

# Natural enemies and host-plant asynchrony contributing to the failure of the introduced moth, *Coleophora parthenica* Meyrick (Lepidoptera: Coleophoridae), to control Russian thistle

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## ABSTRACT

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Host-plant synchronization, predators, and parasitoids limited the population growth of *Coleophora parthenica* Meyrick (Lepidoptera: Coleophoridae), a moth introduced into California for the biological control of Russian thistle, *Salsola australis* R. Brown (Chenopodiaceae), that was studied in the Coachella Valley of southern California during 1979/80 and 1985/86.

The oviposition period of the overwintered F<sub>3</sub> generation largely coincided with the highest mortality of young plants. Field observations indicated that this plant mortality caused the death of the *C. parthenica* larvae living on these plants, and was mainly responsible for the drastic population decrease of *C. parthenica* in early spring. During summer generations, rodent predation and parasitism of the larvae were minimal; spider predation accounted for 28.7 and 30.4% of the F<sub>1</sub> and F<sub>2</sub> moths, respectively. The *C. parthenica* population slightly increased during summer 1979 and was highest in the desiccated plants during winter 1979/80. During winter 1979/80, intrinsic larval mortality was 8.5%; rodents removed 25% of the larvae, and larval parasitism reached 42.1%, as compared with only 13.5 and 11.0% larval parasitism in 1984/85 and 1985/86, respectively. Rodent predation was limited by the diameter of the branches, reaching highest rates in the second order branches. Parasitoids did build up high densities, especially during mild winters, as in 1979/80 and predominantly attacked larvae in the thinner third order branches, which the rodents could not reach. Thus, poor host-plant synchronization, predators, and parasitoids considerably limited the population growth of *C. parthenica*. The extent of these mortality factors, together with the limited impact of the larval mining, helps to explain the failure of this moth to control Russian thistle.

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## INTRODUCTION

The stem- and branch-boring moth *Coleophora parthenica* Meyrick (Lepidoptera: Coleophoridae) was introduced into southern California from Egypt, Pakistan and Turkey in 1973 and 1974 for the biological control of Russian thistle, *Salsola australis* R. Brown (Chenopodiaceae) (Hawkes et al., 1975; Goeden et al., 1978; Hawkes and Mayfield, 1978). The colonization, establishment and impact of *C. parthenica* on the introduced annual *S. australis* was studied in the Coachella Valley by Goeden et al. (1978) and Goeden and Ricker (1979). Up to three generations per year were reported from this low-elevation, Colorado Desert location. Larvae of the last generation overwintered within the branches and emerged from the dead plants the following spring.

Spider and rodent predators of *C. parthenica* were studied by Nuessly and Goeden (1983, 1984). Müller and Goeden (1990) described the parasitoid complex of *C. parthenica* 10 years after its introduction into southern California.

Compared with generalist predators, parasitoids have less impact on the establishment and effectiveness of introduced species of phytophagous insects (Goeden and Louda, 1976; Carl, 1982; Crawley, 1986, 1987). The present study sought to estimate the relative importance of host-plant population dynamics and native parasitoids and predators in limiting population growth by *C. parthenica* in the Coachella Valley.

## MATERIALS AND METHODS

### *Study sites*

Studies were conducted during 1979/80 and 1985/86 at three sites in the Coachella Valley located between the cities of Indio and Coachella and within 2 km of the 1974 release site of *C. parthenica* (Goeden et al., 1978). The climate and the most common plant species at these Colorado Desert locations were described by Müller and Goeden (1990).

### *Plant parameters*

To estimate host-plant density, a 50×2-m transect established using the method of Whaba (1970) at each of the three sites was sampled at different times of the year. Interpolated values of these Russian thistle densities were used to calculate moth densities (per area) during the three flight periods in 1985, which then were used to estimate predation rates by spiders. To follow host-plant growth, the basal diameter and the height of each of 20 randomly selected Russian thistles were measured at several occasions at all sites. Plant volumes were then estimated by calculating their volume as half-spheroids ( $V = 1/2(4/3\pi \times ab^2)$ ; where  $a$  = plant height, and  $b$  = radius).

### *Branch samples*

Ten larger to 25 smaller, randomly selected Russian thistles were collected at each of the three sites on 8 March, 4 July, 17 September, 28 October and 9 December 1985 and again on 30 January and 1 April 1986 to obtain overwintering  $F_3$  larvae, and on 7 June and 23 July 1985 to obtain  $F_1$  and  $F_2$  larvae, respectively.

### *Branch dissections and rearings*

Branches were classified as main or first order ( $1^\circ$ ) branches, second order ( $2^\circ$ ) branches, and third order ( $3^\circ$ ) branches (generally  $< 2$  mm in diameter and without flowers) to reflect the architecture of Russian thistle. Ten-meter aggregate lengths of  $1^\circ$  branches and 25-m each of  $2^\circ$  and  $3^\circ$  branches were included in each sample, which approximated the proportions of each type in a plant. Immediately after collection, 20% of each branch type was dissected under a microscope using a single-edged razor blade to slit each branch lengthwise. Larvae and pupae of *C. parthenica* and its parasitoids were held individually in gelatin capsules in the laboratory for adult emergence. The remaining 8 m of  $1^\circ$  branches and 20 m each of  $2^\circ$  and  $3^\circ$  branches were placed in separate emergence cages in an air-conditioned glasshouse at the University of California, Riverside, where temperatures approximated those at the sample sites.

### *Predation and parasitism studies of C. parthenica during 1979/80*

Seven large, randomly selected Russian thistle plants were collected in January 1980, at the three study sites, of which pre-dissection measurements were taken of the location of each  $2^\circ$  branch (measured from the base of the  $1^\circ$  branch) to calculate larval densities and record the distribution of parasitism and predation within each plant. Numbers of *C. parthenica* larvae alive, dead or parasitized and chew-marks left by rodents (cf. Nuessly and Goeden, 1984) were recorded separately for each  $2^\circ$  branch.

## RESULTS

### *Host-plant synchronization*

Germination times and success of annual *S. australis* are determined by the winter rainfall patterns and amount (Young and Evans, 1972). Mean seedling density reached 176 plants  $10\text{ m}^{-2}$  (range 132–207) on 5 April 1985, but dropped to less than 5% 7 weeks later. Plant growth rate was highest between mid-April and the end of June (Fig. 1b). On 1 April 1986, 114 seedlings  $10\text{ m}^{-2}$  (range 10.3–246.8) were recorded, of which less than 10% were left 2 months later.

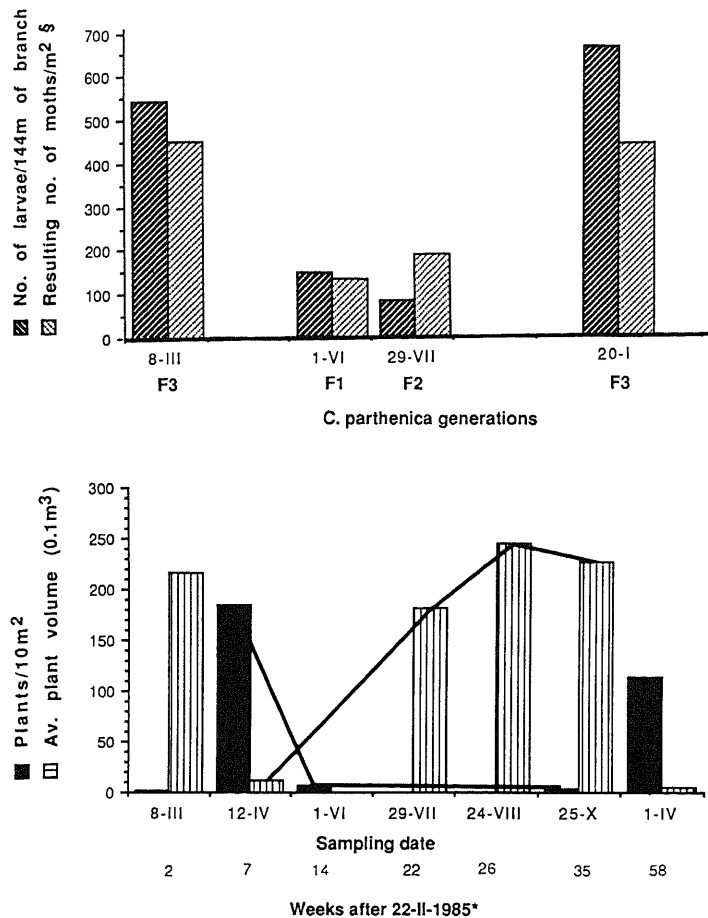


Fig. 1. Patterns of moth occurrence and host-plant availability. Top graph: densities of *C. parthenica* larvae and moths during 1985/86 from combined branch samples (8 m of 1° branches and 20 m of each of 2 and 3° branches from each of three localities), and interpolated values of plant densities from lower graph. Lower graph: Seasonal fluctuations of host-plant density and average plant volume (the lines connect corresponding values of a plant cohort). Roman numerals indicate months.

Figure 2 shows the 1985/86 emergence pattern of the moths. Approximately half the larvae collected on 17 April 1985 pupated and emerged as adults in 1985, as a partial fourth generation. In 1986, emergence of the overwintering generation started in mid-April, peaked in early May, and lasted until the beginning of July. Eggs were found from 14 April 1986 on, indicating that oviposition began a few days after emergence.

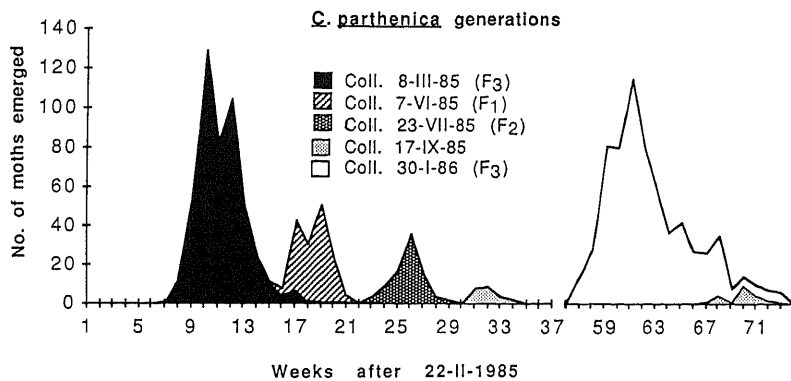


Fig. 2. Emergence pattern of *C. parthenica* adults during 1985/86 from combined branch samples (8 m of 1° branches and 20 m each of 2 and 3° branches from each of three localities). Roman numerals indicate months.

The oviposition period almost coincided with the time of high host-plant mortality. Because many eggs were found on wilting young succulent plants 30–50 cm tall, it was assumed that a large portion of the  $F_1$  generation of *C. parthenica* died in the egg or early larval stage following desiccation and death of their host plants. Unfortunately, this loss was not quantified because data on ovipositional selectivity (e.g. on early-dying versus surviving plants), and detailed knowledge of plant demography were lacking. Host-plant desiccation may also affect subsequent *C. parthenica* generations as laboratory observations indicated that older branch tips in these desert locations were too tough for hatching larvae to penetrate.

#### *Parasitism of C. parthenica during 1985/86*

Impact of parasitoids on *C. parthenica* varied widely between generations. No parasitized egg was found in all three generations studied in 1985, and only two individuals of a single parasitoid species emerged from over 800 larvae and pupae collected during the two summer generations (Müller and Goeden, 1990). The sample collected on 8 March 1985 yielded 11% parasitism. Overwintering larvae were sampled on five occasions in 1985/86. On 17 September, 28 October and 9 November, 1985, rates of parasitism were less than 1%, but reached 5.5% on 30 January and 8.8% on 1 April 1986 (Müller and Goeden, 1990). If parasitoids that emerged from the 1 April 1986 sample are treated as a subsequent generation of the parasitoids from the 30 January 1986 sample, losses from parasitoids in the winter 1985/86 generation reached 13.5%. Some of the moths and parasitoids, however, had already emerged in the field from stems collected on 1 April 1986. In addition, later dissection of branches revealed dead *C. parthenica* from which no parasitoids had emerged that either did not complete development or died as adults within the branch

mine. Hence, the rate of parasitism calculated above underestimated the actual loss from parasitoids. The two dominant species during both winters were *Norbanus perplexus* Ashmed (Pteromalidae; 58% on average) and *Eurytoma strigosa* Bugbee (Eurytomidae; 25% of the total), both of which are solitary, hymenopterous ectoparasitoids (Müller and Goeden, 1990).

#### *Mortality of overwintering C. parthenica larvae collected in January 1980*

Figure 3 gives the results from detailed dissections of seven branches collected in January 1980. The house mouse, *Mus musculus* L., was identified as the dominant predator (Nuessly and Goeden, 1984). House mice and parasitoids reduced the overwintering population of larvae by 67.5%, but mortality was probably greater, as these branches were collected before larval parasitism had ended. Rodent predation accounted for 25% larval mortality and were highest in the 2° branches; parasitism reached 42.1%, and was highest in the 3° branches (61%). The mild winter of 1979/80 may have allowed parasitoids to produce several generations, resulting in relatively high parasitization rates compared with the winters of 1984/85 and 1985/86 (Anonymous, 1980; cf. Fig. 3).

Intrinsic mortality associated with the biology and behavior of the larvae within the plants was 8.5%. The level of this mortality was significantly higher in the 3° branches, where most of the larvae start their feeding.

#### *Interference between parasitism and predation*

According to Müller and Goeden (1990) the level of parasitism of overwintering larvae is positively correlated with branch diameter and position

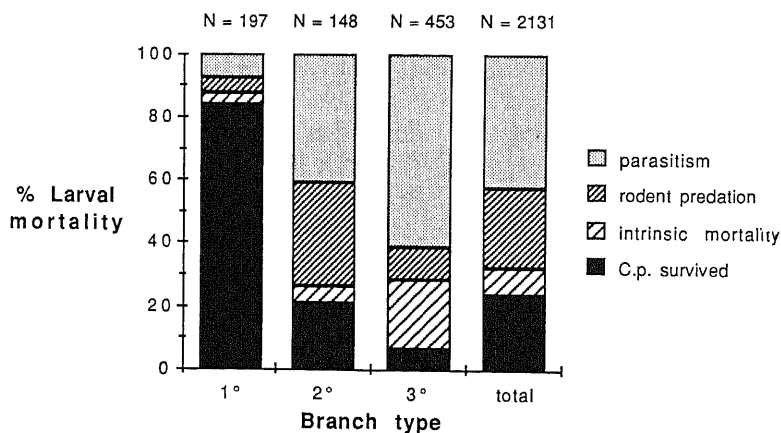


Fig. 3. Mortality factors for overwintering *C. parthenica* larvae in different branch types of Russian thistle collected in January 1980.

( $r=0.66$ ,  $P<0.001$ ), increasing from 2% in the 1° branches to 45% in the 3° branches in spring 1985, and from 2 to 19% in spring 1986 (Fig. 3).

Predation by house mice was found to be restricted to overwintering larvae, with the rodents preferentially foraging for larvae within the 2° branches (Nuessly and Goeden, 1984). To detect any differences in the searching ability or preferences of the two groups of natural enemies, the larval densities at which predation ( $n=169$ ) and parasitism ( $n=242$ ) occurred were compared. Although both groups of natural enemies attacked larvae at densities of 0.01–0.4 individuals  $\text{cm}^{-1}$  branch, the mean larval densities at which they attacked larvae were significantly different (pooled  $t=2.6$ ,  $P=0.001$ ), rodents attacking larvae at a higher density ( $0.1319 \pm 0.0659$ ) than the parasitoids ( $0.1146 \pm 0.0667$ ).

As larval densities increased from 3 to 1° branches (Nuessly and Goeden, 1984; Müller and Goeden, 1990), the locations of 2° branches on the 1° branches were compared to determine whether the results of the previous test were an artefact of the distribution of predation on the branches. A significant difference (pooled  $t=-4.1$ ,  $P=0.001$ ) between the distribution of larval mortality due to rodents and parasitoids was found along the primary branches, with the rodents apparently preferring larvae on lower 2° branches ( $41.83 \pm 63.397$  cm) than parasitoids ( $53.65 \pm 55.634$  cm). The parasitoids attacked larvae in the thinner branches, which the relatively heavier rodents were less able to reach. Therefore, partitioning of the energy source by natural enemies, both temporally and spatially, limited competition and increased overall utilization of larvae.

#### *Estimated spider predation on C. parthenica adults*

In 1980, Nuessly and Goeden (1984) conducted field studies on spider predation on *C. parthenica* adults in the same area. Spiders were the only predators observed to feed on the moths. Moth densities recorded in 1985 (Fig. 1a) and 1980 data on web densities and capture rates of the two dominant spiders, *Dictyna reticulata* Gertsch & Ivie (Dictynidae) and *Diguetia mojavea* Gertsch (Diguetidae), allowed for the predation rate to be estimated at 7.1, 28.7 and 30.4%, respectively, for each of the three moth generations in 1985/86.

#### DISCUSSION AND CONCLUSION

Field observations on Russian thistle indicate that suitable microsites for early plant development probably are limited by water supply in the soil, causing high density- and herbivore-independent mortality of young plants. Spider predation on moths was estimated to be relatively low in spring when larval predation and parasitism is also minimal (Fig. 3). Hence, the threefold decrease in moth density (Fig. 1a) between the overwintering and first generation seems to be mainly because of this poor host-plant synchronization.

Its colonization period of 10 years did not allow *C. parthenica* to adapt to this host-plant phenology. A delay in the emergence and oviposition period of 1–2 weeks would probably increase the survival rate of the F<sub>1</sub> generation.

Spider predation on moths was the only biotic mortality factor observed during summer. The number of larvae per branch length, however, further decreased in the F<sub>2</sub> generation, mainly as a consequence of plant growth. However, high numbers were found again in the dead or dying plants during the winter. The *C. parthenica* population (moth density per area) slightly increased during summer and peaked again the following spring despite high levels of predation and parasitism of the overwintering larvae (Figs. 2 and 3).

Little information is available on the most important effect of poor host-plant synchronization on the population dynamics of introduced specialized phytophages. Host-plant incompatibility because of misidentifications of insects and plants was found to be a major cause of failure in establishment for introduced biological control agents (Crawley, 1986), but food resources seem to be virtually limitless for biological control agents when they are first introduced. However, asynchronization, like the observed herbivore-independent mortality of seedlings and young plants causing the death of endophagous young larvae unable to move to new host plant individuals, may prevent establishment of introduced biological control agents or reduce the level of weed control (cf. Goeden and Ricker, 1985).

Localized rodent predation of insects imported for biological control of weeds has been reported, but few studies quantified this predation. Petty (1947) reported that three species of rodents were exclusively responsible for the failure of colonies of *Dactylopius* sp. near *confusus* to control *Opuntia aurantica* Lindley in South Africa. Bess and Haramato (1958) found that rodents destroyed up to 51% of populations of *Procecidocares utilis* Stone in Hawaii, where it had been imported to control *Eupatorium adenophorum* Sprengal.

Although several workers mentioned spiders as predators of imported insects (Petty, 1947; Williams, 1950; Wilson, 1960; Huffaker, 1967), the study by Nuessly and Goeden (1984) represents a rare example in which spiders were identified and their impact quantified.

The impact of natural enemies on accidentally or purposely introduced phytophages is highly variable. Crawley (1986) found predators to be about twice as important as parasitoids in preventing establishment and reducing the degree of weed control. Parasitoids often became efficient only after a considerable time lag (Goeden and Louda, 1976; Carl, 1982). In the present study, the two dominant species, *N. perplexus* and *E. strigosa* are both congeners of the native parasitoid fauna of *C. parthenica* in Pakistan, and presumably polyphagous, with a wide range of ecological niches (Müller and Goeden, 1990). Hence, it is not surprising that specialist parasitoids, e.g. endophagous Braconidae, which dominate the native parasitoid complex of *C. parthenica* in Pakistan and the U.S.S.R. (Müller and Goeden, 1990) are



missing in southern California, as species with a closer association with the host plant take longer to adapt than generalists (Carl, 1982; Strong et al., 1984).

The various mortality factors, together with the limited destructive impact of the *C. parthenica* mining, even at relatively high larval densities (Pember-ton, 1986), explain that no measurable impact on plant mortality, plant size or fruiting of Russian thistle has so far occurred in southern California (R.D. Goeden, personal observations, 1977–1989) and, perhaps, elsewhere in North America (Julien, 1987).

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