SYSTEMATICS

Life History of *Megamelus scutellaris* with Description of Immature Stages (Hemiptera: Delphacidae)

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Ann. Entomol. Soc. Am. 98(1): 66–72 (2005)

ABSTRACT The five immature stages of *Megamelus scutellaris* Berg (Hemiptera: Delphacidae) are described and illustrated. The main characters that distinguish the various stages are body size, number of tarsomeres and tibial spines, color, and number of teeth on the metatibial spur. New biological data based on laboratory rearing and field observations show that *M. scutellaris* can carry out its biological cycle successfully on water hyacinth, *Eichhornia crassipes* (Martius) Solms Laubach (Pontederiaceae). Mating occurs close to the water level and one to four eggs per scar are laid in apical portion of petiole and pseudolaminae. Ovipositional scars are recognized by three parallel marks. In addition, the efficient rearing in captivity, the high survivorship registered, and overwintering on only water hyacinth suggest *M. scutellaris* as a potential biocontrol agent of this invasive aquatic weed.

KEY WORDS biological control, *Eichhornia crassipes*, immature stages, *Megamelus scutellaris*, water hyacinth

THE CENUS *Megamelus* Fieber 1866 (Hemiptera: Delphacidae) includes 24 species in the Americas, of which five are found in the Neotropical region: *M. bifurcatus* Crawford, *M. iphigeniae* Muir, *M. electrae* Muir, *M. timheri* Muir, and *M. scutellaris* Berg (Asche 1985). Although there are limited biological data on species of this genus, it is known that some of them are associated with aquatic plants (Au 1941, Wilson and McPherson 1979, O'Brien and Wilson 1985, and Wilson et al. 1994). Only the life cycle of the North American *M. davisi* Van Duzee on water lily *Nuphar advena* (Aiton) has been studied in detail (Wilson and McPherson 1981a, b).

Among South American *Megamelus*, only two species, *M. electrae* in Trinidad and Tobago (Cruttwell 1973) and *M. scutellaris* in Peru, Brazil, Uruguay, and Argentina (Sosa et al. 2004), are associated with *Eichhornia crassipes* (Martius) Solms-Laubach (Pontederiaceae), commonly called water hyacinth. This plant is an invasive aquatic tropical species native to the Amazonian and Paraná basins in South America. It is considered the most serious aquatic weed in the invaded areas of the tropical and subtropical regions (United States, Central America, Australia, Papua New Guinea, southeastern Asia, Africa, and southwestern Europe) (Gopal 1987, Julien et al. 1999, Julien 2000). Recently, the diagnostic characters, winged forms, and records from Argentina, Uruguay, Brazil, and Peru of *M. scutellaris* have been considered (Sosa et al. 2004). Because *M. scutellaris* reaches high densities on the native range of water hyacinth (unpublished data) and may be considered a potential biological agent, further biological information is required.

This article contributes to the knowledge of the biology and postembryonic development of *M. scutellaris* based on laboratory rearing and field observations.

Materials and Methods

Laboratory Rearing

In a 3-yr period (1999–2001), adults and nymphs of *M. scutellaris* were periodically collected by aspirating on water hyacinth in Argentina, Brazil, and Peru and used to establish a laboratory colony. Several generations were reared in two cages (61 by 61 by 61 cm), in outdoor conditions, on *E. crassipes.* Plants were added every week or when required.

Morphological Studies

The description of each stage was based on 24-h hatched nymphs from the laboratory colony. Specimens were anesthetized with 95% ethyl ether to register coloration, and then cleared in cold 10% KOH solution and fixed in Faure liquid for microscopic examination and illustration. Scanning electron microscopy was used to illustrate some cephalic sensorial structures: nymphs were cleaned by soaking in chlo-

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Fig. 1. M. scutellaris eggs. Bar, 0.5 mm.

Once adult, the parasitoid specimens were preserved in 70% ethyl alcohol and sent for identification.

In the descriptions, the average is expressed as mean \pm SE.

All specimens studied were deposited at Museo de Ciencias Naturales de La Plata.

Specimens Examined. ARGENTINA: Formosa Province, Comandante Fontana, Rt 81, 16-XII-1998, two nymphs III, one nymph IV, six nymphs V, Sosa & Cordo col; Palo Santo, Rt 81, 16-XII-1998, one nymph I, one nymph II, one nymph III, five nymphs IV, 19 nymphs V, Sosa & Cordo col; Riacho He He Chico, 26-XI-1995, two nymphs IV, five nymphs V, Cordo col; Chaco Province, Traffic circle, junction Rt 16 and Rt 11, 13-XII-1998, two nymphs I, one nymph II, three nymphs III, six nymphs IV, nine nymphs V, Sosa & Cordo col; Rt 5, 7 km southwestern Río Bermejo, 15-VII-1998, two nymphs I, two nymphs IV, two nymphs V, Sosa & Cordo col; Santa Fe Province, Rt 168 9 km east Río Colastiné, 31-X-2000, two nymphs I, one nymph II, one nymph III, two nymphs IV, Sosa & Cordo col; Buenos Aires Province, Baradero, Baradero River, 26-XII-1998, two nymphs V, Hernández col; INTA Delta, 09-XI-1999, one nymph V, Sosa, Cordo & Hernández col; INTA Delta, 09-XI-1999, one nymph V, Sosa & Cordo col; San Pedro, 29-X-1999, three nymphs V, Sosa & Cordo col; Hurlingham, SABCL, 04-II-2000, three nymphs I, two nymphs II, three nymphs III, four nymphs IV, 10 nymphs V, Sosa col. PERÚ: Iquitos, Muringo Cocha, 27-IV-1999, three nymphs III, 10 nymphs IV, 24 nymphs V, Cordo col. BRAZIL: Paraná, outskirts of Foz do Iguaçu, road to international border with Argentina, 22-IV-2000, one nymph I, one nymph II, two nymphs III, one nymph IV, Sosa & Cordo col.; Rio Grande do Sul, BR 116 outskirts of Guaiba, 9-IV-2000, one nymph II, three nymphs III, 16 nymphs IV Sosa & Cordo col., Rio do Janeiro, Cabo Frio, 16-I–V-2000, one nymph I, two nymphs II, Sosa & Cordo col; Sao Paulo, SP 55, 4 km western Humaita, 13-IV-2000, one nymph V, Sosa & Cordo col; Sao Paulo, SP 55, Jaguehy, 13-IV-2000, two nymphs II, one nymph III, four nymphs IV, two nymphs V, Sosa & Cordo col.

roform (3 min) and washing twice in 70% ethanol, afterwards they were dehydrated by placing them in increasing concentrations of ethanol and finally the critical-point technique (dried and coated with a 65–70- μ m gold-palladium film) was used.

The first instar is described in detail; only major changes that differ from the previous instars are highlighted in the later stages. The brachypterous form of the fifth instar is described from laboratory colony specimens and the macropterous form from field specimens. The reported measurements derive from 10 specimens of each sex and winged form and are given in millimeters. The dimensions are expressed as total body length (L) from the tip of the vertex to the distal apex of the abdomen; width (W), measured across the widest part of the metathorax; and thoracic length (TL), from the anterior margin of the pronotum to the posterior margin of the metanotum. The nomenclature for arrangement of pits follows Vilbaste (1968). Drawings were made with the aid of a camera lucida on a Leica stereomicroscope.

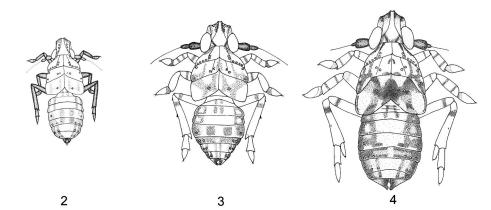
Biological Studies

Fifth instars of *M. scutellaris*, collected in Isla Talavera in January 2004 (Buenos Aires Province, Argentina), were isolated in small plastic containers (10.5 cm in diameter by 6.3 cm in depth) in a rearing chamber at 25°C, 80% RH, and a photoperiod of 14:10 (L:D). Ten groups of newly emerged adults, each consisting of four planthoppers of each sex, were placed for 3 d on a water hyacinth in plastic containers (40 cm in length by 30 cm in width by 25 cm in depth) with 10-cm soil and filled with water. Each group was put in separate cages (61 by 61 by 61 cm) and kept in outdoor conditions. To register mating, daily observations were made.

The oviposition samples were made in outdoor conditions $\approx 25.9^{\circ}$ C (range 12.9–38.7°C) from 6 to 12 January 2004. Ten groups of three 4-d-old fertilized females were isolated in the apical portion of two petioles of water hyacinth in plastic cylinders (7.8 cm in diameter by 13.9 cm in length) closed at both extremes with pieces of fine mesh gauze covering $\approx 50 \text{ cm}^2$ of the stem. Twice a day the mesh was sprayed with water to maintain high humidity. Number and distribution of eggs and oviposition scars were obtained by removing the plant tissue after 6 d.

To study the life cycle, leaves with oviposition scars were taken from the laboratory colony. Because eggs failed to hatch after being removed from plant tissue, these leaves were kept in separate petri dishes in rearing chamber (photoperiod of 14:10 [L:D]) at $25 \pm 0.5^{\circ}$ C and 80% RH until egg hatch. Fifty newly emerged nymphs were arbitrarily chosen and reared in groups of five in 10 plastic containers (10.5 cm by 6.3 cm), with moistened paper on the bottom. Leaves, or pieces of leaves of water hyacinth, were used daily as food. Duration and survival of each immature stage was recorded.

Eggs and nymphs from the field and laboratory were examined daily to detect parasitoids. Those with sacs were isolated and observed until the larval emergence.



Figs. 2–6. Immature stages of *M. scutellaris*, dorsal view. (2) First instar. (3) Second instar. (4) Third instar. (5) Fourth instar. (6) Fifth instar. Bar, 1 mm.

Results

Morphological Studies

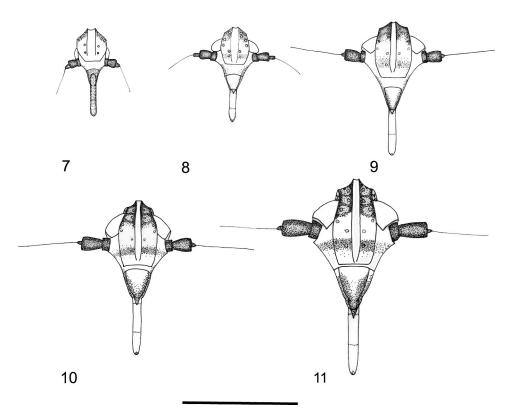
Eggs. (Fig. 1) L: 0.97 ± 0.06 , W: 0.20 ± 0.01 .

Eggs ellipsoidal with cephalic apex sharp and opposite end rounded; ventral surface slightly concave, dorsal convex. Color milky white when laid, turning yellowish white before hatching. Chorion translucent, smooth.

First Instar. (Fig. 2). L: 0.92 ± 0.02 ; W: 0.32 ± 0.02 ; TL: 0.34 ± 0.01 .

Pale yellowish body with light brown markings, legs brown and eyes red. Light brown on fastigium between median and lateral carinae of frons, clypeus, labrum, rostrum, two vertex posterolateral spots, two pronotum anterolateral spots and four metanotum longitudinal stripes; brown on antennae, legs (except from middle portion of pro and mesocoxae), abdominal segments VI to IX, medial marks on I, II, III, IV, and VII; and four lateral marks aligned longitudinally on VIII.

Elongated subcylindrical in form, widest across metathorax. Vertex longer than broad (1.6:1), posterior margin straight, lateral margins carinate; projecting beyond eyes about one-half its length. Frons oval, convex in profile; as long as wide; tricarinate, two median carinae, not reaching apical margin with distance between them shorter than distance between lateral carinae and eyes. Clypeus convex, broader than long, narrowing distally (Fig. 7). Rostrum three-segmented, extending beyond mesocoxae, segment I almost completely obscured by anteclypeus, II and III



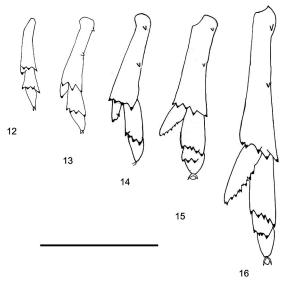
Figs. 7-11. Immature stages of *M. scutellaris*, front view of head. (7) First instar. (8) Second instar. (9) Third instar. (10) Fourth instar. (11) Fifth instar. Bar, 1 mm.

subequal. Antennae three-segmented, relatively long, without sensory pits; segment I short; II subcylindrical, as long as wide; III bulbous basally bearing a plaqueorgan, ending in an elongated bristle as long as pronotum + mesonotum.

Thoracic nota divided into three pairs of plates by longitudinal mid-dorsal line. Pronotal plates subtrapezoidal, lateral carinae divergent, slightly convex toward posterior margin. Mesonotum and metanotum plates subrectangular, posterior margin convex, metanotum longer laterally. Legs subcylindrical (Fig. 12); metatrochanter bearing cuticular folds medially; metatibiae unarmed laterally, bearing apical row of three black-tipped spines and a short, moveable subconical spike-like spur; spur slightly longer than longest apical spine, without marginal teeth. Tarsi twosegmented; protarsi and mesotarsi with divisions between tarsomeres obscure, metatarsomeres equal in length, metatarsomere I bearing apical row of four black-tipped spines, with external longest; tarsomeres II of all legs subconical, slightly curved, with pair of black claws and pulvilli apically.

Abdomen nine-segmented, subcylindrical, getting wider in segments III to V; IX elongate vertically, surrounding anus. Segments III to IX with tergites curving around lateral margins to ventral side.

Arrangement of pits (Figs. 2 and 7). Head: four on vertex, behind lateral carinae, four on fastigium, eight on frons, a medium pair near lateral carinae and more ventral pair near submedian carinae. Thorax: 12 on pronotum, two between midline and carinae, four between carinae and lateral margin bordering posterior margin; eight on mesonotum, two on each side of midline, four on antero-lateral and postero-lateral angles; two on met-



Figs. 12–16. Apical portion (from tibiae) of hind leg of immature stages of *M. scutellaris*. (12) First instar. (13) Second instar. (14) Third instar. (15) Fourth instar. (16) Fifth instar. Bar, 0.5 mm.

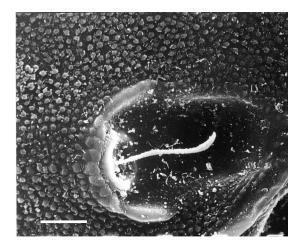


Fig. 17. Scanning micrograph of a sensory pit of the mesonotum of the second instar of M. scutellaris. Bar, 10 μ m.

anotum on both sides of midline. Abdomen: tergum of segments V: 1 + 0; VI to VIII: 1 + 1 and IX: 3 + 3.

Second Instar. (Fig. 3). L: 1.12 \pm 0.02; W: 0.46 \pm 0.02; TL: 0.37 \pm 0.01.

Body pale yellow, heavily marked in brown. Legs yellowish, pale brown annular stripes in middle of procoxa and mesocoxa, base of trochanter, apex of femur, base and apex of protibiae and mesotibiae, base of metatibiae, and base of tarsi.

Vertex twice as long as wide. Frons broadest just beneath eyes; median carinae conspicuous, slightly divergent in basal third, convergent apically. Rostrum segment II slightly longer than III. Antennal segment II narrower than I, 1.5 times longer than wide, bearing two sensory pits (Fig. 8).

Mesonotum with lateral carinae divergent posteriorly. Metatibiae bearing two small black-tipped spines on lateral margin, one near base, other nearly midlength; spur twice length of longest apical spine, bearing one apical tooth. Tarsi with visible divisions between tarsomeres. Metatarsomere I bearing apical row of four black-tipped ventral spines (Fig. 13).

Arrangement of pits (Figs. 3 and 8 and 17): as for first instar except 10 on frons (adding a lower pair); abdominal segment VIII: 1 + 2.

Third Instar. (Fig. 4). Measurements. L: 1.38 ± 0.17 ; W: 0.60 \pm 0.01; TL: 0.53 \pm 0.03.

Coloration similar to former instar but darker, two transversal stripes on frons, a dark broad stripe below the eyes and a whitish one on frontoclypeal margin. A distinguishable V-like brown spot on mesonotum and metanotum.

Frons longer than wide (1.5:1). Length antennal segment II twice its width, bearing four sensory pits (Fig. 9).

Mesonotal wingpads posterolaterally lobate, reaching basal third of metanotum; posterior margin straight. Metanotum slightly longer than mesonotum at midline, wingpads posterolaterally lobate.



Fig. 18. Dorsal view of fifth-instar antenna of *M. scutel*laris. Bar, 100 μ m.

Metatibiae bearing apical row of four black-tipped ventral spines; spur slightly flattened, as long as twothirds of metatarsomere I, bearing one apical and one or two marginal subapical teeth. Metatarsomere I bearing apical row of five black-tipped, ventral spines (Fig. 14).

Arrangement of pits (Figs. 4 and 9): similar to former instars, except 12 on frons (adding the other pair, completing the total number of frontal pits).

Fourth Instar. (Fig. 5). Measurements. L: 1.56 ± 0.07 ; W: 0.74 ± 0.04 ; TL: 0.66 ± 0.08 .

Coloration pattern similar to former instar but darker.

Frons longer than wide (1.6: 1). Antennal segment II increasing to eight sensory pits (Fig. 10).

Mesonotal wingpads extending more than one-third of length of midline, covering one-half of metanotum plates laterally; metanotal wingpads extending to first abdominal segment.

Metatibiae bearing five apical spines; spur length >two-thirds metatarsomere I, bearing apical tooth and row of three to five marginal teeth; metatarsi with tarsomere I bearing an apical row of five black-tipped ventral spines; tarsomere II with row of three weakly developed black-tipped ventral spines near middle of partially subdivided tarsomere (Fig. 15).

Arrangement of pits (Figs. 5 and 10): similar to former instars, adding two on both sides of lateral carinae of mesonotum.

Fifth Instar. (Fig. 6) Measurements. L: 2.37 ± 0.09 ; W: 1.07 ± 0.06 ; TL: 0.87 ± 0.01 .

Coloration pattern similar to former instar but darker.

Head considerably longer than previous instars. Frons twice as long as wide, parallel submedian carinae approaching each other, convergent at apical margin. Antennal segment II with 12 sensory pits (Figs. 11 and 18).

Wingpads lobate, brachypterous form with mesonotal wingpads slightly overlapping metanotal plates, metanotal wingpads extend to third abdominal segment (Fig. 6). Macropters with wingpads much more developed, narrower and longer, with mesonotal extending laterally to apex of metanotal wingpads, metanotal reaching fourth abdominal segment.

Spur foliaceous, shorter than basal metatarsomere, 5 times longer than broad at base, 5–8 marginal blacktipped teeth of varying size. Metatarsi three-segmented, tarsomere I bearing ventral apical row of six black-tipped spines and II bearing four ventral blacktipped spines, tarsomere III similar to earlier instar (Fig. 16).

Arrangement of pits: similar to former instar (Figs. 6 and 11).

Key to Instars

- Metatibia with two lateral spines on shaft. Metatibial spur >2 times length of longest apical spine (Figs. 13–16). Antennal pedicel with several sensorial pits (Fig. 18) 2
 - Metatibia without lateral spines on shaft (Fig. 12). Metatibial spur less 2 times length of longest apical spines. Antennal pedicel without sensorial pits
- Metatibial spur without marginal teeth (Fig. 13). Metatarsomere I with apical transverse row of four spines second instar
 - Metatibial spur with one or two marginal teeth (Fig. 14). Metatarsomere I with apical transverse row of five spines third instar
- 4. Metatibial spur with three to five marginal teeth (Fig. 15). Mesonotal wingpads covering half of metanotum plates laterally (Fig. 5). fourth instar
 - Metatibial spur with five to eight marginal teeth (Fig. 16); mesonotal wingpads overlapping
 - metanotal plates (Fig. 6) fifth instar

Biological Studies

Mating occurs on the bottom of the plant, close to water level. A few days after mating, females lay one to four eggs per scar into the septa of aerenchyma in apical portion of petiole and pseudolamina of water

Table 1. Egg distribution per oviposition scar from 30 females during 6 d in 50 $\rm cm^2$ of water hyacinth petiole

 One	Two	Three	Four
egg/scar	eggs/scar	eggs/scar	eggs/scar
142 39.6	194 54.0	9 2.5	

hyacinth (Fig. 19a). Ovipositional scars are characterized by three recognizable parallel marks, which turn dark brown after ≈ 3 d. The eggs are aligned with the shortest central mark (Fig. 19b).

According to the observations on the oviposition pattern test, the three-female group laid 30.8 ± 4.9 eggs in 17.9 ± 2.7 oviposition scars; most frequently recorded were two egg scars (54%), less frequent one egg scar (39.6%), and rarely three and four egg scars (2.5 and 3.9%, respectively) (Table 1). Egg density was 4.1 ± 0.7 eggs/cm², and density of ovipositions scars was 0.7 ± 0.1 scars/cm².

Nymphs emerge after ≈ 7 d, covered by an embryonic membrane that is left behind when the nymph escapes the plant tissue (an intermediate molt). The first instars were frequently found feeding in groups near the water hyacinth pseudolamina.

According to laboratory observations, the entire immature stage lasts ≈ 15 d under controlled conditions (Table 2), whereas in outdoor conditions it lasts ≈ 25 d. Only brachypterous forms were obtained under controlled conditions. From May to August, in localities in Argentina, water hyacinth decays due to frost but the base of the plant remains protected by litter where the planthoppers reside. The immature stages of *M. scutellaris* represent by far the most abundant stage collected overwintering. This suggests that this planthopper could overwinter as nymphs, at least in the prospected area.

Two species of parasitoids, *Gonatopus hilaris* Olmi (Hymenoptera: Dryinidae) and *Kalopolynema poema* Triapitsyn and Berezovskiy (2002) (Hymenoptera: Mymaridae), were found parasitizing nymphs and eggs of *M. scutellaris*, respectively. The dryinid was observed parasitizing young nymphs of *M. scutellaris*, with the pupal cocoon attached to the upper side of water hyacinth leaves. The cocoon looks like a spider egg mass and was frequently observed in the field.

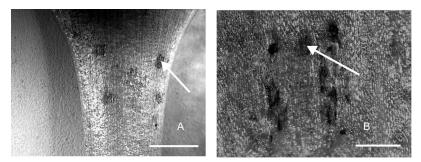


Fig. 19. Oviposition scars of *M. scutellaris*. (a) Ovipositions scars in a petiole of a leaf of water hyacinth (indicated with an arrow). Bars, 0.5 cm. (b) Magnification of one of these. The place where eggs are inserted is indicated with an arrow. Bars, 0.5 mm.

 Table 2.
 Duration (in days) and nymphal mortality of M. scutellaris under laboratory conditions

Nymph	No. nymphs	No. nymphs completing instar	Duration (d)	
	beginning instar		Range	Mean \pm SE
First	50	47	2.0-3.5	2.98 ± 0.07
Second	47	46	2.0 - 3.5	2.99 ± 0.06
Third	46	45	2.5 - 4.0	3.24 ± 0.08
Fourth	45	39	2.5 - 4.0	3.23 ± 0.07
Fifth	39	36	2.5 - 4.0	3.38 ± 0.07
Total immature stage	50	36	14.0-18.0	15.83 ± 0.21

In conclusion, immature stages of *M. scutellaris* differ from the American species M. davisi not only in the morphological features and coloration pattern but also in biological aspects. We noticed that M. davisi nymphs have a larger body size, the fourth instar has a spur with 5–10 marginal teeth, and the fifth instar has a spur with 12-19 marginal teeth. According to the coloration, the most relevant differences are frons of first instar yellow with brownish gray dorsal markings and legs yellow infused with brown, and from of second instar with a dark brown longitudinal line between each inner and outer carinae. About biological data, Wilson and McPherson (1981b) were not able to record eggs from field-collected or laboratory-reared females of *M. davisi*, only registered one egg per scar, and, in late fall, found the fifth instars feeding on "several" other plants after the water lilies had died. Instead, *M. scutellaris* shows a reproductive success in laboratory, a different oviposition pattern, and only one overwinter host plant. The easily detectable oviposition marks on E. crassipes, the efficient rearing in captivity, and the high survivorship registered (Table 2) show that M. scutellaris can carry out its biological cycle on this plant successfully. Preliminary field and laboratory observations (Sosa et al. 2004) and host specificity (unpublished data) suggest M. scute*llaris* as a promising agent for the classical biological control of water hyacinth.

Acknowledgments

We thank E. Virla and S. Triapitsyn for the identifications of Dryinidae and Mymaridae, respectively; M. Szudruk for laboratory assistance; and P. Sarmiento for technical assistance on the scanning electron microscope. We also thank the anonymous reviewers for valuable comments that improved the manuscript. This work was supported by USDA– South American Biological Control Laboratory and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET-Argentina).

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Received 13 April 2004; accepted 7 October 2004.