

Three primary factors determine the suitability of a weed for biological control: great damage caused, small beneficial value, and a good chance for success. Snakeweeds, in their present unnaturally abundant population levels, are among the most damaging weeds of rangelands (Huddleston and Pieper, 1990) and also damage natural ecosystems, they have no notable economic or ecological beneficial value (DeLoach, 1981), and several insects have been found in Argentina that are promising biological control agents (Cordo and DeLoach, 1992). Since snakeweeds are native plants, their importance in the ecosystem must be carefully considered as well as their taxonomic affinity to other plant species that might be subjected to nontarget attack by introduced control agents (DeLoach, 1995).

Several species of snakeweeds, especially *Gutierrezia sarothrae* and *G. microcephala*, and also broomweeds in the closely related genus *Amphiachyris*, have become serious weeds under the environmental changes brought about by our agricultural and social system (DeLoach, 1995). Under "natural" (pre-European settlement) conditions these plants were not weedy. In fact, Wooten (1915) recorded that when the first settlers reached the Southwest from the eastern United States, snakeweeds were so uncommon that when they began increasing, local ranchers brought specimens to him thinking they were a newly introduced species.

Possible effects on nontarget plant species. *Gutierrezia* has 16 species native in North America (Lane, 1985). It is very closely related to the native genera *Gymnosperma* (1 sp.), *Amphiachyris* (2 spp.), and *Grindelia* (40 spp.) and is less closely related to several other genera in the subtribes Solidagininae and Machaerantherinae of the tribe Astereae, family Asteraceae. North America is probably the origin of the family Asteraceae, which is well represented here with many genera and species. Only sunflower and lettuce are

major crops, but several species are important ornamentals (Bailey and Bailey, 1976).

Our tests predict that some of the nontarget species in the genera *Gutierrezia, Grindelia,* and *Gymnosperma* may be attacked by *H. ventralis.* Annual species are unlikely to be attacked to any important degree, because the life cycle of the weevil is longer than the life cycle of the plant. The larvae probably cannot, or can only rarely, survive through the fall and winter after the annual plants die. Therefore, of the 16 species of *Gutierrezia* in North America (Lane, 1985), the six annual species, along with the two annual species of *Amphiachyris,* would be little attacked. Since two of the annuals, *Gut. texana* (DC.) Torrey and Gray and *Gut. sphaerocephala* Gray, along with the two *Amphiachyris* species, are serious rangeland weeds, any attack that might occur on them would be beneficial.

The perennials *Gut. sarothrae* and *Gut. microcephala* are very weedy and are the major targets for biological control. *Gutierrezia serotina* Green and *Gut. californica* (DC.) Torrey and Gray are also weedy although less so. *Gutierrezia alamanii* Gray and *Gut. sericocarpa* (Gray) Lane are rather widespread Mexican species which probably are not weedy, or only occasionally so. These species are sufficiently abundant and occur over a wide enough area in sufficiently diverse habitats that *H. ventralis* is not likely to threaten their existence, although it might reduce their populations. *Gutierrezia triflora* (Rose) Lane, in addition to being an annual, could also be protected because it grows only along the Texas Gulf Coast, outside the range of other snakeweeds.

The remaining four species, *Gut. petradoria* (Welsh and Goodrich) Welsh from Utah, *Gut. ramulosa* (Green) Lane from Baja California, *Gut. argyrocarpa* Greenman from Hidalgo, and *Gut. grandis* from the mountain tops of the eastern Chichuahuan Desert, although not rare, are not abundant and are not weedy. If nonabundant species are little attacked because of the density-dependent nature of their natural enemies (Harris, 1988), then several species of *Gutierrezia* and *Grindelia* could be protected from overexploitation by *H. ventralis* because they are not abundant.

The perennial *Gym. glutinosum* is a widespread, common species throughout much of Mexico to southern Arizona, New Mexico, and western Texas. It would probably be considerably attacked, but its occurrence in a wide variety of habitats would protect it from overexploitation by *H. ventralis;* it has no known value as wildlife food or for use by man.

Of the 45 species of *Grindelia* recognized by Steyermark (1934), 17 are perennials, 3 are biennials or perennials, 4 are biennials, 1 is annual or biennial, none are true annuals, and 20 were not identified as to perennation. Some of these perennial species, and possibly some of the biennials also, may be considerably attacked by *H. ventralis. Grindelia squarrosa* (Pursh) Dunal, an annual species, is a moderately serious rangeland weed in Utah and other western states. None of the species have any but very minor beneficial value. Bailey and Bailey (1976) listed nine species (including the introduced Argentine *Grin. chiloensis*) as minor ornamentals, stating they were "sometimes grown as ornamentals in regions where they grow, succeeding on poor land"; they also noted that two species are used medicinally as home remedies. Several species of *Grindelia* would be protected from overexploitation by *H. ventralis* because they are not abundant, because of spatial separation from large *Gutierrezia* populations, and because of habitat incompatibility. Examples are *Grindelia littoralis* Steyermark, which grows only in the Galveston Bay area of Texas, *Grin. oolepis* Blake, which grows on black clay soils near Brownsville, Texas, *Grin. howellii* Steyermark, which grows along the St. Maries River in Idaho, and possibly other species. The species of *Grindelia* that grow in West Coast salt marshes are also protected because *H. ventralis,* being a root-boring desert weevil, probably cannot survive in submerged roots.

Only one endangered or threatened plant species is present in any of the genera on which *H. ventralis* is expected to feed. This is the Ash Meadows gumplant, *Grindelia fraxino-pratensis* Reveal & Barneby, described by Reveal and Beatley (1971). This species would likely be protected from attack by *H. ventralis* because it grows best in water-saturated soils where the root-boring larvae of *H. ventralis* would probably drown. This plant would be further protected because only *Gut. microcephala* occurs, but is infrequent, at Ash Meadows National Wildlife Refuge, Nevada, thus precluding population buildup that could spill over onto *Grin. fraxino-pratensis.* We did not test the plant.

Effects on snakeweed consumers. We found no reports in the literature which indicated that any species of vertebrates depend to any important degree on snakeweeds or on other closely related plant genera.

In fact, few species of the family Asteraceae have any but minor value as food for wildlife, except for ragweeds whose seeds are a valuable food resource for birds (Martin *et al.,* 1951). Martin *et al.* (1951) listed *Grindelia* only once (as "gumweed"), as a minor food plant (2–5% of the diet) for the bighorn sheep, *Ovis canadensis,* in California, but did not mention *Grindelia* as a foodplant in any of the other four geographical areas listed. No endangered or threatened vertebrates are listed as consumers of snakeweeds or of the related genera *Grindelia, Gymnosperma,* or *Amphiachyris* (Anonymous, 1995; U.S. Fish and Wildlife Service, 1997).

However, some 50 species of native North American insects can feed and develop on snakeweeds (*G. saro-*

thrae and *G. microcephala*) of which ca. 15 species feed mostly or entirely on them (Richman and Thompson, 1999). Populations of some species of insects or other arthropods that feed on snakeweeds (or of the parasitoids or predators of those arthropods) probably will be reduced if biological control is successful. However, none are likely to be placed in jeopardy, even if snakeweeds are reduced to their pre-Columbian level of abundance, which we regard as highly unlikely. Other species of arthropods that inhabit the plants expected to replace snakeweeds after biological control probably will increase in abundance. No endangered or threatened species of insects or other invertebrates are listed as dependent on snakeweeds (Anonymous, 1995).

Prognosis for efficacy. The degree of control of a weed resulting from the introduction of a given biological control agent always has been more difficult to predict than has host range (McFadyen, 1998), and we do not attempt to do so here. A multitude of biotic interactions are different in the area of release than in the natural range of the control agent overseas, and at the present state of the art, their effects cannot be reliably estimated before release of the control agents. However, evidence from the field in Argentina indicates that the combined attack by *H. ventralis* (Cordo, 1985; Cordo *et al.*, 1999) and by the sesiid moth root borer, *Carmenta haematica* (Ureta) (Cordo *et al.*, 1995a,b), seriously damages roots of *Gutierrezia* spp. in Argentina and, when the plants additionally are drought-stressed, cause die-off of the plants in large areas. This is similar to the die-offs observed in New Mexico (Richman and Huddleston, 1981), which although dramatic, are too sporadic in time and space to provide sufficient control. We expect that the addition of *H. ventralis* to the guild of insects that attack snakeweeds in North America will increase the amount of control currently provided by only the native insects.

In Argentina, snakeweeds never attain a density of more than 10 to 30% that of the dense stands often seen in the United States. The causes are incompletely known, but in Argentina grazing intensity probably is less, the snakeweed species are different and maybe less aggressive, the climate and soil (though similar) are somewhat different, and the snakeweeds are attacked by guilds of insects different from those in North America. More than 50% control of snakeweeds in the United States by the introduction of *H. ventralis* is unlikely and greater control probably would require the introduction of some of the additional natural enemies found in Argentina by Cordo and DeLoach (1992).

The most likely (and the intended) consequence of biological control of snakeweeds (if successful) is that the affected native plant communities in both rangelands and natural areas will be improved by the reduction in competition from the presently overabundant snakeweeds. Such an increase in biodiversity and abundance of native grasses and forbs was well documented following biological control of St. Johnswort (*Hypericum perforatum* L.) in California (Huffaker and Kennett, 1959). Snakeweeds themselves would be substantially reduced in abundance, but would not be threatened with eradication, which has never occurred in the history of biological control of weeds (Julien, 1992). Some nontarget species in the genera *Grindelia* and *Gymnosperma* also may be reduced in population but, again, not to critical levels.

Based on our research, and that in Argentina (Cordo, 1985; Cordo *et al.*, 1999), a petition was submitted to the Technical Advisory Group on the Introduction of Biological Control Agents of Weeds, of USDA-APHIS, in April 1987, requesting permission to release *Heilipodus ventralis* in the field. The petition was approved December 1, 1987, and releases began in early summer, 1988. To date, establishment of *H. ventralis* on snakeweeds or on any nontarget plants has not been confirmed and no further releases are planned at this time. Our attempts to establish it in the field are the subject of another paper, now in preparation. Under the present climate of concern about harm to nontarget plants, even if they are somewhat weedy and have (as *Grindelia*) little or no beneficial values, probably only a control agent with a more restricted host range can or should be released.

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