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Bionomics of *Carmenta haematica* (Ureta) (Lepidoptera: Sesiidae) Which Attacks Snakeweeds (*Gutierrezia* spp.) in Argentina

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Adult *Carmenta haematica* are day-flying moths with orange (female) or clear (male) wings and a wingspan of 20 to 24 mm. Adults mated in bright sunlight. Females lived an average 2.3 days and laid an average 240 eggs each on stems and twigs of the host plant. Only 66% of the eggs hatched, mostly in the 4 h before dawn. Larvae had seven instars and reached ca. 24 mm long when full grown. Larvae entered the plant at the base of twigs or leaves or sometimes directly into the crowns. They were cannibalistic after the second instar and usually only one large larva occurred in a plant in the field. Larger larvae tunneled in the larger roots and made an exit hole in a large stem 5–8 cm above the crown where they pupated; a silken tube often protruded from the exit hole. The life cycle required ca. 139.5 days at 30°C: 15 days for the egg, 107 days for the larva, 16.5 days for the pupa, and 1 day for the adult to reach peak oviposition. Larval survival decreased below 0°C, and all larvae died after 1 day at −15°C. Larvae pupated in midsummer, adults emerged in late summer, and larvae developed during the fall, winter, and spring. The species was mostly univoltine, but the presence of some large larvae and pupae during most months indicated some variation. In the field, larvae infested 20 to 25% of medium-sized or large plants. At three locations of unusually high larval populations, the combined attack by *C. haematica*, other root borers, and drought killed most plants of *Gutierrezia solbrigii* Cabrera and *Grindelia chiloensis* Cabrera.

KEY WORDS: ***Carmenta haematica;* Sesiidae; *Gutierrezia;* snakeweed; broomweed; biocontrol-weeds; range weeds; weeds-biocontrol.**

INTRODUCTION

Snakeweeds (*Gutierrezia* spp.: Asteraceae) are major pests of rangelands in the southwestern United States and northern Mexico (Platt, 1959). They compete with beneficial forage plants (Gesink *et al.*, 1973; Ueckert, 1979; McDaniel, 1990) and are poisonous to livestock (Dollahite and Anthony, 1956; Smith and Flores-Rodriquez, 1990). Snakeweeds cause $17 million annual losses in Texas and at least two- or threefold that amount in the entire infested area. Herbicidal controls are relatively expensive in these areas of low production per unit area (10 to 25 ha per animal unit) and most ranchers do not use them (McGinty and Welch, 1987). The irregular cyclical nature of snakeweed populations makes economical control uncertain (Torell *et al.*, 1990). Biological control is feasible and is the most economical method for controlling several of the more important weeds of this area, including several native species (DeLoach, 1981, 1995; DeLoach *et al.*, 1986).

Gutierrezia is of North American origin, with 16 native species (Solbrig, 1960; Lane, 1985). Two species of snakeweeds (perennials), *Gutierrezia sarothrae* (Pursh) Britton & Rusby and *Gutierrezia microcephala* (DC.) Gray, and two species of annuals (broomweeds) are serious weeds. Many species of native insects attack snakeweeds in the United States (Falkenhagen, 1978; Richman and Huddleston, 1981; Foster *et al.*, 1981; Wangberg, 1982; Thompson and Richman, 1990) but do not give satisfactory control.

Eleven species of snakeweeds are also native in Argentina and Chile (Solbrig, 1966), and we have found several insects in Argentina that are possible candidates for biological control in the United States (Cordo and DeLoach, 1992). The first of these, the root-boring weevil, *Heilipodus ventralis* (Hustache), was tested at the Hurlingham laboratory (Cordo, 1985) and in quarantine in Temple, Texas (DeLoach, unpublished data) and was released in the field in 1988. The biology of another candidate, the root-boring sesiid moth, *Carmenta haematica* (Ureta), is reported here. Its host range in Argentina was reported by Cordo *et al.* (1995).

Several workers have determined the biology of three pest species of sesiids in the closely related genus *Synanthedon:* the peachtree borer, *Synanthedon exitiosa*

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(Say) (Snapp and Thomson, 1943), the lesser peachtree borer, *Synanthedon pictipes* (Grote and Robinson) (Cleveland *et al.*, 1968), and the rhododendron borer, *Synanthedon rhododendri* (Beutenmuller) (Neal, 1984). These studies provided guidance in determining the biology of *C. haematica.* Subsequent to our investigations, Forno *et al.* (1991) reported the biology of *Carmenta mimosa* Eichlin and Passoa from Mexico and Central America, used as a biocontrol agent for the woody *Mimosa pigra* L. in Australia.

Heppner and Duckworth (1981) listed 31 species of *Carmenta,* mostly from the Western Hemisphere and a few from the Australian region, from a genus that may contain 200+ mostly neotropical species. Duckworth and Eichlin (1977) considered 25 species to be in the genus north of Mexico, with 3 more added since: 20 of these occur in the southwestern United States and northern Mexico. Of the 13 species for which reliable host records are available, 7 have larvae that bore in the roots and stems of Asteraceae (Eichlin,[1] personal communication). So far, none have been reported to attack *Gutierrezia.*

C. haematica was described from Chile as *Synanthedon haematica* by Ureta (1956), but nothing was known about its biology prior to our investigations. *C. haematica* does not occur in the United States and probably not in the Northern Hemisphere (Eichlin,[1] personal communication).

MATERIALS AND METHODS

The various stages of *C. haematica* used in laboratory tests were reared from larvae collected from roots of *Grindelia chiloensis* (Corn.) Cabrera and *Gutierrezia solbrigii* Cabrera growing in rangelands and along roadsides between San Rafael and El Nihuil in central Mendoza, Argentina. These larvae were returned, still within the plant roots, to the laboratory at Hurlingham, where they were removed and placed individually in artificial diet in 28-ml clear plastic cups with cardboard lids (creamers).

Several diets were tried and various modifications were made during the investigations. The diet used was a modification of that of Harley and Wilson (1968) for cerambycids, as follows for ca. 1 liter of diet: 158 g ground stems of *Grindelia pulchella* Dun., 53 g cellulose, 12 g sucrose, 12 g cornstarch, 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, 15.0 ml antimicrobial[2] mix, 7 g vitamin mix,[3] 1.5 ml formol, 25 g agar, and 1100 ml water.

Medium- to large-sized larvae (third instars and larger) collected from the field completed development well on this diet, but small larvae (first and second instars) usually died. From 1855 larvae and 113 pupae obtained in eight site collections in the field, 955 adults emerged in the laboratory for a survival of 48.5%. Nearly all pupae collected in the field emerged in the laboratory unless they were injured during removal from the plant.

The larvae pupated in the diet, and the pupae were placed in clean creamers with a 5- to 10-mm layer of damp tissue paper in the bottom until the adults emerged. After mating in cages outdoors, the females were held in creamers with damp tissue paper for oviposition. We made several attempts to feed the adults by offering them various solutions of honey-water in cotton balls suspended from the cages but we never saw them feeding or appearing to be attracted to the food. They laid many eggs without feeding and we assumed that they probably do not feed in nature or, at least, that feeding is not necessary for reproduction. Therefore, we did not feed them in the test to measure adult longevity, oviposition, or for obtaining eggs or larvae for other tests. Adult longevity was measured at room temperature; the adults were placed in the mating cages within an hour after emerging.

C. haematica, as with certain other sesiid species, requires very special conditions for mating. Our first attempts to rear this moth for host-range testing were unsuccessful because the adults would not mate. The following method produced the greatest proportion of matings: Male and female pupae, held individually in creamers, were separated by sex and held in different rooms in the laboratory or on opposite sides of the same room for ca. 10 days before they emerged. When adults were ready to emerge (the pupae turned black), they were taken outside in the creamers during mid-morning and placed in the sunlight. The pupae usually began moving and often emerged within ca. 15 min. The adults were then placed in 24 by 27 by 34-cm-high screen cages with a glass door. The cages were first washed with a detergent and then rinsed with tap water, sprayed with 95% ethanol, rinsed again with tap water, and dried with a clean towel or air dried. We placed two to three females and two to three males in the cage together.

After mating, the females were placed individually in creamers with moist tissue paper, where they oviposited. The eggs were held in the same creamers until they hatched, without adding more water. For shipment, the eggs were surface-sterilized for 1 min in 1% chlorox, rinsed in water, then transferred to glue-papers for storage or shipment. These papers were prepared by brushing a thin water–flour paste (boiled for a few minutes) onto notebook paper and letting them dry. When the eggs were ready to transfer, the paper was wet, and the eggs were transferred to it with a small brush and let dry again. During rearing, the culture of *C. haematica* was

[1] T. D. Eichlin, Insect Taxonomy Laboratory, California Department of Food and Agriculture, Sacramento.

[2] Antimicrobial mixture: 20.0 g sorbic acid, 15.0 g methyl *p*-hydroxybenzoate, 170.0 ml ethanol (95%).

[3] Vanderzant modification vitamin mix for insects, NBCo Biochemicals (Cleveland, OH).

usually held in a growth cabinet at ca. 25°C and 14/10 h day/night photophase or at room temperature when this approximated 25°C.

To determine the number and duration of instars, we reared neonate larvae on artificial diet in creamers in a growth chamber at ca. 30°C and a 14/10 day/night photophase. The test began in April, using 226 neonates in nine lots by date of hatch, from eggs laid by three females. Since early instars are difficult to rear in diet, we made the first examination only after 23 days (121 alive) and the second 32 days after eclosion (51 alive) to minimize disturbing them. Subsequent examinations were made each 2 to 3 (range 1 to 8) days until they reached the adult stage or died. Measurements used in the analysis were only from the 35 individuals that developed beyond the third instar. Duration of instars was estimated by the mean age (from egg hatch) at which individuals of a given instar were present at each examination.

To measure larval survival at low temperatures, large larvae collected from the field were held in the laboratory for 3 months in 28-ml creamers with diet at ca. 7°C. They were then placed in 15-ml vials, one larva per vial, without food but with moist tissue paper in the bottom, and the vials were plugged with cotton. They were then tested, 10 larvae at each of 26 different temperature/exposure periods (0 to −18°C, 1 to 32 days) maintained in a separate refrigerator for each temperature.

Two tests measured longevity of adults. The first began in March 1985 using adults reared from larvae collected from *Gu. solbrigii* at San Antonio Oeste, Río Negro, during January and February 1985. The second test began on December 30, 1985, using adults reared from larvae collected from *Gr. chiloensis* at El Nihuil, Mendoza, on December 10. Two temperature regimes were used: continuous room temperature (ca. 25°C) day and night, and room temperature (14 h) day and in a darkened temperature cabinet (ca. 7°C) at night (10 h).

Three tests measured the behavior and success of neonate larvae in entering the stems of their host plants. In the first laboratory test, neonate larvae or eggs were placed on potted plants of *Gr. chiloensis* and *Gu. solbrigii* (10 to 15 per plant) by three methods: (1) larvae placed on small twigs of the upper part of the canopy, (2) larvae placed on the sand surrounding the plant, and (3) eggs glued with a boiled, thick, water–flour paste to large- and medium-sized stems. The plants were dissected after 3 months.

In a second laboratory test, we glued a total of 82 eggs just before hatching on various sized stems of potted plants of two species of *Gutierrezia* and on two species of *Grindelia*. The plants had been grown from seed, so they had no previous larval tunneling. The plants were 8 to 12 months old and 20 to 30 cm high. The eggs were glued with thin water–flour paste to the stems of each plant from 1 to 15 cm (mostly 3 to 10 cm) above the soil. The plants were dissected after 2 to 3 weeks and the number and location of the larvae recorded.

In a field test, we placed 10 eggs per plant on 17 to 20 plants of both *Gu. solbrigii* and *Gr. chiloensis* at each of two locations: at Península Valdés, Chubut, on March 22–24, 1990, and at San Rafael, Mendoza, on March 27–29, 1990. Eggs with embryos just before hatching were applied to the plant stems with a flour paste and small brush at three levels on each plant, one level only on a given plant: on the main stem or main branches from the soil level to 5 cm high (base), on woody branches from 5 cm high to within 10 cm of the tip of the stems (middle), and on green terminals within the distal 10 cm of the stems (top). The plants selected were 17 to 40 cm high. The plants remained in place in the field for ca. 2 months, when they were excavated, placed in plastic bags, and returned to the laboratory, where they were dissected over the next 30 to 40 days and the location and size of the larvae were recorded. The plants at Península Valdés were much more drought stressed and the natural population of *Carmenta* was much lower than at San Rafael.

In the field, we attempted to attract adults of *C. haematica* with the clearwing-moth sex attractant, predominantly the Z,Z isomer of 3,13-octadecadien-1-ol acetate (Z,Z-ODDA), obtained from J. L. Sharp, Insect Attractants Laboratory, USDA-ARS, Gainesville, Florida. At Arroyito, Neuquén, we tested the lure during three trips during December and February 1983. We attached a capillary tube of the lure to a branch of a few plants and attached a tube to a sweep net we used.

The geographic distribution of *C. haematica* was determined by collecting plants at various sites in Argentina on several extensive field trips made from 1978 to 1990. Collections were made within the distribution of the known host plants, *Gr. chiloensis*, *Grindelia tehuelches* Cabrera, and *Gutierrezia* spp., as determined from museum collections and our own previous collection records (Cordo *et al.*, 1995). We dissected plants in each area where host plants were found. The larvae found were left in the roots and returned to the laboratory for rearing to the adult stage for identification.

Statistical analyses were performed where applicable, expressed as mean ±SD, and are specified in the tables and figures. Unspecified small tests discussed in the text list mean ± SD. Methods for some of the small tests are given under Results and Discussion along with the results of the tests.

RESULTS AND DISCUSSION

Adult

Wingspan averaged 22.2 ± 1.7 (range 18.7 to 24.3) mm for 11 females and 21.3 ± 0.8 (range 19.7 to 22.2) mm for 11 males. These adults were reared from larvae collected

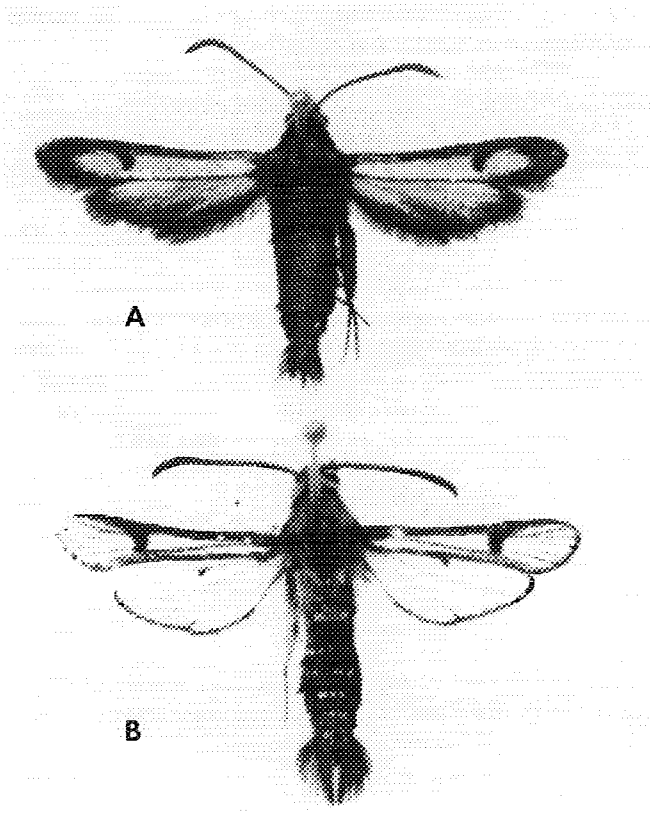

FIG. 1. Adults of *Carmenta haematica:* (A) female, (B) male.

at El Nihuil, Mendoza. Females have orange wings and males have clear wings (Fig. 1).

Emergence. In the laboratory, adults emerged mostly from midmorning to early afternoon. Emergence of 104 adults observed during 1 day in midsummer was as follows: 6–8 AM = 7 adults, 8–10 AM = 37 adults, 10 AM–12 PM = 19 adults, 12–2 PM = 18 adults, 2–4 PM = 8 adults, 4–6 PM = 9 adults, and 6–8 PM = 6 adults. This emergence schedule was similar to that of the peachtree borer (Snapp and Thomson, 1943).

Longevity. In two tests to determine longevity in the laboratory, adults lived an average of 1.8 to 4.5 days (Table 1). Longevity of *C. haematica* in our tests was much less than the average 6.7 ± 1.5 days in the insectary or 4.2 ± 1.0 days in the orchard reported for the peachtree borer (Snapp and Thomson, 1943) or the 9.2 days for males and 3.8 days for females of the lesser peachtree borer held at 27°C (Cleveland *et al.,* 1968). Most female *C. mimosa* live 6 days, with a few surviving to 12 days (Forno *et al.,* 1991).

Mating. As soon as the adults emerged in the laboratory, they crawled up the screen sides of the mating cage where they hung until their wings expanded and hardened. They often mated within ca. 30 min after emerging. Before mating, the female usually crawled around for a short period and then settled in one place and "called" the males by elevating the distal portion of the abdomen and exserting the cream-colored tip of the ovipositor (as described for the lesser peachtree borer (Cleveland *et al.,* 1968) and as illustrated for the rhododendron borer (Neal, 1984), which she moved slowly from side to side). When this occurred, we placed one to three males in the cage. The males flew rapidly about the cage, sometimes passing near a female: a male then usually alighted a short distance from her for a few minutes. This male then flew in a slow, hovering pattern back and forth over the female, then brought the abdomen forward under the body and, facing the same direction as the female, flew upside down, quickly grasped the female's ovipositor with its claspers, straightened its abdomen, and turned facing downward in the opposite direction from the female which was facing upward, and hung from the female with abdomens joined until mating was completed. In our observations of 81 matings, the pairs remained in copula from 3 to 28 (mean = 15.4) min.

In our tests, adults mated well in the 24 by 27 by 34-cm-high screen cages, when placed in bright sunlight, between 10:00 AM and 3:00 PM, at a temperature of 30 to 32°C, with gentle air movement, and when the male and female pupae were isolated during rearing, and the oviposition cages were washed after each exposure (see Materials and Methods).

If females did not mate within ca. 1 h after being exposed to males, we removed them, separated the males from the females, washed the cage with the detergent, alcohol, and water, and placed the adults in the cage again in the early afternoon. Females that still did not mate, and males, were held overnight in separate containers at 10 to 15°C, then were held at room temperature for 1 h the next morning, and were again placed together in the mating cage. Females that did not mate in the morning of the first day often mated the same af-

TABLE 1

Longevity of Adults of *Carmenta haematica* in the Laboratory

Test	Conditions	No. and sex	Adult longevity (days) $\bar{x}$ ± SD (range)
1	Room temperature, continuous	23 ♀	4.5 ± 1.6 (3–8)
2a	Room temperature	37 ♂	2.3 ± 1.0 (1–5)
	day, 7°C night	48 ♀	2.9 ± 1.4 (1–6)
2b	Room temperature,	26 ♂	1.8 ± 1.1 (1–5)
	continuous	64 ♀	2.9 ± 1.2 (1–5)

ternoon, but only on occasional female mated the second day. By this method, 67% (39 of 54) of the females in one test mated. Males often mated twice and mated a maximum of four times; sometimes they mated with two females within 1 h.

In earlier attempts to induce mating in unwashed cages (as used for the lesser peachtree borer (Cleveland *et al.*, 1968)), only one-third of the females mated. Washing the cage after use by each mating pair (or group of pairs) greatly increased the changes that the next pair would mate (washing apparently removed pheremones left on the cage by the previous pair, which seemed to confuse the next males). Also, adults appeared to disturb one another if more than six were present in a cage, resulting in reduced frequency of mating. Adults held in an outdoor 2 by 2 by 1.5-m screen cage mated only occasionally. Pairs mated only occasionally when held in glass tubes 11.5 cm in diameter by 23 or 35 cm high with a nylon mesh cover. Adults held in the 24 by 27 by 34-cm cages never mated when held in the 25°C growth chamber under a bank of 10 40-W fluorescent tubes. Under these conditions, the females appeared to "call" normally but the males always flew wildly about inside the cage. Adults mated only occasionally on cloudy days. Changing the sex ratio did not increase mating. We could not associate fertility of the eggs with duration of copula or any of the conditions of mating. Females of *C. mimosa* mated only once, nearly always when 1 or 2 days old (Forno *et al.*, 1991). The rhododendron borer mated between 10:00 AM and 2:00 PM on bright sunny days (Neal, 1984).

Oviposition. When the mating pair separated, we placed the females individually in creamers with damp paper tissue in the bottom. They often began ovipositing the black eggs almost immediately (within 10 min). Females laid most eggs on the day of mating and the following day. We left the females in the creamers until they died after 3 or 4 days so we did not know the number of eggs laid each day. A few observations indicated that females oviposited very little at night. Subsequently, we held them under continuous light to increase oviposition.

In the laboratory, we measured oviposition by 84 mated females reared from 33 collected as larvae from *Gu. solbrigii* at San Antonio Oeste in January and February 1985 and 51 from *Gr. chiloensis* at El Nihuil in February 1990, all held in creamers at 20 to 30°C and constant light. The 71 apparently mated females (28 from *Gutierrezia* and 43 from *Grindelia*) laid an average 239.8 ± 87.2 (range 94 to 430) eggs each. The apparent occurrence of two peaks at 230 to 239 and at 353 to 381 eggs per female (Fig. 2) is probably due to the random occurrence of two or three low- or high-producing females in the valley and the last peak and is not significant. We observed no differences between females from the two

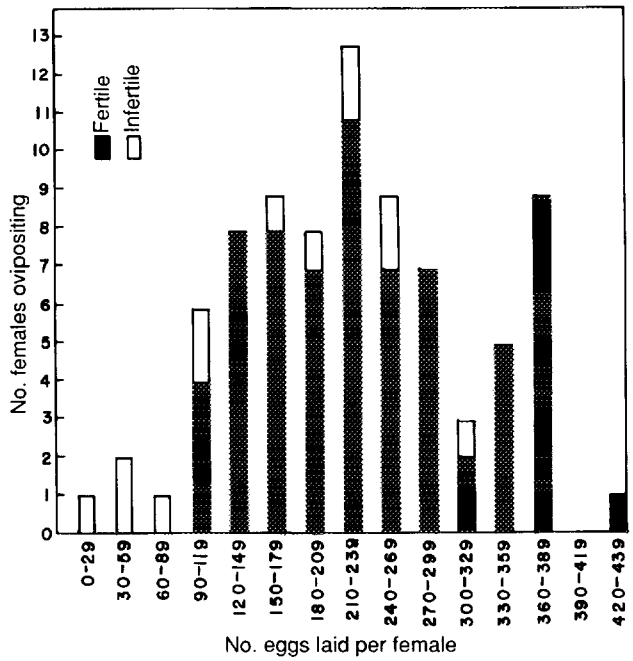

FIG. 2. Frequency distribution of the number of eggs laid by 84 females of *C. haematica* in the laboratory. Empty bars represent females laying only infertile eggs.

host species. Some of the apparent matings we observed probably were unsuccessful since 12 females which laid 34 to 303 eggs each produced only infertile eggs and one laid no eggs. We omitted these 13 females from the analysis.

Ovipositional behavior was similar to that of the peachtree borer which also began oviposition on the day of emergence. It also laid most of its eggs between 9:00 AM and 4:00 PM and laid none at night (Snapp and Thomson, 1943). Female *C. mimosa* laid an average of 295 eggs each, mostly on Days 1 and 2 (Forno *et al.*, 1991).

Behavior in the field. The adults we observed in the field were all flying during midday, indicating that *C. haematica* are day fliers as is characteristic of the Sesiidae. We never observed mating in nature. However, on March 30, 1990, near San Rafael, Mendoza, we observed mating by a wild female and male in our mating cage and observed oviposition by this female and another one in the field. We caught the first female at 11:30 AM just after she emerged from a plant and put her in our standard mating cage on top of the vehicle. She soon began "calling," and within 30 min a wild male arrived which we caught and put in the cage with her. They copulated for 30 min, and at 1:50 PM we released the female at the base of a large plant of *Gr. chiloensis.* She soon flew up into the center of the canopy and laid eight eggs, after which she flew to other plants. During 25 min of observations, she laid two eggs on each of 10 plants and one egg on

each of 32 plants. She then flew across the highway and was caught and killed by a large adult robber fly (Asilidae).

She laid most of the eggs on the upper and middle parts of the plant in the interior of the canopy. She laid 19 eggs on leaves (2 on the upper and 9 on the lower surface of green leaves and 2 on the upper and 6 on the lower surface of dry leaves). She also laid 9 eggs on stems (8 near the terminals and 1 near the middle), 2 on flowers (1 on a dry receptable and 1 on a dry peduncle), and 1 on a dry stem lying on the ground. Our second observation was of a passing wild female which we spotted at 3:00 PM and followed for 35 min before losing her; she laid on 62 plants.

Both females searched by flying in a zig-zag pattern 30 to 40 cm above the ground. They seemed to sense the plant at a distance of 40 to 50 cm, then flew briefly over and around the plant and entered the canopy where they laid one or two eggs within 3 or 4 s, and then resumed the zig-zag pattern until finding the next plant. They rested occasionally on the ground for 30 s to 3 min. They selected plants that were 10 by 10 cm to 40 by 40 cm in size, although larger and smaller plants were present, without regard to the age or health of the plant, but they ignored other species of plants growing among the stand. The first female entered the canopies from the top or side whereas the second entered always from the bottom.

These observations were made on a day that was cloudy, cool (18 to 20°C), and windy (30 km/h with gusts to 50 km/h), which our previous laboratory observations indicated were unfavorable for mating. During this period, adults emerged from eight of the female pupae we brought with us and mated readily in the cage.

In the field in late April 1986 at El Nihuil, Mendoza, we found 33 eggs laid naturally by females on 10 of the 25 plants collected: 19 were located on large stems, 10 on the upper part, 6 on the middle, and 3 near the base; 6 on small stems; 7 on the upper small twigs; and 1 on the base of a leaf.

In a preliminary attempt to attract adults in the field at Arroyito, Neuquén, during December and February 1983, using the clearwing-moth sex lure, Z,Z-ODDA, we observed three to five male *C. haematica* that flew to within 1 m of the lure. Although the numbers attracted were very small, these were probably half of all the adults we ever observed in the field. This lure has been used in Florida to trap several species of sesiids to measure seasonal occurrence and to trap *C. mimosa* (Eichlin and Passoa, 1983) and other sesiids (Sharp *et al.*, 1978; Neal and Eichlin, 1983). The low numbers we collected could indicate that populations of adults in the area were very low, partly as a consequence of adults emerging over a long period of time and having a short life span. The trial also may have indicated that the lure had small activity but was not optimal for *C. haematica*.

Egg

The egg is 0.80 ± 0.04 (range 0.74 to 0.91) mm long by 0.54 ± 0.03 (range 0.49 to 0.63) mm wide (n = 19), ovoid, slightly depressed, and slightly broader on the end with the micropyle and becoming biconcave with age. The chorion is hard, entirely black even when just laid, and without sculpturing. Females laid the eggs singly and glued them to the surface of the stems.

Duration and viability. Duration of the egg stage averaged 16.4 days for 2836 eggs observed from 18 females in the laboratory at 26.3 °C. Eggs began hatching on the 13th day, peak hatching occurred on the 15th day, and all fertile eggs had hatched by the 22nd day. Once eggs from a given female began hatching, 35% hatched on the 2nd day and 88% had hatched by the end of the 4th day. When eggs from additional females were included, 65.8% of 6620 eggs from 38 mated females hatched. Percentage of hatch varied from 19.4 to 96.5% among females. Eggs of *C. mimosa* hatched after 11 days (Forno *et al.*, 1991).

Time of hatching. The eggs hatched mainly at night, in the 4-h period just before dawn. In the laboratory in March, 87.9% of the eggs exposed to a 12/12 h photophase hatched during the dark phase (which correspond to nighttime outdoors), half of the total in the third 4-h period just before dawn outdoors. When eggs were held in continuous darkness, 65.6% hatched during the 12-h period corresponding to outdoor night; when held in continuous light, only 41.8% hatched in the periods corresponding to night (Table 2). Thus, light probably suppressed hatching.

Snapp and Thomson (1943) found that the eggs of the peachtree borer also hatched mostly at night, and duration was slightly less (mostly 10 to 13 days) than for *C. haematica*. However, viability of the peachtree borer eggs was 93.7 to 96.8%, which was much higher than the 65.8% for *C. haematica* in our tests. We could not determine whether this low viability was caused by the artificial condition at mating or is inherent in the species.

Larva

Larvae are whitish with tan head capsules, typically sesiid-shaped, and without notable markings. Neonate larvae were ca. 1.5 mm long and full-grown larvae were 20 to 25 mm long.

Development and number of instars. Development and head-capsule size of each instar were measured in the laboratory for a cohort of 35 larvae reared on artificial diet at 30°C. The larvae were observed frequently and the cast exuviae were recovered so that the instar of each individual was known. The larvae in this test had seven instars. Head-capsule diameter varied from an average of 0.28 mm in the first instar to 1.34 mm in the seventh instar. First and second instars could be identi-

TABLE 2

Influence of Light on Hatching of Eggs of *Carmenta haematica* in the Laboratory[a]

Treatment	Percentage of eggs hatching[b]							
	1st 4 h	2nd 4 h	3rd 4 h	Total	4th 4 h	5th 4 h	6th 4 h	Total
Continuous darkness	20.9	29.5	15.2	65.6	9.5	8.6	16.2	34.3
Continuous light	13.6	19.1	9.1	41.8	25.4	10.9	21.8	58.2
	12-h darkness					12-h light		
Light/darkness 12/12 h	19.8	18.7	49.4	87.9	6.6	1.1	4.4	12.1

[a] Total of 360 eggs from one female, placed in test shortly before hatching, 120 eggs per treatment.
[b] Four-hour periods beginning at midnight.

fied from measurements of the head capsules, but diameter of the head capsules of the later instars overlapped considerably (Fig. 3). The growth ratio between instars averaged 1.30 and was greater between the second and the third and between the third and the fourth instars than between the younger and the older instars (Fig. 3). The rhododendron borer also has seven larval instars (Neal, 1984), and *C. mimosa* has seven or eight (Forno *et al.*, 1991).

We also determined the mean age when each instar was present from the above cohort of 35 larvae reared at 30°C. This provided a measure of the progressive development of the cohort until adults were produced. The difference in the mean of each instar or stage seen in Fig. 4 approximates the mean duration of that stage, although development periods of individuals in each instar or stage overlapped considerably. The mean age at which last instar larvae were present was 122 days, less 15 days for the egg stage, which left 107 days as an approximation of the period required for larval development at 30°C (Fig. 4). Forno *et al.*, (1991) reported that larvae of *C. mimosa* completed their development in 68 days.

Behavior. Neonate larvae of *C. haematica,* although very small, were very active and could crawl 8 cm over moist sand in 10 min. Activity of unfed larvae greatly decreased with increasing age and they died after ca. 8 h if not fed. Three tests measured larval behavior and success in entering the stems of their host plants, two tests in the laboratory and one in the field. In the first laboratory test, we placed 10 or 15 neonate larvae or eggs on each of five potted plants of *Gu. solbrigii* and three of *Gr. chiloensis,* in each of three treatments: neonate larvae on stems or on the sand at the base of the plant and eggs glued to stems. After 3 months, we found only 6 larvae (third and fourth instars) and one pupa in the stems from 305 neonate larvae and eggs that began the test. A few had entered stems of both test-plant species and from all treatments. Many embryos were dead inside the eggs, indicating that the paste was too thick. We could not determine why the neonate larvae were unable

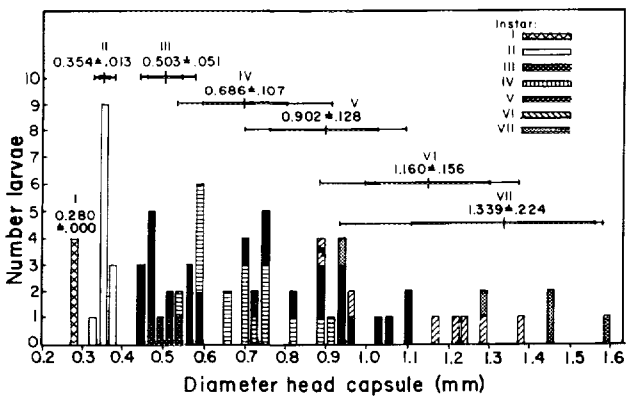

FIG. 3. Head capsule diameters for each instar larva of *C. haematica* from a cohort of 78 larvae reared on artificial diet. Instars of all larvae were determined from cast exuviae. Numbers and heavy horizontal bars, mean ± SD; light bars, range.

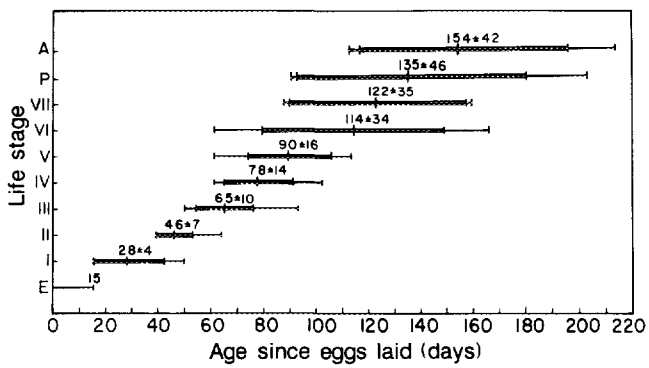

FIG. 4. Presence of each life stage of *C. haematica* developing in a cohort of 35 larvae reared on artificial diet at 30°C. Numbers, means of the ages of each stage present on the observation dates: heavy bars, ± SD; light bars, range. Data for the egg stage were taken from a different test at 26.3°C and extrapolated to 30°C.

TABLE 3

Egg Hatching and Entry of Larvae of *Carmenta haematica* in Stems of Four Species of Potted Host Plants in the Laboratory Garden

Host plants	No. plants	No. eggs used	No. eggs hatched (%)	No. larvae entered (%)
Common hosts				
Gutierrezia solbrigii	4	32	20 (63)	16 (80)
Grindelia chiloensis	3	26	14 (54)	13 (93)
Total		58	34 (59)	29 (85)
Occasional hosts				
Gutierrezia mandonii subsp. *gilliesii*	1	8	6 (75)	3 (50)
Grindelia tehuelches	2	16	10 (62)	4 (40)
Total		24	16 (67)	7 (44)

to enter, but possibly it was because they became exhausted during the few hours before we put them on the plants. In the next tests, we used only eggs and a thinner glue.

In the second laboratory test, using only eggs glued on with a thin past, 61% of the total 82 eggs had hatched when we examined them after 2 to 3 weeks. Egg hatching was about the same on all four plant species, but a greater percentage of larvae entered the two common hosts (85%) than the two occasional hosts (44%) (Table 3). When we dissected the plants of *Gr. chiloensis* and *Gu. solbrigii*, we found no larvae in stems below 3 cm from the soil, 14 larvae at 3 to 7 cm above the soil, 3 at 10 cm, 5 at 15 cm above the soil line, and 7 larvae in roots. Eleven eggs were placed on stems 3 mm or less in diameter but no larvae entered stems this small; 34 eggs were placed on stems 4 to 8 mm in diameter and 20 larvae were found in these stems. No eggs were placed on larger stems or on roots, but 2 larvae were found in stems 10 mm in diameter and 7 were found in roots. Many larvae had entered the stem within 1 to 3 cm from the egg but not through the base of the egg or beside the egg. When examined, 7 larvae were feeding toward the center of the stems, 3 underneath the bark and in the outer woody tissue, and 8 had entered and were feeding inside the base of small side stems and in the base of the small leaves at the axils of the stems. The location of 4 larvae was not recorded.

All seven larvae found in *Gutierrezia mandonii* (Sch. Bip.) Solbrig ssp. *gilliesii* Solbrig and *Gr. tehuelches* were in the roots, but no tunnels were found going down toward the roots. Apparently, those larvae that had entered the roots had crawled down the stem and below the soil line where they entered. Alternatively, they may have fed for a short time, exited, and entered at another site or in the roots. The number of larvae recovered was greater in this test than in the first, probably because we used a thinner paste to glue the eggs on the plants and because we dissected the plants sooner, before the larvae became cannibalistic. Forno *et al.* (1991) reported that *C. mimosa* larvae sometimes exited from their tunnels in stems of *M. pigra* and reentered below the soil surface, where they fed in or on the roots.

In the field test where we glued eggs to plants (Table 4), larvae entered equally well in *Gr. chiloensis* and *Gu. solbrigii* at San Rafael and slightly more entered *G. chiloensis* at Península Valdés. The overall level of entry at the two locations also was not different. When we dissected the plants, most larvae were in the crowns and roots. Slightly more larvae had entered the plants when eggs were glued to the base of the stems but many also had entered from eggs placed in the middle or top of the plant and had found their way to the crown or roots. Overall recovery was only 133 larvae from 2200 eggs (6%) but mortality included the period when cannibalism would be expected and included our unnatural handling methods. We found larvae in 40 to 60% of the plants at Península Valdés and in 50 to 65% of the plants at San Rafael.

In natural populations in the field, we found large tunnels in the larger stems and the tunnels extended into the taproot. We found larvae in these stems, indicating that they sometimes moved up and down in the tunnels. Before pupating, larvae tunneled into the crown or into large stems up to 5 to 8 cm above the crown where they cut an exit hole. The larvae then lined the tunnel, up to 10 cm long, with silk. This silk tube sometimes extended 5 to 10 mm outside of the stem through the exit hole. The mature larvae then pupated, usually at the bottom of the silken tube at the level of the crown. Sometimes larvae pupated in the larger stems and in the taproot. In our rearing cups, the larvae also sometimes cut through the plastic cup or the cardboard lid and extended the tube to the outside.

Survival at low temperatures. Large larvae collected from the field were held in the laboratory at temperatures from −0.3 to −17.8°C for periods of 1 to 32 days. All larvae survived all exposures at −0.3°C and all died at −15.5 and −17.8°C. At −5.6 and −7.3°C, survival decreased with increasing exposure time (Table 5).

Pupa

Male pupae averaged 11.9 ± 1.4 mm long by 2.6 ± 0.2 mm wide and female pupae averaged 14.4 ± 0.7 mm long by 2.9 ± 0.3 mm wide in a sample of 11 males and 11 females reared from large larvae dissected from roots of *Gr. chiloensis* from Santa Isabel, La Pampa, in June 1989. In the male, the genital suture, with rounded pads on either side, is on the ventromedial aspect of segment A9, but in the female, the genital suture is on segment

TABLE 4

Entry and Development of Larvae of *Carmenta haematica* in Plants in the Field, Artificially Infested with Eggs

Plant species	Location and no. of eggs placed per plant	No. plants used	Finding when dissected: No. plants with larvae (%)	No. larvae per plant ($\bar{x} \pm$ SD)	No. and instar of larvae found	Number of larvae and location in plant: Base of stem	Crown	Root
			San Rafael					
Grindelia chiloensis	Base 10	20	10 (50.0)	0.55 ± 0.60	11 (6-II + 5-III)	1	3	7
	Mid. 10	19	9 (47.4)	0.53 ± 0.61	10 (7-II + 3-III)	1	3	6
	Top 10	19	12 (63.2)	0.68 ± 0.58	13 (6-II + 7-III)	3	4	6
Total		58	31 (53.4)	0.59 ± 0.59	34 (19-II + 15-III)	5	10	19
Gutierrezia solbrigii	Base 10	17	11 (64.7)	0.88 ± 0.70	14 (8-I + 4-II + 2-III)	1	9	4
	Mid. 10	18	11 (61.1)	0.67 ± 0.59	12 (10-I + 2-II)	3	8	1
	Top 10	14	7 (50.0)	0.57 ± 0.65	8 (1-I + 6-II + 1-III)	2	3	3
Total		49	29 (59.2)	0.67 ± 0.63	34 (19-I + 12-II + 3-III)	6	20	8
			Península Valdés					
Grindelia chiloensis	Base 10	20	12 (60.0)	0.85 ± 0.81	17 (3-I + 8-II + 6-III)	1	10	6
	Mid. 10	19	9 (47.3)	0.68 ± 0.94	13 (2-I + 7-II + 4-III)	3	7	3
	Top 10	19	10 (52.6)	0.58 ± 0.51	10 (1-I + 6-II + 3-III)	2	4	4
Total		58	31 (53.3)	0.68 ± 0.78	40 (6-I + 21-II + 13-III)	6	21	13
Gutierrezia solbrigii	Base 10	17	7 (41.2)	0.47 ± 0.62	8 (5-II + 3-III)	2	4	2
	Mid. 10	18	8 (44.4)	0.44 ± 0.51	8 (1-I + 5-II + 2-III)	0	4	4
	Top 10	20	8 (40.0)	0.45 ± 0.60	9 (2-II + 7-III)	1	3	5
Total		55	23 (41.8)	0.45 ± 0.57	25 (1-I + 12-II + 12-III)	3	11	11

A8 and is without the rounded pads (Fig. 5). Both sexes have a dorsal row of large spines on the anterior margin of segments A3 to A8. In the male, a dorsal row of small spines is present on the posterior margin of segments A3 to A7, but in the female, these are present only on segments A3 to A6 and are absent on A7. The sexes of *C. mimosa* pupae can be distinguished by a similar difference in spines on segments A7 (Forno *et al.*, 1991).

TABLE 5

Survival of Late Instar Larvae of *Carmenta haematica* at Low Temperatures[a]

Temperature in °C ($\bar{x} \pm$ SD)	Number of larvae surviving by exposure period: 1 day	2 days	4 days	8 days	16 days	32 days
−0.3 ± 0.4	10	10	10	10	10	10
−5.6 ± 2.1	9	4	2	3	2	0
−7.3 ± 2.4	2	1	1	1	0	0
−15.5 ± 3.8	0	0	0	0	0	—
−17.8 ± 2.6	0	0	0	—	—	—

[a] Ten field-collected larvae at each temperature/exposure period. —, not tested.

Duration. Development time (Y) for a sample of 26 pupae (5 or 8 at each temperature) decreased with temperature (X) by the function $Y = 0.003X^{-0.031}$ from 65.8 days at 15°C to 16.5 days at 30°C in the laboratory (Fig. 6). The calculated lower threshold was 10.2°C, and 330 day-degrees were required for development. In a sample of 54 pupae collected in December at Arroyito, Neuquén, and held at room temperature, 90.7% produced adults; the 25 males emerged in 22.2 ± 3.5 days and the 24 females in 22.2 ± 3.1 days. From another group of 220 pupae from San Antonio Oeste, Río Negro, collected in January and February and held at 20–30°C, 84.1% produced adults; the 95 males emerged in 17.8 ± 3.5 days and the 90 females in 18.5 ± 4.7 days. Males tended to emerge 1 day sooner than the females in this latter group. Males of the peachtree borer, the lesser peachtree borer, and the rhododendron borer also emerged earlier than the females (Snapp and Thomson, 1943; Cleveland *et al.*, 1968; Neal, 1984).

At a lower temperature (10 to 15°C), only 30% of the

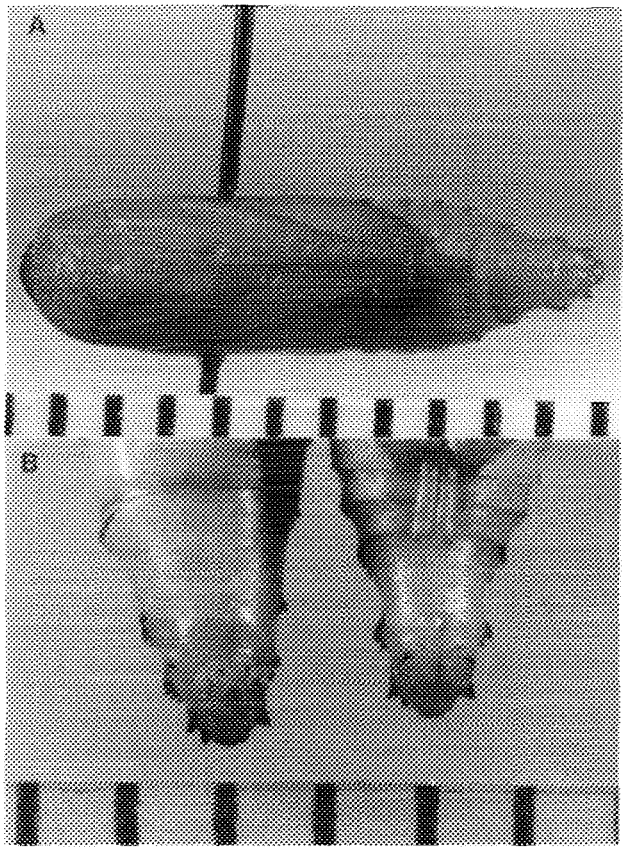

FIG. 5. Pupae of *C. haematica*: (A) Entire male pupa, (B) sexual characters of female on left and male on right (mm scale at bottom).

pupae produced adults vs 90% at room temperature. Many of the adults were deformed at the low temperatures, and the adults emerged over a longer time period.

Behavior. In the field, we found pupae easily by locating the protruding silk tubes. Pupae occurred at various levels in the silk tubes and we observed them moving up or down within the tube using the rows of spines on the body. Pupae that had turned black just before eclosion were usually found inside the tunnel near the exit hole.

Life Cycle

Our best estimate of the length of the entire life cycle of *C. haematica* at 30°C was ca. 139.5 days: 15 days for the egg stage, 107 for the larva, 16.5 for the pupa, and 1 day (estimated) for the adult female to lay half of her eggs; this total development time should be near the minimum for the species. These periods were measured at 30°C except for the egg stage which was at 26.3°C and extrapolated to 15 days at 30°C.

For 25°C, we calculated the development time for the egg stage at 17 days and for the larval stage at 150.4 days, assuming that the increase in development time from 30 to 25°C was proportional to that of the pupal stage at these temperatures (Fig. 6); development time for pupae was measured as 22.6 days at 25°C and 1.5 days was estimated for the adult female to lay half of her eggs. This gave a total of 191.5 days for the entire life cycle at 25°C. At cooler temperatures in the field during part of the year, development could be prolonged sufficiently such that more than a year might be required for some individuals. Snapp and Thompson (1943) reported that the larval feeding period of the peachtree borer required 272 to 383 days under field conditions.

Mortality Factors

Natural enemies. We reared two species of parasitoids from 1367 larvae collected in the field from nine collections in Mendoza, Neuquén, and Río Negro during 6 years. Parasitism by the braconid *Ipobracon weyenberghi* (Cameron) varied from 0 to 21.0% in seven collections. Parasitism by *Sarcophaga* sp. varied from 0 to 65.4% in six collections. Parasitism by *Ipobracon* was greater in *Grindelia* and that by *Sarcophage* was greater in *Gutierrezia*; however, the samples were too small and too infrequent to establish trends by date or location (Table 6).

Cannibalism and interspecific competition. In the field, we found no more than one larva of *C. haematica* per plant in small or medium-sized plants. In large roots, we sometimes found two larvae and in very large roots (7 to 8 cm in diameter) of *Gr. chiloensis* we occasionally found four or five larvae. In the laboratory, first instars were not cannibalistic; however, third and larger instars fiercely attacked each other if more than one was placed in an empty petri dish. In the creamers of diet, only one larva survived more than 1 or 2 days.

In the field, we commonly found one to several larvae of the weevil *H. ventralis* and one of *C. haematica* in the

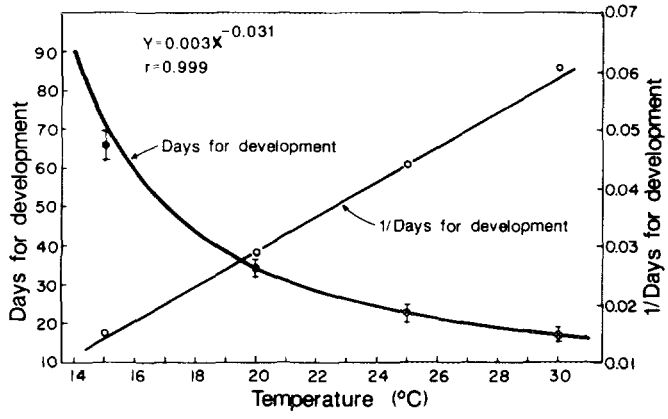

FIG. 6. Development of pupae of *C. haematica* at four constant temperatures; vertical bars, ± 1 SD.

same root and rarely those of buprestids (*Dactylozodes* spp.). Also, although these latter usually inhabited smaller plants than *Carmenta*, we saw no evidence in the field that *C. haematica* attacked these other species of stem borers.

Larvae of the peachtree borer (Snapp and Thomson, 1943) and the rhododendron borer (Neal, 1984) were not cannibalistic, even when several larvae were confined together in small containers.

Predation. We never observed predation on larvae or pupae of *C. haematica* in the field. When infested roots were dug up, they often contained many ants in the old tunnels and decayed portions, but the larvae appeared to be well protected in their tunnels and were not attacked. We observed predation on adults once, when one of the two ovipositing females we followed in the field was caught by a robber fly.

Seasonal Occurrence in the Field

Larvae of *C. haematica* were present in the field during every month (no examinations were made during July or March) in 74 examinations made at 47 sites from 1978 to 1988. We collected pupae from *Gr. chiloensis* during every month (except March) from October to June but from *Gu. solbrigii* only during November and February. Peak population appeared to occur in February when we found pupae at all but 2 of the 16 examination sites where we found larvae (Table 7).

C. haematica probably has one generation a year in the field. This conclusion is consistent with the 139.5-day generation time measured at ca. 30°C in the laboratory. Pupae and adults are present during February (adults were only very rarely seen in the field) and since the adults are short-lived (ca. 2 to 4 days), oviposition probably also occurs during February (mid- to late summer). Larvae then develop during the fall, continue slow development through the winter on warm days, and complete development during the spring and early summer. Although most sesiids have a 1-year life cycle (Neal, 1984), some individuals of the peachtree borer, lesser peachtree borer, and rhododendron borer, in the closely related genus *Synanthedon*, are known to require 2 years to complete their development and some may have two generations per year (Snapp and Thomson, 1943; Smith, 1951). This could also account for the large larvae and pupae of *C. haematica* that we found in the fall.

TABLE 6

Parasitism of Larvae of *Carmenta haematica* Collected in the Field

Location	Date collected	No. larvae collected	No. and (% parasitized)	
			Ipobracon	*Sarcophaga*
		From *Grindelia*		
El Nihuil, Mendoza	Feb. 86	260	25 (9.6)	0
El Nihuil, Mendoza	Dec. 85	19	4 (21.0)	0
Total (or mean)		279	29 (10.5)	0
		From *Gutierrezia*		
Arroyito, Neuquén	Dec. 85	41	0	5 (12.2)
Cutral-có, Neuquén	Sep. 80	107	0	70 (65.4)
S. Ant. Oeste, Río Negro	Sep. 85	50	5 (10.0)	6 (12.0)
S. Ant. Oeste, Río Negro	Jan. 83	20	2 (10.0)	1 (5.0)
S. Ant. Oeste, Río Negro	Feb. 85	540	7 (1.3)	75 (13.9)
S. Ant. Oeste, Río Negro	Feb. 88	300	3 (1.0)	2 (0.7)
Sargento Vidal, Río Negro	Feb. 86	30	2 (6.7)	0
Total (or mean)		1088	19 (1.7)	159 (14.6)

Damage to Host Plants in the Field

We found larvae in ca. 20% of the plants of both *Gu. solbrigii* and *Gr. chiloensis* as an average of all sites and all dates. The maximum number found at our major collection sites was 64.5 larvae per 100 plants in November. We found an average of 20.0 larvae and pupae per 100 plants on *Gu. solbrigii* and 23.7 per 100 plants on *Gr. chiloensis* (Table 7).

We found three locations in the field where attack by root-boring larvae apparently had caused great mortality of *Gu. solbrigii* or *Gr. chiloensis*. One location was in Chubut ca. 40 km N of Península Valdés in 1986 and another near La Ahumada, Mendoza, in 1989. Both of these were areas of mostly medium-sized plants of *Gr. chiloensis*, ca. 2- to 3-cm crown diameter and 40 to 50 cm high. These areas appeared to be suffering severely from drought, as evidenced by the appearance of other vegetation present. In both locations, ca. 80% of the plants were dead and all or nearly all of the roots of the dead plants were very heavily damaged by root-boring larvae. The few living plants were also heavily attacked, especially by larvae of the weevil *H. ventralis* but also by some larvae of *C. haematica*.

At the third location at San Antonio Oeste, Río Negro, we followed the decline of a stand of snakeweed over a 5-year period. When we found the location in May 1983, it was excellent for collecting, with many large plants of *Gu. solbrigii* and *Gr. chiloensis* that extended at least 30 km along the highway. The plants were flowering and

TABLE 7

Seasonal Occurrence of Immatures of *Carmenta haematica* in the Field (Summed over Various Sites and Years)

	Gutierrezia solbrigii			*Grindelia chiloensis*		
		No. per 100 plants			No. per 100 plants	
Date	No. plants examined	Larvae	Pupae	No. plants examined	Larvae	Pupae
Jan	1,030	32.6	0	0		
Feb	6,400	10.9	1.9	3,752	14.7	4.2
Mar	0			0		
Apr	500	10.0	0	2,000	18.2	1.0
May	80	17.5	0	1,550	25.2	1.0
Jun	0			3,070	22.1	0.1
Jul	0			0		
Aug	1,140	10.9	0	0		
Sep	3,315	8.3	0	20	20.0	0
Oct	1,350	18.2	0	3,100	21.3	2.3
Nov	752	64.1	0.4	1,550	32.8	1.3
Dec	4,610	5.1	0	2,015	24.2	1.7
Total	19,177			17,057		
Mean		19.7	0.3		22.3	1.4

had little foliage but few were dead. Many larvae of *H. ventralis*, *C. haematica*, and *Daclylozodes* spp. were present in the roots. In January and February 1985, the area appeared very dry, the *Gutierrezia* plants were dying, only a few large plants of *Grindelia* remained, and the remaining living plants were infested with many large larvae in the roots. We collected 300 larvae of *Carmenta* and 218 adults and many larvae of *H. ventralis* (these larvae were not counted but were returned in the roots to the laboratory for removal) from ca. 1000 plants. In February 1988, the plants of *Grindelia* were nearly all dead and only a few medium-sized plants of *Gutierrezia* remained alive; we collected 80 larvae of *C. haematica* and 80 adults and many larvae of *H. ventralis* from 300 plants.

The effects of drought and attack by two species of root-boring insects on plant mortality are difficult to separate in the field. However, we believe the insects kill the plants during times of drought stress, as reported by Richman and Huddleston (1981) when snakeweeds in New Mexico attacked by the root-boring cerambycid *Crossidius pulchellus* Le Conte were killed during droughts.

Geographical Distribution

We found the natural host plants of *C. haematica* (*Gu. solbrigii, Gu. mandonii, Gu. spathulata, Gr. chiloensis,* and *Gr. tehuelches*) at 78 sites during 43 trips over a 12-year period from 1978 to 1989. From this and additional information from the literature and museum records, we depicted the generalized distribution of the host species (Fig. 7). We found larvae and/or pupae of *C. haematica* in roots of its host plants at 39 locations from Abra Pampa in Jujuy Province in the north (22° 40′ S. latitude) at 3350 m (11,000 ft) elevation to Comodoro Rivadavia in Chubut Province in the south (45° 51′ S. latitude) near sea level.

C. haematica occurred most commonly in the provinces of Río Negro, Neuquén, Mendoza, and La Pampa, where its host plants were most abundant. Levels of infestation of the host plants in various areas were presented by Cordo *et al.* (1995). Routes taken during the surveys and descriptions of the biogeography of the major sites were described by Cordo and DeLoach (1992).

GENERAL DISCUSSION

According to Cordo and DeLoach (1992) and Cordo *et al.* (1995), *C. haematica* has the narrowest host range of any of the candidate biocontrol agents of *Gutierrezia* thus far investigated in Argentina, being restricted to two genera of the tribe Astereae (Asteraceae), *Grindelia* and *Gutierrezia*. The larvae cause considerable damage to medium- and large-sized plants and sometimes appear to contribute to the death of plants in the field.

The number of larvae per 100 plants generally was greater in *Gr. chiloensis* than in *Gu. solbrigii*, except in November, indicating that in the field *Grindelia* was either more attractive to ovipositing females or it was more suitable for larval development. However, the number of pupae per 100 plants on *Gu. solbrigii* averaged only one-fifth that on *Gr. chiloensis* and substantial numbers were found only during February on *Gu. solbrigii*. The few pupae we found indicates substantial mortality of prepupae or pupae in both plant species but

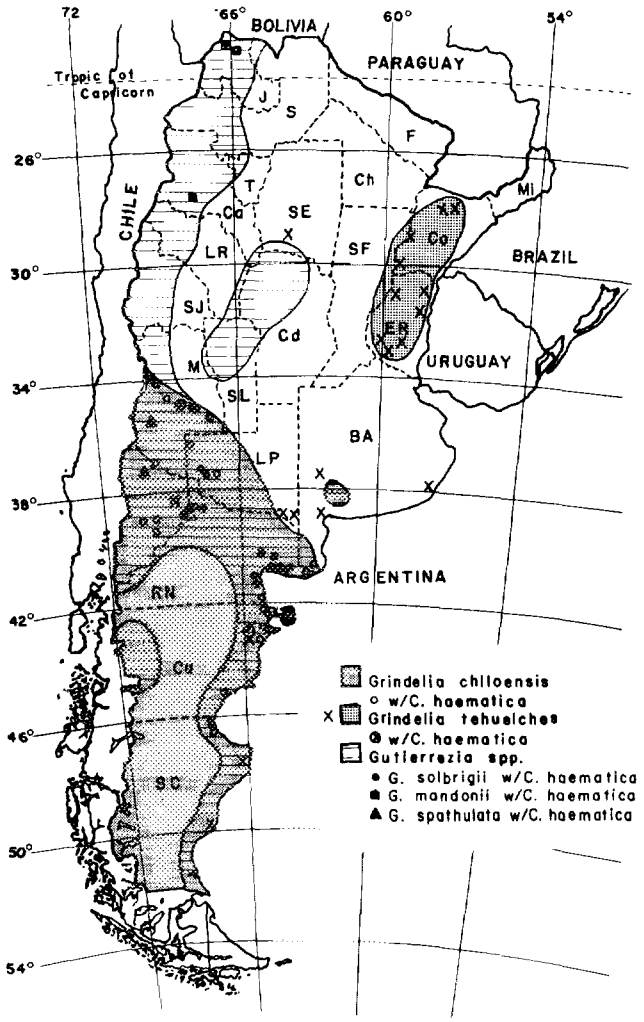

FIG. 7. Distribution of *C. haematica* (circles, triangles, squares) on each of its five natural host plants (shaded areas) in Argentina. Provincial names: BA, Buenos Aires; Ca, Catamarca; Cd, Córdoba; Ch, Chaco; Co, Corrientes; Cu, Chubut, ER, Entre Ríos; F, Formosa; J, Jujuy; LP, La Pampa; LR, La Rioja; M, Mendoza; Mi, Missiones; N, Neuquén; RN, Río Negro; S, Salta; SC, Santa Cruz; SE, Santiago del Estero; SF, Santa Fe; SJ, San Juan; SL, San Luis; T, Tucumán. The X's outside the main area of distribution of *Gr. tehuelches* are small isolated areas of plants.

greater mortality in *Gu. solbrigii.* We found no cause for this mortality in the field.

The species is generally univoltine, although some individuals may complete two generations a year as evidenced by our finding pupae during the spring and again during midsummer. Some individuals may require 2 years to complete the life cycle. For a moth, *C. haematica* has a relatively low fecundity of 240 eggs per female with egg viability of only 66%. However, reproduction in the field (which we were unable to measure) may have been greater than in our laboratory measurements. In a biological control program, the reduced effectiveness caused by this low fecundity would be at least partially compensated for by the probability of good dispersal, based on our observations that the adults are strong fliers. The reproductive rate does not appear to be so low as to handicap the insect as a biocontrol agent. The only other biocontrol agent released to date in the United States for control of snakeweed, the root-boring weevil *H. ventralis,* also has a low fecundity and a poor dispersal capability. Both insects are expected to have a low level of mortality in the field since they are partially protected inside the roots of the host plant from predators and insect parasitoids.

C. haematica, like certain other sesiid moths, has very special behavioral requirements for mating. It also has distinctive behavioral patterns for entry of the larvae into the host plant. We have discovered these patterns in sufficient detail to culture the moth and to conduct host-range testing in the laboratory. Our rearing experiments also revealed that development of larvae and pupae could be delayed at low temperatures. Therefore, emergence of adults can be synchronized with the development of the host plants in the Northern Hemisphere so that shipments can be made at the appropriate time for testing and release there.

C. haematica occurs over a wide geographical area of Argentina (from the northernmost province of Jujuy (22°S. latitude) to the southern province of Santa Cruz (46°S. latitude). This range includes nearly the entire range of *Gutierrezia* in Argentina. Theoretically, this would allow establishment of *C. haematica* from northern Mexico to the Canadian border, which is almost the entire range of *Gutierrezia* in North America. However, *C. haematica* was found in the southern areas of Argentina only near the Atlantic coast in a climate much milder than that of Montana and Wyoming. Therefore, we might expect the moth to become established no further north than Arizona, New Mexico, and Texas.

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REFERENCES

Cleveland, M. L., Wong, T. T. Y., and Lamansky, K. W. 1968. Rearing methods and biology of the lesser peach tree borer, *Synanthedon pictipes,* in the laboratory. *Ann. Entomol. Soc. Am.* **61,** 809–814.

Cordo, H. A. 1985. Host specificity of the Argentine weevil, *Heilipodus ventralis,* for the biological control of snakeweeds (*Gutierrezia* spp.) in the U.S. In "Proceedings, VI International Symposium Biological Control of Weeds, Vancouver, Canada, 19–24 Aug. 1984" (E. S. Delfosse, Ed.), pp. 709–720. Agric. Canada, Canadian Govt. Print. Centre, Ottawa.

Cordo, H. A., and DeLoach, C. J. 1992. Occurrence of snakeweeds (*Gutierrezia:* Compositae) and their natural enemies in Argentina: Im-

plications for biological control in the United States. *Biol. Control* **2,** 143–158.

Cordo, H. A., DeLoach, C. J., and Ferrer, R. 1995. Host range of the Argentine root borer *Carmenta haematica* (Ureta) (Lepidoptera: Sesiidae), a potential biocontrol agent for snakeweeds (*Gutierrezia* spp.) in the United States. *Biol. Control* **5,** 1–10.

DeLoach, C. J. 1981. Prognosis for biological control of weeds of southwestern U.S. rangelands. In "Proceedings, V International Symposium on Biological Control of Weeds, Brisbane, Australia, 22–29 July 1980" (E. S. Delfosse, Ed.), pp. 175–199. CSIRO, Melbourne.

DeLoach, C. J. Progress and problems in introductory biological control of native weeds in the U.S. In "Proceedings VIII International Symposiom on Biological Control of Weeds, Canterbury, New Zealand, 2–7 Feb. 1992" (E. S. Delfosse, Ed.), in press.

DeLoach, C. J., Boldt, P. E., Cordo, H. A., Johnson, H. B., and Cuda, J. P. 1986. Weeds common to Mexican and U. S. Rangelands: Proposals for biological control and ecological studies. In "Management and Utilization of Arid Land Plants: Symposium Proceedings" (D. R. Patton, C. E. Gonzales V., A. L. Medina, L. A. Segura T., and R. H. Hamre, Eds.), pp. 49–68. USDA-Forest Service General Technical Report RM-135.

Dollahite, J. W., and Anthony, W. V. 1956. "Experimental Production of Abortion, Premature Calves and Retained Placentas by Feeding a Species of Perennial Broomweed." Texas Agricultural Experimental Station Progress Report 1884.

Duckworth, D. W., and Eichlin, T. D. 1977. "A Classification of the Sesiidae of America North of Mexico (Lepidoptera: Sesioidae): Occasional Papers in Entomology." California Department of Food and Agriculture Division of Plant Industry, Sacramento, CA.

Eichlin, T. D., and Passoa, S. 1983. A new clearwing moth (Sesiidae) from Central America: A stem borer in *Mimosa pigra*. *J. Lepidopt. Soc.* **37,** 193–206.

Falkenhagen, T. J. 1978. "Root Boring Insects in *Guitierrezia sarothrae*." M. S. Thesis, Univ. Arizona, Tucson.

Forno, I. W., Kassulke, R. C., and Day, M. D. 1991. Life cycle and host testing procedures for *Carmenta mimosa* Eichlin and Passoa (Lepidoptera: Sesiidae), a biological control agent for *Mimosa pigra* L. (Mimosaceae) in Australia. *Biol. Control* **1,** 309–315.

Foster, D. E., Ueckert, D. N., and DeLoach, C. J. 1981. Insects associated with broom snakeweed (*Xanthocephalum sarothrae*) and threadleaf snakeweed (*Xanthocephalum microcephala*) in west Texas and eastern New Mexico. *J. Range Manage* **34,** 446–454.

Gesink, R. W., Alley, H. P., and Lee, G. A. 1973. Vegetative response to chemical control of broomweed on a blue grama range. *J. Range Manage.* **26,** 139–143.

Harley, K. L. S., and Willson, B. W. 1968. Propagation of a cerambycid borer on a meridic diet. *Can. J. Zool.* **46,** 1265–1266.

Heppner, J. B., and Duckworth, W. D. 1981. Classification of the superfamily Sesioidae (Lepidoptera: Ditrysia). *Smithson. Contrib. Zool.* **314,** 1–144.

Lane, M. A. 1985. Taxonomy of *Gutierrezia* (Compositae: Astereae) in North America. *Syst. Bot.* **10,** 7–28.

McDaniel, K. C. 1990. Snakeweed populations in New Mexico, 1979–1989. In "Snakeweed: Problems and Perspectives" (E. W. Huddleston and R. D. Pieper, Eds.), pp. 13–25. Proceedings, Symposium, 9–10 Nov. 1989. Agricultural Experiment Station Bulletin **751,** New Mexico State Univ., Las Cruces.

McGinty, A., and Welch, T. G. 1987. Perennial broomweed and Texas ranching. *Rangelands* **9,** 246–249.

Neal, J. W., Jr. 1984. Bionomics and instar determination of *Synanthedon rhododendri* (Lepidoptera: Sesiidae) on rhododendron. *Ann. Entomol. Soc. Am.* **77,** 552–560.

Neal, J. W., and Eichlin, T. D. 1983. Seasonal response of six male Sesiidae of woody ornamentals to clearwing borer (Lepidoptera: Sesiidae) lure. *Environ. Entomol.* **12,** 206–209.

Platt, K. B. 1959. Plant control—Some possibilities and limitations. II. Vital statistics of range management. *J. Range Manage.* **12,** 194–200.

Richman, D. B., and Huddleston, E. W. 1981. Root feeding by the beetle *Crossidius pulchellus* LeConte and other insects on broom snakeweed (*Gutierrezia* spp.) in eastern and central New Mexico. *Environ. Entomol.* **10,** 53–57.

Sharp, J. L., McLaughlin, J. R., James, J., Eichlin, T. D., and Tumlinson, J. H. 1978. Seasonal occurrence of male Sesiidae in north central Florida determined with pheromone trapping methods. *Florida Entomol.* **61,** 245–250.

Smith, E. H. 1951. Control of peach tree borer and lesser peach tree borer in New York. *J. Econ. Entomol.* **44,** 685–690.

Smith, G. S., and Flores-Rodriquez, G. I. 1990. Toxicity of snakeweeds. In "Snakeweed: Problems and Perspectives" (E. W. Huddleston and R. D. Pieper, Eds.), pp. 13–25. Proceedings, Symposium, 9–10 Nov. 1989. Agricultural Experiment Station Bulletin **751,** New Mexico State University, Las Cruces.

Snapp, O. I., and Thomson, J. R. 1943. "Life History and Habits of the Peachtree Borer in the Southeastern States." U.S. Department of Agriculture Technical Bulletin **854.**

Solbrig, O. T. 1960. Cytotaxonomic and evolutionary studies in the North American species of *Gutierrezia* (Compositae). *Contributions Gray Herb.* **188,** 2–63.

Solbrig, O. T. 1966. The South American species of *Gutierrezia*. *Contributions Gray Herb.* **197,** 3–42.

Thompson, D. C., and Richman, D. B. 1990. The role of native insects as snakeweed biological control agents. In "Snakeweed: Problems and Perspectives" (E. W. Huddleston and R. D. Pieper, Eds.), pp. 179–187. Proceedings, Symposium 9–10 Nov. 1989, Agricultural Experiment Station Bulletin **751,** New Mexico State Univ., Las Cruces.

Torrell, L. A., Williams, K., and McDaniel, K. C. 1990. Economics of broom snakeweed control. In "Snakeweed: Problems and Perspectives" (E. W. Huddleston and R. D. Pieper, Eds.), pp. 113–138. Proceedings, Symposium 9–10 Nov. 1989, Agriculture Experiment Station Bulletin **751,** New Mexico State Univ., Las Cruces.

Ueckert, D. N. 1979. Broom snakeweed: Effect on shortgrass forage production and soil water depletion. *J. Range Manage.* **32,** 216–220.

Ureta, E. 1956. Revision de la familia Aegeriidae (Lep. Het.) en Chile. *bol. Museo Nacional Historia Natural* **26,** 261–267.

Wangberg, J. K. 1982. Destructive and potentially destructive insects of snakeweed in western Texas and eastern New Mexico and a dioristic model of their biotic interactions. *J. Range Manage.* **35,** 235–238.