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LIFE HISTORY AND BEHAVIOR OF *SYNAXIS CERVINARIA* (GEOMETRIDAE), A DEFOLIATOR OF *ARCTOSTAPHYLOS PATULA* (ERICACEAE)

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ABSTRACT. The life stages and behavior of *Synaxis cervinaria* are described from laboratory and field studies conducted in Shasta Co., California, using greenleaf manzanita, *Arctostaphylos patula*, as a host plant. Instars 1 and 2 resemble the green surface and red edges of the expanding leaves, and third instars begin to resemble twigs. The first three instars remain in the crown during the day. Instars 4 and 5 resemble twigs and stems, maintaining stick-like resting positions near the main stem below the crown during the day. The pupae overwinter. Adults emerge in late spring/early summer and oviposition occurs prior to and during manzanita leaf expansion. There is one generation per year.

Additional key words: greenleaf manzanita, crypsis, flight period, leaf consumption.

Synaxis cervinaria (Packard) (Geometridae) was described from an adult male collected in West Springs, California (Packard 1871). McGuffin (1987) described the adult female and genitalia of both sexes but noted that the egg, early larval instars, and pupa were unknown: a description based on a single preserved specimen of a "mature" larva (presumably fifth instar) was given. *Synaxis cervinaria* ranges from British Columbia south to California, and the reported hosts include: Oregon white oak, *Quercus garryana* Hooker (Fagaceae) (Jones 1951); an unidentified *Quercus*; poplar, *Populus* sp. (Populaceae) (McFarland 1965); *Arbutus* (Ericaceae) (McGuffin 1987); willow (Salicaceae); bitterbrush (Rosaceae); cascara and species of *Ceanothus* (Rhamnaceae) (Miller 1995).

In 1990, as part of a broader study of the insect fauna associated with *Arctostaphylos patula* E. Greene (Ericaceae) (Valenti 1994), we found larvae of *S. cervinaria* on this plant near Hat Creek, Shasta Co., California. This manzanita commonly occurs throughout the western United States in montane forest zones (Ball et al. 1983) and is of concern to forest land managers because it often inhibits the survival, regeneration, and growth of conifers (Radosevich 1984). In response to a general lack of information regarding insect fauna associated with chaparral commu-

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nities (Force 1990), especially species of manzanita (Haws et al. 1988), we conducted a study of *S. cervinaria* and its interactions with greenleaf manzanita.

This paper presents life history and behavioral information for *S. cervinaria*, one of six geometrids encountered during our faunal survey (Valenti & Zack 1995) that utilizes greenleaf manzanita as a host plant. The goals of this study were to: 1) determine adult flight period; 2) describe larval stages and behavior and determine stadium lengths; 3) measure leaf consumption of *A. patula* by larvae; 4) establish a list of acceptable foodplants associated with greenleaf manzanita communities in the Hat Creek area; and 5) identify natural enemies of eggs and larvae.

MATERIALS AND METHODS

Synaxis cervinaria laboratory studies, rearings, and adult collections were conducted at the Forest Insect Laboratory, USDA Forest Service, Hat Creek, California. Field studies were conducted at two sites in Shasta Co., California. The first site was adjacent to the USDA Forest Service Work Center at Hat Creek (T34N R4E S16) (elev. 1018 m) and contained a variety of woody plant species. Greenleaf manzanita accounted for less than 30% (canopy coverage) of the total vegetation. Other common plants included: sagebrush (*Artemesia tridentata* Nuttall) (Compositae), curl-leaf mountain-mahogany (*Cercocarpus ledifolius* Nuttall), birch-leaf mountain-mahogany (*C. betuloides* Torrey & A. Gray), antelope bitterbrush (*Purshia tridentata* [Pursh] de Candolle) (Rosaceae), California black oak (*Quercus kelloggii* Newberry) (Fagaceae), ponderosa pine (*Pinus ponderosa* Lawson), sugar pine (*P. lambertiana* Douglas), white fir (*Abies concolor* [Gordon & Glendinning] Lindley), Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco), incense cedar (*Calocedrus decurrens* [Torrey] Florin), and western juniper (*Juniperus occidentalis* Hooker) (Pinaceae). The second site (elev. 1512 m) was 3.2 km northwest of California Route 89 near Logan Lake in Old Station, ca. 24 km south of Hat Creek (T32N R4E S2&3). Dominant vegetation (canopy coverage) consisted of greenleaf manzanita (74%), tobacco brush (11%), *Ceanothus velutinus* Hooker (Rhamnaceae), and ponderosa pine (9%). This 50+ ha site is on an east-facing slope and was mechanically cleared of all vegetation in 1976 and planted with ponderosa pine in 1977.

During 1991 and 1992, a 15 watt black light was used at the Hat Creek Forest Insect Laboratory to determine the flight period of *S. cervinaria*. All adults collected from 2100–2300 h each evening were tallied, a portion of the males was retained as vouchers, and most females were placed in covered 236 ml plastic cups for egg collection. Be-

havioral data, including egg-laying, were obtained by observing adults in the field and in screen cages (45 × 45 × 75 cm).

Larval rearing containers were constructed from clear plastic cylindrical tennis ball containers 20 cm in height and 7 cm in diameter. A single neonate larva was placed on a greenleaf manzanita branch in each of 30 containers. Larval development under ambient conditions was observed daily until pupation. Foliage was replaced once, following the fourth instar molt. Frass of the first four instars was collected from the bottom of each rearing container when foliage was changed, and again after pupation. All leaves damaged by the fifth instars were collected, pressed, mounted to sheets of standard card stock, and missing portions of each leaf were drawn freehand. A digitizer was then used to measure leaf area consumed (cm^2). Frass weight was used to estimate leaf area consumption for first through fourth instars. Head capsule widths and total body lengths of 30 individuals in each instar (reared in 45 × 45 × 75 cm cages) were measured to the nearest 0.05 mm using an ocular micrometer.

A host suitability study was conducted by placing 15–40 unfed first instars onto foliage from various plants in the families Pinaceae, Compositae, Ericaceae, Fagaceae, Rhamnaceae, and Rosaceae. Observations were made daily to determine if larvae were feeding and continuing to develop. This procedure was repeated for a group of fourth instars that had previously fed on greenleaf manzanita foliage.

One day old egg masses collected from captured females were placed in the field. Prior to larval eclosion (ca. 10 days), egg masses were collected and transferred to Petri dishes. Adult parasitoids that emerged from eggs were collected and preserved. Larvae from a laboratory colony were periodically placed onto greenleaf manzanita branches in the field; those recovered several days later were reared individually to obtain parasitoids.

Statistix© was used to perform all statistical analyses (Siegel 1992), following methods of Steel & Torrie (1980). Representative voucher specimens of all taxa have been deposited in the Maurice T. James Entomological Collection at the Department of Entomology, Washington State University, Pullman, Washington.

LIFE HISTORY

Adult. Adult *S. cervinaria* flew at Hat Creek from early June to late July in 1991 and mid-May to late June in 1992 (Fig. 1). Adults have historically been collected in April, May, and June (Jones 1951), and early July (one specimen in the Essig Museum of Entomology, University of California Berkeley). Thus, based on these collection records and our data there appears to be one generation per year.

During 1991, 160 males and 166 females were collected giving a capture sex ratio of nearly 1:1. In 1992, 102 males and 114 females were collected (1.0:1.1 ratio). Adults survived up to 11 days in captivity. More than 94% of captured females produced eggs. All egg-producing females were fertile. Many *S. cervinaria* females attracted to the black light

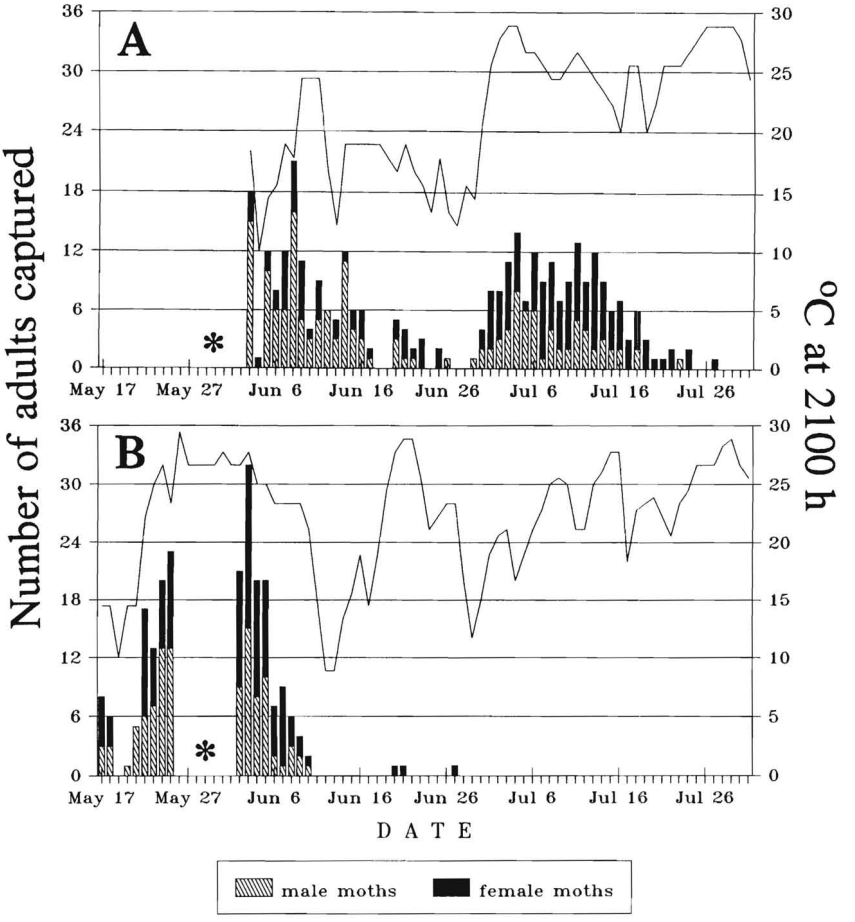

FIG. 1. Flight period of *Synaxis cervinaria* in 1991 (A) and 1992 (B). All adults attracted to a 15 watt black light were collected nightly from 2100–2300 h at the Forest Insect Laboratory, USDA Forest Service, Hat Creek, California. Asterisks indicate adults not collected before 2 June 1991 nor between 26 May and 1 June 1992.

showed little or no sign of wear (Fig. 2A), and had likely emerged within a few days of capture. Virgin females placed in screen cages with adult males for 24 h produced viable eggs. These observations strongly suggest mating occurs soon after emergence from overwintering pupae. Although mating in the field or laboratory was never observed, adults of at least some other geometrid species (e.g., *Stamnodes animata* [Pearsall]) are known to mate prior to flight (Furniss et al. 1988). An adult female collected in 1989 had seven spermatophores within her bursa (K. Bolte, pers. comm.).

Female *S. cervinaria* use their papillae anales to locate a leaf edge. Eggs are deposited along the leaf edge, in a single row of several to about 30 (Fig. 2B). Under cramped artificial conditions egg deposition also occurred along the edges of any available substrate (container lids, folded wax paper, cage frames, etc.), and they were often layered two or three deep. Eggs were always oriented with the micropylar end near the substrate edge.

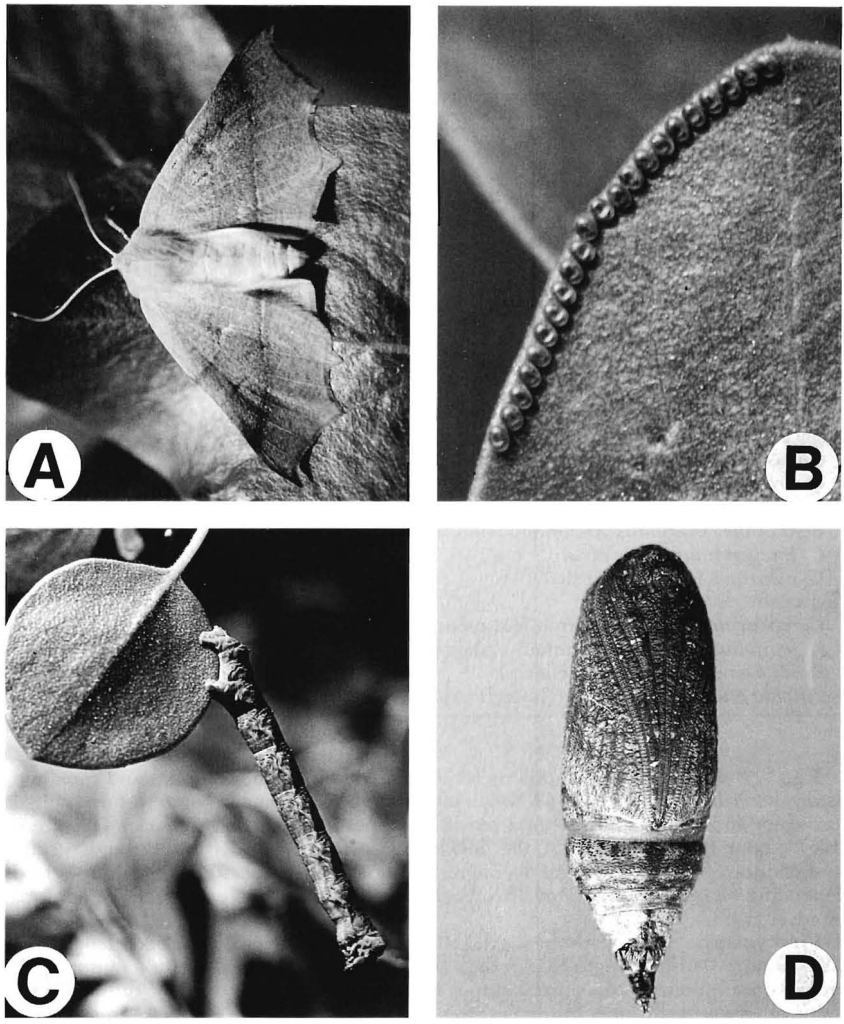

FIG. 2. *Synaxis cervinaria* life stages. A, adult female. B, typical egg mass along leaf edge. C, fifth instar in a typical resting position on a greenleaf manzanita leaf. D, female pupa.

Several egg masses were encountered in the field on greenleaf manzanita leaves and one egg mass was collected from a tobacco brush leaf at the Logan Lake site.

More than 90% of the eggs produced by females in captivity were deposited after 2100 h over a period of three or four nights. In 1991 a total of 159 captured females produced 11,474 eggs for an average of 72 eggs per female (range: 0–230). In 1992, 94 captured females produced 5207 eggs for an average of 55 eggs per female (range: 0–139). Some of these females may have deposited a portion of their eggs before flying to the black light. From a sample of 2110 eggs deposited by 30 females, 1846 produced larvae (87.5% hatching rate).

TABLE 1. Host suitability tests for *Synaxis cervinaria* larvae. No indicates that larvae do not feed and eventually starve to death; yes indicates that larvae feed and continue to grow and develop.

Host family/species	Feeding/frass
Pinaceae	
Abies concolor (white fir)	no
Calocedrus decurrens (incense cedar)	no
Juniperus occidentalis (western juniper)	no
Pinus lambertiana (sugar pine)	no
P. ponderosa (ponderosa pine)	no
Pseudotsuga menziesii (Douglas-fir)	no
Compositae	
Artemesia tridentata (sagebrush)	no
Chrysothamnus viscidiflorus (yellow rabbitbrush)	no
Ericaceae	
Arctostaphylos patula (greenleaf manzanita)	yes
Fagaceae	
Chrysolepis sempervirens (bush chinquapin)	yes
Quercus kelloggii (California black oak)	yes
Rhamnaceae	
Ceanothus cordulatus (mountain whitethorn)	yes
C. integerrimus (deer brush)	yes
C. velutinus (tobacco brush)	yes
Rosaceae	
Cercocarpus betuloides (birch-leaf mountain-mahogany)	yes
C. ledifolius (curl-leaf mountain-mahogany)	yes
Prunus emarginata (bitter cherry)	yes
Purshia tridentata (antelope bitterbrush)	yes

Egg. Smooth, somewhat oblong (0.75 mm wide by 0.95 mm long) and remaining a pale yellowish-green for ca. 24 h following deposition. The eggs begin to turn a pinkish-rose color and then crimson after a second 24 h period (eggs that remain yellow are inviable). About 12 h before hatch, the developing larva becomes visible through a translucent chorion, giving the eggs an overall reddish-gray appearance. Eggs hatch in 7–10 days depending on temperature. Parasitized eggs turn black prior to emergence of adult parasitoids.

First instar. Head capsule width (HCW) 0.45 ± 0.02 mm, total body length (TBL) 2.8–6.9 mm, stadium length (SL) 5 days (range: 4–7 days). Head capsule uniformly light brown; crimson dorsal and ventral stripes from pronotum to A9 dorsally, through A5 ventrally, otherwise translucent until feeding commences, whereupon these areas take on a greenish hue; body lacks protuberances.

Second instar. HCW 0.74 ± 0.03 mm, TBL 6.1–13.3 mm, SL 6 days (range: 5–8 days). Head capsule light brown with three sets of herring-bone patterns, more black than brown; crimson ventral region from cervix to A6 (first pair of prolegs); dorsum and lateral areas greenish-yellow due to food plant material visible through translucent integument; body lacks protuberances.

Third instar. HCW 1.19 ± 0.07 mm, TBL 11.9–21.1 mm, SL 6 days (range: 4–8 days). Head capsule with more pronounced brown herring-bone pattern; fleshy dorsolateral lobes begin to appear on the metathoracic segment late in this stadium; body color varies to some extent; mottled black, brown, and crimson dorsally; ventrally and laterally an array of colors are exhibited including white, yellow, gray, brick red, crimson, brown, and black.

Fourth instar. HCW 1.91 ± 0.10 mm, TBL 18.2–25.5 mm, SL 8 days (range: 5–13 days). Head capsule mottled/stippled brown, crimson, and white; fleshy tubercle at apex

TABLE 2. Greenleaf manzanita leaf consumption by *Synaxis cervinaria* larvae (n = 30). Total number leaves consumed determined by measuring the area of 528 mature leaves from 30 greenleaf manzanita branches to calculate a mean leaf area value (5.32 ± 1.69 cm^2/leaf).

	1st–4th Instars		5th Instar		Percent of total foliage consumed		
	Frass wt. (mg)	Leaf area consumed (cm^2)	Frass wt. (mg)	Leaf area consumed (cm^2)	1st–4th Instars	5th Instar	Total number leaves consumed
Mean	131	8.47	743	47.17	15.2	84.8	10.45
SE	16	1.82	13	6.60	2.2	2.2	1.82

of clypeus; dorsolateral metathoracic fleshy lobes more pronounced; A4, A5, and A8 dorsally with prominent paired chalazae; paired, dark colored ventrolateral and lighter colored ventromedial chalazae on A1; body coloration varies from crimson red to mottled gray with whitish hourglass patterns dorsally. These color variations are similar to those observed in both live and dead greenleaf manzanita twigs and branch stubs.

Fifth instar. HCW 2.83 ± 0.10 mm, TBL 24.3–35.2 mm, SL 14 days (range: 9–21 days). Head capsule mottled/stippled light to dark brown, crimson, and white; fleshy tubercle at apex of clypeus; dorsolateral metathoracic fleshy lobes less pronounced; A4, A5, and A8 with prominent, paired chalazae dorsally, paired dark colored ventrolateral and lighter colored ventromedial chalazae on A1; body coloration and color patterns, as in instar four, extremely variable. Stem/twig mimicry by cryptic morphology and behavior are pronounced in the fifth instar (Fig. 2C).

Pupa. Obtect, mottled brown or tan, about 5 mm at the widest point and up to 19 mm in length. Female genitalia span the 8th and 9th abdominal segments (Fig. 2D) whereas the male genitalia on the 9th segment only has a raised longitudinal border. Pupation occurs in leaf litter below host plants.

BIOLOGICAL NOTES

Larval behavior. Larvae developed normally on a variety of woody plants, but not on conifers or composites in the feeding trials (Table 1). Feeding tests on greenleaf manzanita showed that larvae (n = 30) consumed, on average, a total of 55.64 ± 7.48 cm^2 of foliage or 10.45 ± 1.82 expanded leaves (Table 2).

Neonate larvae emerge from eggs by using their mandibles to chew along a visible circular suture on the micropylar end of the egg, leaving a whitish-translucent shell with an apical exit hole. No parts of the chorion are consumed. There was no evidence of cannibalism for this or any subsequent instar, even under crowded conditions with no available food. Early instars feed by grazing the outer layers of cells from old and new foliage (greenleaf manzanita is a broadleaf evergreen that retains its leaves for more than one year), and although new foliage is preferred, larvae can develop normally on old foliage. Larval activity in late spring coincided with greenleaf manzanita leaf expansion. At the Logan Lake site, leaves first began to expand between 14–21 June in 1991 and 1–5 June in 1992, about 10 days later than at Hat Creek (494 m lower in elevation) where adults were surveyed.

First instars released onto greenleaf manzanita branches in the field usually remained on or close to (within 15 cm) the leaf on which they were originally placed. Occasionally a larva would be found on a lower stem, possibly forced from an upper branch after disturbance by wind or predator. Unidentified species of ants (Formicidae) were ubiquitous and occasionally approached larvae which then dropped from their perch on a silken thread. Eight such encounters were observed in the field but none resulted in captured larvae.

Prior to the first molt, the ventral area remains crimson but the dorsal stripe degenerates, and the dorsum and lateral areas become greenish-yellow. Laboratory-reared larvae were often observed in the evening suspended from silken threads (1.5–2.5 cm) or maintaining a characteristic stick-like appearance on the edge of a leaf (typical resting posture). The body is held in a straight and stiff position at a 30–45° angle to the substrate (usually a leaf or branch) to which the prolegs are attached, always with a silk thread from the head to an attachment site on the substrate. Larval feeding was observed both day and night.

Second instars feed by grazing on leaf surfaces and occasionally create a small hole in maturing leaves. Newly expanding leaves are sometimes consumed by feeding along the leaf edge. Larvae released in the field tended to remain on or near the point of placement if left undisturbed, similar to behavior observed for first instars.

Third instars released in the field begin to move about on the foliage, more so than the first and second instars, but they still remain relatively close to the point of release. A stick-like resting posture is maintained on or near foliage. Feeding usually occurs along leaf edges and whole leaf sections are removed.

The significance of cryptic coloration in the first three instars is not well understood. They are exposed in the canopy and presumably would be vulnerable to bird predation. However, field exclosure experiments revealed that birds had no significant effect on the survival of instars 1–3 (Valenti 1994).

Stem mimicry and crypsis in the fourth instars is made possible by a combination of resting posture, morphology, and coloration. During the day, larvae in this stadium begin to move down and away from the crown. Typically, fourth instars released in the field would be found in a 30–45° resting posture on a main stem below the crown. Larvae at this stage can consume entire leaves and feed nocturnally.

The molt to the fifth instar begins with the late fourth instar terminating its feeding and hanging by the prolegs with its head downward for several hours (the process described here is similar for the other instars). The cuticle splits at the vertex and the old head capsule is sloughed off by the thoracic legs. With undulating body movements, the

old skin is forced up towards the prolegs. Once the exuvium is slipped over the first pair of prolegs (A6) the larva transfers its anterior end back up to the leaf or branch, secures a perch with the thoracic legs, and then slips its posterior end out of the remaining old cuticle. The prolegs are then firmly attached to the branch along with a silk thread near the head. Once initiated, the entire molting period lasts about five minutes. The larva maintains itself in a typical motionless, stick-like appearance while it hardens and darkens. The shriveled exuvium remains attached to the branch, often long after molting is complete.

Fifth instars account for ca. 36% of the entire larval developmental period and inflict the most damage to greenleaf manzanita foliage (85% of the total amount of foliage consumed) (Table 2). They feed at night on entire leaves and remain in the lower crown or near the plant base during the day.

Fourth and fifth instars avoid detection by visually searching predators (e.g., birds) by resting during the day below the crown. Their resemblance to stems and twigs and their resting posture make them very difficult to detect. Although we never observed significant defoliation in the field and there have been no outbreaks of *S. cervinaria* reported in the literature, caged larvae completely defoliated greenleaf manzanita plants, suggesting that this geometrid is strongly regulated at low densities by natural enemies. Exclosure experiments in the field supported this supposition; in the absence of birds and ants larval survival increased nearly five-fold (Valenti 1994).

Pupae. The fifth instar drops or crawls to the ground and burrows one to two cm beneath the leaf litter surface where it spins a loose cocoon attached to pieces of litter and detritus. After 4 days (range: 3–7 days) the molting period is complete and a hardened and darkened pupa is formed. The pupa overwinters. The average weight of 30 pupae was 233 ± 22 mg. Adults emerged from pupae cold treated at 4°C for 90–120 days.

Natural enemies. Two species of wasps were reared from parasitized *S. cervinaria* eggs: *Trichogramma* sp. (Hymenoptera: Trichogrammatidae) and *Telenomus alsophilae* Viereck (Hymenoptera: Scelionidae). Individual parasitized *S. cervinaria* eggs produced two to five individuals of *Trichogramma* sp. or a single individual of *Telenomus alsophilae*.

Several parasitoids were reared from *S. cervinaria* larvae (instars attacked are in parentheses): *Campylochaeta* sp. (Diptera: Tachinidae) (4,5), *Aleiodes* n. sp. (Hymenoptera: Braconidae) (3), *Meteorus rubens* (Nees) (Hymenoptera: Braconidae) (1–5), *Dusona nigritibialis* (Viereck) (Hymenoptera: Ichneumonidae) (3–5), *Euplectrus* sp. poss. *plathypenae* Howard (Hymenoptera: Eulophidae) (1–5).

In the field, a female *Goniozus gracilicornis* (Kieffer) (Hymenoptera: Bethylidae) was observed dragging a moribund third instar of *S. cervinaria* across a greenleaf manzanita leaf. It is unknown if it had paralyzed the larva. On three occasions spiders where observed successfully attacking *S. cervinaria* larvae. These were *Misumenops celer* (Hentz) (Araneae: Thomisidae), *Xysticus* sp. (Araneae: Thomisidae), and *Metaphidippus* sp. (Araneae: Salticidae).

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