

# Bioecology of *Stenoma catenifer* (Lepidoptera: Elachistidae) and Associated Larval Parasitoids Reared from Hass Avocados in Guatemala

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**ABSTRACT** A 10-wk study of the avocado seed-feeding moth *Stenoma catenifer* Walsingham (Lepidoptera: Elachistidae), was conducted in a commercial ‘Hass’ avocado (*Persea americana* Miller [Lauraceae]) orchard in Guatemala. Up to 45% of fruit in the orchard were damaged by larval *S. catenifer*. Larval-to-adult survivorship for 1,881 *S. catenifer* larvae in Hass fruit was 37%, and adult sex ratio was 51% female. Four species of larval parasitoid were reared from field-collected *S. catenifer* larvae. The most common parasitoid reared was a gregarious *Apanteles* sp., which parasitized 53% of larvae and produced on average eight to nine cocoons per host. *Apanteles* sp. sex ratio was 47% female and 87% of parasitoids emerged successfully from cocoons. *Apanteles* sp. longevity was  $\approx 1.5$  d in the absence of food, and when provisioned with honey, parasitoids survived for 5–7 d. The mean number of cocoons produced by *Apanteles* sp. per host, and larval parasitism rates were not significantly affected by the number of *S. catenifer* larvae inhabiting seeds. Oviposition studies conducted with *S. catenifer* in the laboratory indicated that this moth lays significantly more eggs on the branch to which the fruit pedicel is attached than on avocado fruit. When given a choice between Hass and non-Hass avocados, *S. catenifer* lays up to 2.69 times more eggs on Hass.

**KEY WORDS** *Apanteles* sp., *Brachycyrtus* sp., life table, *Macrocentrus* sp., oviposition choice tests

California is the largest producer of avocados (*Persea americana* Miller [Lauraceae]) in the United States (Hoddle et al. 2003). In the 2005–2006 growing season, the avocado harvest in California was worth  $\approx$ US\$341 million, and ‘Hass’ accounted for 95% of the  $\approx$ 273,000 tonnes harvested from 25,500-bearing ha (CAC 2007). California avocado production is under increasing risk from invasive arthropod species that originate in areas outside of California (Hoddle 2004). Some of the most worrisome infiltration threats to California producers are specialist herbivores that have evolved to feed on avocado fruit and foliage in the home range of this plant in Mexico and Central America. Of most concern are moths, weevils, and fruit flies that feed internally on fruit. These internal fruit feeders are currently absent in California, but they have the potential to invade, establish, and cause substantial economic damage. The threat posed by specialist internally feeding fruit pests has increased markedly with the legalization of fresh fruit imports into California from Mexico. Imports from Mexico began for the first time in February 2007, thereby ending a Federal ban on fresh avocado imports that had been in place since 1914.

One pest insect of particular interest for California from a biosecurity viewpoint is the avocado seed-feeding moth *Stenoma catenifer* Walsingham (Lepi-

doptera: Elachistidae), a specialist herbivore on members of the Lauraceae (Cervantes Peredo et al. 1999). *S. catenifer* is native to Neotropical areas, and it is considered to be one of the most important pests of avocados in Mexico, Central, and South America (Wysoki et al. 2002). It has been recorded attacking avocados in Mexico (Arellano 1975; Mendez Villa 1961; Muniz Velez 1958; Wolfenbarger and Colburn 1966, 1979), El Salvador (Wolfenbarger and Colburn, 1966), Guatemala (Popenoe 1919), Honduras (Sasscer 1921), Venezuela (Boscán de Martínez and Godoy 1984), Guyana (Cervantes Peredo et al. 1999), Peru (Wysoki et al. 2002), and Argentina (Wysoki et al. 2002). In Brazil, *S. catenifer* is the major pest limiting commercial avocado production (Hohmann et al. 2003). The principle economic loss is caused by larvae feeding on fruit, which not only disfigures fruit externally and internally but also can promote premature fruit drop. Crop losses of 60 and 80% have been recorded in Brazil and Venezuela, respectively, despite intensive broad-spectrum pesticide use (Boscán de Martínez and Godoy 1982, Nava et al. 2005a). Similarly in Mexico, up to 95% of fruit can be attacked and monthly insecticide treatments are recommended for control (Wysoki et al. 2002). In addition to fruit, *S. catenifer* larvae can attack and kill young twigs and stems (Wolfenbarger and Colburn 1979), and heavy infestations of stem-mining larvae can kill young avocado trees (Cervantes Peredo et al. 1999). Colored photographs of *S. catenifer* eggs, larvae, pupae, and

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adults, along with fruit damage are available (Hoddle 2007).

Trichogrammatids can parasitize up to 60% of *S. catenifer* eggs in Brazil, which is insufficient to prevent substantial economic losses (Hohmann et al. 2003), but augmentative field releases of these natural enemies may be feasible (Nava et al. 2007). A variety of braconid and ichneumonid parasitoid species have been recorded attacking *S. catenifer* larvae (Cervantes Peredo et al. 1999, Hohmann et al. 2003, Nava et al. 2005a), with *Apanteles* sp. (Braconidae) inflicting  $\approx 30$ –40% mortality (Boscán de Martínez and Godoy 1982, Nava et al. 2005a).

Most of the published field and laboratory work on *S. catenifer* has come from Brazil, and it has focused on the commercial avocados 'Margarida', 'Breda', and 'Beatriz' (Ventura et al. 1999, Nava et al. 2006). In addition to these three cultivars, Hohmann et al. (2000) field evaluated the susceptibility of an additional 19 avocado cultivars to attack by *S. catenifer*. Hass, the avocado cultivar of most commercial importance to California, Mexico, and emerging industries in Costa Rica and Guatemala, has not been surveyed extensively for *S. catenifer* activity in the latter three countries in which *S. catenifer* has been recorded. In response to this lack of published information, an  $\approx 10$ -wk study of *S. catenifer* was undertaken in a commercial Hass avocado orchard in Guatemala. The objectives of this study were to 1) document the larval parasitoid fauna attacking *S. catenifer* and parasitism levels by parasitoid species; 2) quantify basic life history parameters of the most common parasitoid species (e.g., emergence rates, adult longevity, and sex ratio) in the laboratory; 3) investigate in the field attack patterns and levels on Hass fruit by *S. catenifer*; and 4) study in the laboratory the oviposition behavior of this moth.

## Materials and Methods

**Field Site and Fruit Collections for *Stenomoma catenifer*.** An  $\approx 5$ -ha commercial Hass avocado orchard consisting of  $\approx 800$  trees in San Miguel Dueñas, Sactepequez, Guatemala ( $14^{\circ} 31.461$  N,  $90^{\circ} 46.579$  W; elevation 1,500 m) was used for this study over the period 19 January 2007 to 31 March 2007. This study site was selected based on results of a broader survey of avocados in Guatemala for fruit-feeding Lepidoptera (Hoddle and Hoddle 2008). Trees in the Hass orchard were  $\approx 5$ -yr old,  $\approx 4$ –5 m in height, and canopies were separated by  $\approx 5$ –7 m of clear ground allowing full sun exposure. The orchard was treated with malathion three times (rate of application and interval frequency data were not available) in December 2006, and no subsequent treatments were made during this study. Every 2–4 d, at least 50–60 randomly selected trees in the orchard were inspected for *S. catenifer* damaged fruit. From each sampling event,  $\approx 200$  damaged fruit exhibiting frass accumulations, periseitoid exudates, or obvious holes were harvested and returned to the laboratory for rearing of *S. catenifer* larvae.

**Attack Levels and Damage Patterns in the Field.** On three sampling dates (12 and 27 February and 19 March 2007), 20 randomly selected trees had each of 10 randomly selected fruit examined for *S. catenifer* damage. Of these 600 examined fruit that had been set on trees during the principle flowering period, the number damaged was recorded by sampling date. Additionally, on four separate occasions (25 January, 12 and 25 February, and 2 March 2007), a cumulative total of 253 damaged fruit were inspected for *S. catenifer* holes. The number of holes and their position in either the top, middle, or bottom third of the fruit were recorded.

**Rearing of *S. catenifer* Larvae and Estimation of Parasitism Levels under Laboratory Conditions.** Damaged Hass avocados collected at the field site were returned to the laboratory, and they were kept for 10–14 d in collapsible ventilated insect rearing cages (BugDorm-2120, [60 by 60 by 60 cm], Mega-View Science Education Services, Taichung, Taiwan) that were labeled by collecting date. Fruit were inspected daily, and emerged mature *S. catenifer* larvae wandering in cages searching for pupation sites were isolated and kept in labeled clear plastic cups with ventilated lids. After the 10–14-d holding period, all fruit from a particular harvest date were opened, and avocado seeds showing recent *S. catenifer* activity were cleaned of fruit pulp and isolated individually in labeled clear plastic cups with ventilated lids. The total number of larvae living in each seed was recorded as the number of larvae emerging from each seed, which was combined with the number of *S. catenifer* (pupae, dead, or parasitized larvae) found within cavities after the dissection of seeds after larval emergence ceased.

Immature larvae feeding on pulp were removed from fruit and used to inoculate clean uninfested avocado seeds. A no. 2 cork borer (4.0 mm in diameter) was used to punch a  $\approx 1.5$ -cm-deep hole into a seed. The head of the walking *S. catenifer* larva that had been extracted from pulp was aligned with the artificial hole, and  $\approx 99\%$  of immature larvae readily entered seeds in this manner. Most larvae quickly closed the entrance of the artificial tunnel with a very thin silk barrier, and within 20–30 min accumulating frass sealed the tunnel opening. Hass avocado seeds inoculated in this manner readily supported the complete development of *S. catenifer* larvae as seed deterioration was not significant enough to cause rearing problems. All rearing cups were observed daily until the fate of *S. catenifer* larvae was recorded as having pupated, or died from parasitism or unknown causes. Survivorship and mortality data for 1,881 *S. catenifer* larvae reared from field collected Hass avocados were used to construct a partial life table for this pest.

All rearing and laboratory experiments were conducted in a well-lit room under natural daylight and lengths ( $\approx 12$  h) at  $22.14 \pm 0.13^{\circ}\text{C}$  and  $74.12 \pm 3.76\%$  RH (temperature and humidity measured with a Hobo data logger [Onset Corp., Bourne MA] at 60-min intervals).

**Parasitoid Studies.** All larval parasitoids reared from *S. catenifer* were kept for identification. The most

common parasitoid was a gregarious *Apanteles* sp. (Braconidae) (see below). Larvae of this parasitoid emerged from fifth instars of *S. catenifer*, remained externally attached to the host until it died, and then pupated in silk cocoons on the withered host cadaver. The following data were collected for this parasitoid: 1) number of *Apanteles* sp. cocoons externally attached to each parasitized *S. catenifer* larva at time of death, 2) proportion of larvae successfully spinning cocoons, and 3) sex ratio and emergence rates of adult parasitoids. 4) Longevity of male and female *Apanteles* sp. that emerged from cocoons into plastic vials either provisioned with honey or lacking honey was determined by observing parasitoids at 9:00 a.m., 1:00 p.m., and 5:00 p.m. daily. Parasitoid longevity was calculated in hours, and when mortality occurred within a given time interval, the length of the observation window was halved and added to the total time alive up to the point of death. 5) Parasitism rates and whether the number of parasitoids produced per *S. catenifer* larva was affected by the number of individual *S. catenifer* larvae inhabiting a single avocado seed were investigated. The number of *S. catenifer* larvae reared per seed ranged from 1 to 7 (see below), and seeds with >2 larvae produced noticeably smaller fifth instars in comparison with seeds with one larva. Based on these observations, two hypotheses were tested to investigate the effect of increasing numbers of *S. catenifer* larvae per seed and parasitism. Hypothesis 1: the mean number of parasitoids emerging and successfully coooning from small hosts would be reduced as a consequence of resource limitation, and 2) as the number of larvae inhabiting a seed increased, the proportion of larvae successfully parasitized would decline because of egg limitation experienced by the female parasitoid exploiting the host patch.

**Statistical Analyses.** Parasitoid longevity data were subjected to Box-Cox transformation, and they were analyzed using two-way analysis of variance (ANOVA) (sex [male or female] by food treatment [honey or no honey]) to determine whether statistically significant differences in longevity existed between sexes and across food treatments. The proportion of *S. catenifer* larvae attacked in relation to the total number of larvae in a seed was analyzed with a chi-square test to determine whether larval density per seed affected the proportion parasitized. A nonparametric one-way ANOVA was performed to determine whether the mean number of parasitoid pupae produced per host was affected by the number of *S. catenifer* larvae inhabiting a single avocado seed. All statistical analyses were conducted at the 0.05 level of significance in SAS (SAS Institute 1990).

**Colony Establishment and Oviposition Studies.** Adult *S. catenifer* reared from pupae that had developed from field collected fruit were maintained in a collapsible ventilated insect rearing cage (BugDorm-2120, [60 by 60 by 60 cm], MegaView) and provisioned with 10% honey water (Nava et al. 2005b). At any time,  $\approx 10$ –15 male and female pairs of moths were present in the oviposition cage. Two different oviposition studies were conducted with this cage set up: 1) de-

termination of egg placement when avocado fruit were presented with the fruit pedicel still attached to a branch, and 2) investigation of egg laying preferences of female *S. catenifer* if given a choice between clonal Hass and non-Hass (i.e., fruit from unmanaged backyard trees that were grown from avocado seeds of unknown heritage) fruit at 85% maturity.

**Experimental Setup of Oviposition Studies.** Hass fruit used in egg placement studies were taken from a commercial Hass orchard (Sumpango, Sactepequez, 14° 40.292 N, 90° 43.195 W; elevation 1,600 m) that was *Stenoma*-free and had received no insecticide treatments for at least 10 wk before fruit harvest for experiments. For the oviposition placement experiment, six to seven thoroughly hand washed and dried avocados that were 85% mature were placed in the *S. catenifer* oviposition cage on egg crating that was raised 10 cm off the ground. Fruit were arranged vertically on egg crating with pedicels and attached branches projecting upwards and were left in the cage exposed to moths for 3–4 d before being removed. The numbers of eggs laid were recorded according to placement in four different areas: 1) on the fruit, 2) in the crevice where the pedicel adhered to the fruit, 3) the pedicel, and 4)  $\approx 20$ -cm piece of branch the pedicel was attached, too. The egg placement experiment was repeated three times. The oviposition preference experiment between Hass and non-Hass avocados was conducted in a similar manner to the egg placement experiment except the oviposition cage was stocked with 10 or 12 avocados half of which were Hass and the remainder being non-Hass. Hass fruit were sourced from the same orchard as fruit used for the egg placement study, whereas 85% mature non-Hass fruit were sourced from an unmanaged backyard plant in San Pedro Las Huertas (Sacatepequez, 14° 31.930 N, 90° 44.073 W; elevation 1,500 m). *S. catenifer* activity was not observed at this site or at other sites in the immediate vicinity with abundant non-Hass avocados despite extensive surveys for this moth on unmanaged avocados in San Pedro Las Huertas. All handpicked fruit were thoroughly hand washed, dried, and presented with pedicels attached to an  $\approx 20$ -cm piece of branch. Fruit were left exposed to ovipositing moths for 4–7 d in the oviposition cage before total numbers of eggs across all structures for each fruit type were recorded. This choice test was repeated four times.

**Statistical Analyses.** Egg placement data were initially analyzed with multinomial logistic regression to determine whether significant differences in proportions of eggs laid by site varied across trials. There was no significant trial date effect (Wald  $\chi^2 = 1.87$ , df = 2,  $P = 0.17$ ). Consequently, trial data were combined and analyzed using chi-square test for specified proportions for each of the four egg placement substrates. For the oviposition preference studies between Hass and non-Hass, logistic regression contrast tests were performed to determine whether significant differences in oviposition preferences existed across the four trials. There was no significant trial date effect (Wald  $\chi^2 = 1.06$ , df = 3,  $P = 0.30$ ). Consequently, trial data were combined and a binomial proportion test was performed to

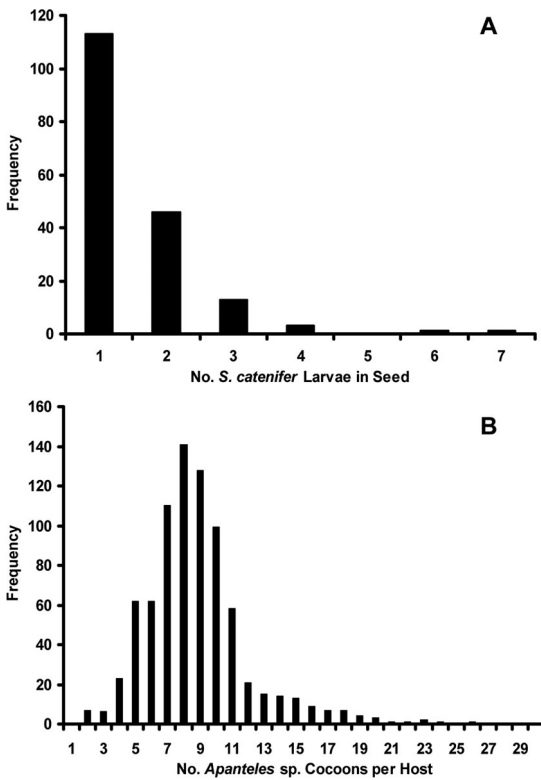


Fig. 1. (A) Density frequency of *S. catenifer* in Hass avocado seeds. (B) Frequency distribution of *Apanteles* sp. cocoons attached to dead *S. catenifer* larvae.

determine whether the proportion of eggs laid on Hass differed significantly from non-Hass. All statistical analyses were conducted at the 0.05 level of significance in SAS (SAS Institute 1990).

## Results

### *S. catenifer* Infestation Patterns in Hass Avocados.

The average level of fruit damage attributable to feeding *S. catenifer* larvae at the field site in San Miguel Dueñas was  $45.50 \pm 1.93\%$ . Of the 253 damaged fruit examined for placement of *S. catenifer* holes, 53, 40, and 7% of holes were in the bottom, middle, and top third of fruit, respectively. The number of holes per fruit ranged from one to four, and  $\approx 14\%$  of fruit had more than one hole. The average number of *S. catenifer* larvae per Hass seed was  $1.52 \pm 0.07$  ( $n = 177$  examined seeds; range 1–7 larvae per seed) (Fig. 1A).

**Parasitism Studies and Partial Life Table for *S. catenifer*.** Four species of hymenopterous parasitoid were reared from *S. catenifer* larvae inhabiting commercially grown Hass avocados. The dominant parasitoid, *Apanteles* sp. (Braconidae: Microgastrinae), accounted for  $\approx 99\%$  of the reared parasitoids. The other parasitoid species reared from *S. catenifer* larvae were *Macrocentrus* sp. (Braconidae: Macrocentrinae; four specimens), *Pristomerus* sp. (Ichneumonidae: Cremastinae; three specimens), and *Brachycyrtus* sp.

Table 1. Partial life table for *S. catenifer* larvae reared from Hass avocados harvested from a commercial orchard in San Miguel Dueñas, Sacatepequez, Guatemala

Life stage	No. entering stage	Cause of mortality	No. dying in stage
Larva	1,881	Parasitism: <i>Apanteles</i> sp.	985
		Parasitism: others	8
		Unknown causes	50
Pupa	838	Unknown causes: females	60
		Unknown causes: males	78
Adult			
Females	357		
Males	343		

Larval-to-adult survivorship, 37%; parasitism, 53%; and sex ratio, 51% female.

(Ichneumonidae: Labeninae; one specimen). Survivorship for *S. catenifer* larvae inside fruit to adulthood was 37%, larval parasitism was 53%, and the sex ratio of emerging moths was 51% female (Table 1).

**Basic Life History Observations on *Apanteles* sp.** The mean number of *Apanteles* sp. cocoons produced per *S. catenifer* host was  $8.78 \pm 0.11$  ( $n = 795$  *S. catenifer* larvae examined; range of cocoons per host 2–26; Fig. 1B). Of the 4,152 adult *Apanteles* sp. sexed, 53% were male, and of the 4,662 parasitoid cocoons examined, 87% of parasitoids emerged successfully. During the course of parasitoid cocooning observations, 19 isolated parasitized *S. catenifer* larvae with a total of 179 externally attached parasitoid larvae were observed daily from the time parasitoids emerged from hosts. Of these parasitoid larvae, 42.46% failed to spin silk cocoons and died, suggesting that estimates of the number of parasitoids produced per host based on cocoon counts may be an under estimate of the number of parasitoid larvae that emerge per host. Parasitoid longevity was significantly affected by access to food ( $F = 45.89$ ;  $df = 3, 97$ ;  $P < 0.001$ ). In the absence of honey, there was no significant difference between males and females with respect to longevity as both sexes lived for  $\approx 35$  h before dying. When provisioned with honey, parasitoid longevity increased significantly by 3.5–4.8-fold in comparison with conspecifics with no food, and males (average longevity of 169.50 h) lived 38% longer than females (122.47 h) (Fig. 2). The proportion of *S. catenifer* larvae parasitized by *Apanteles* sp. was not significantly affected by the number of hosts living in a single seed (Wald  $\chi^2 = 10.39$ ,  $df = 5$ ,  $P = 0.07$ ). The mean number of *Apanteles* sp. cocoons produced per *S. catenifer* was not affected by the number of hosts inhabiting a single seed ( $F = 0.71$ ;  $df = 5, 164$ ;  $P = 0.62$ ). The following was determined from 260 *S. catenifer* larvae reared from 179 individually isolated seeds that were split open and examined for the effect of larval density on parasitism rates and parasitoid cocoon numbers: 32.31% of larvae pupated outside of the seed, 2.69% pupated within the seed, 30.38% died of parasitism outside of the seed where parasitoids spun cocoons, and 34.62% of *S. catenifer* larvae died from parasitism (with parasitoid cocoons attached) within seeds.



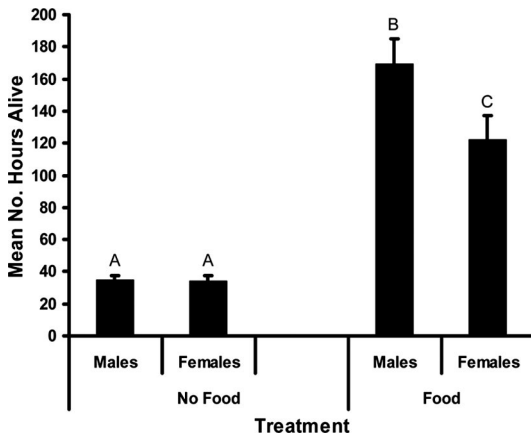


Fig. 2. Longevity of *Apanteles* sp. males and females with-out access to food or provisioned with food (i.e., honey). Different letters indicate significant differences in longevity at the 0.05 level of significance (Tukey-Kramer used for means separation).

**Oviposition Studies.** Results of the chi-square test for specified proportions for *S. catenifer* eggs laid on each of the four egg placement substrates showed significant differences between observed and expected frequencies ( $\chi^2 = 12.40$ ,  $df = 3$ ,  $P < 0.005$ ). This result indicated that *S. catenifer* females showed a very strong preference for ovipositing on branches (especially on the cut ends of the branch) to which the fruit pedicel was attached. No statistical differences existed between proportions of eggs laid on fruit, between the pedicel and fruit, and on the pedicel (Fig. 3A). Ovipositing *S. catenifer* showed a strong preference for Hass avocados over non-Hass when both fruit types were presented simultaneously to female moths and significantly more eggs ( $Z = 12.14$ ,  $P < 0.0005$ ) were laid on Hass (Fig. 3B).

### Discussion

In a commercial Hass avocado orchard in Guatemala, *S. catenifer* populations that had been sprayed with malathion caused observable damage to 45.5% of fruit hanging in surveyed trees. In comparison with fruit damage estimates for other varieties of avocados, this level of damage to Hass fruit ranks this cultivar as extremely susceptible to *S. catenifer*, placing it within the three most susceptible varieties for which damage data have been published (Hohmann et al. 2000). The majority of tunnel entrance holes made by *S. catenifer* were in the middle (40%) and bottom (53%) third of the fruit, supporting previous findings by Hohmann et al. (2003). One possible reason that larvae tunnel into the lower portions of fruit could be to take advantage of gravity for clearing accumulating frass and periseitol from tunnel entrances. Tunnel entrances on the top of fruit (7% of holes) around the pedicel cannot be readily cleared by larvae unless they emerge from holes to push excreta off the shoulder of the fruit. Clearing entranceways in this manner could unnecessarily expose larvae to attacks by natural enemies.

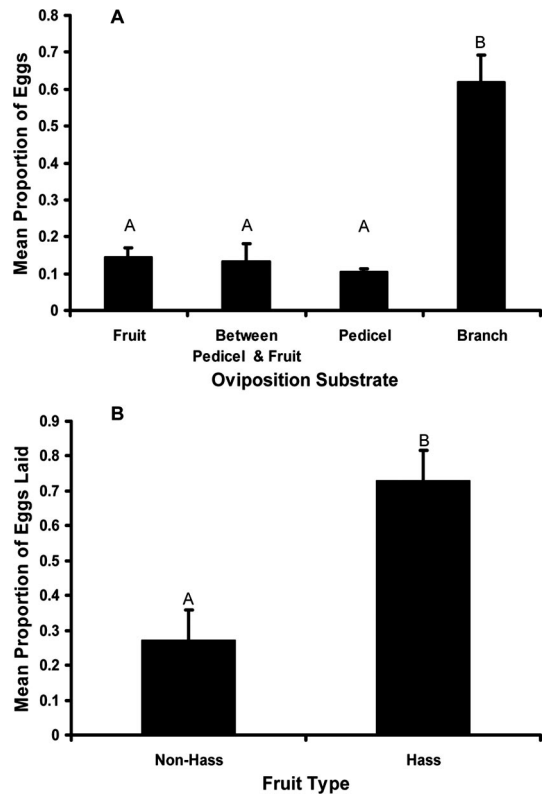


Fig. 3. (A) Mean proportion of eggs laid by female *S. catenifer* in four different places on Hass avocados. (B) Mean proportion of eggs laid by *S. catenifer* when given a simultaneous choice between Hass and non-Hass avocados. Different letters indicate significant at the 0.05 level of significance.

Results from this study indicate that *S. catenifer* larvae infesting Hass avocados were attacked by four undetermined species of koinobiont endoparasitoids in the genera *Apanteles* sp., *Macrocentrus* sp. (both Braconidae, the latter is a solitary parasitoid), *Pristomerus* sp., and *Brachycyrtus* sp. (both Ichneumonidae and solitary parasitoids). This work is the first to document the solitary parasitoid species *Macrocentrus* sp. and *Brachycyrtus* sp. attacking *S. catenifer*. Nava et al. (2005a) and Cervantes Peredo et al. (1999) list *Apanteles* sp., *Dolichogenidea* sp., *Hypomicrogaster* sp., *Chelon* sp., *Hymenochaonia* sp., (all Braconidae), *Euleleboea* sp., and *Pristomerus* sp. (latter two are Ichneumonidae) parasitizing *S. catenifer* larvae in South America.

In this study, the dominant parasitoid accounting for  $\approx 99\%$  of reared parasitoids was a gregarious *Apanteles* sp., which parasitized 53% of field collected *S. catenifer* larvae infesting Hass avocados. The relatively high level of parasitism observed by *Apanteles* sp. in Hass avocados that had been treated repeatedly with a broad-spectrum insecticide strongly suggests that this natural enemy may play an important role in regulating populations of *S. catenifer* in commercial orchards despite insecticide use. In Brazil and Vene-

zuela, solitary *Apanteles* spp. have been documented as being among the most common parasitoids parasitizing *S. catenifer* larvae in avocados at rates ranging from 31 to 33% in Venezuela (Boscán de Martínez and Godoy 1982) and contributing to 30–40% parasitism levels observed in Brazilian avocado orchards that had been treated heavily with insecticides (Nava et al. 2005a).

Basic laboratory studies indicated that adult *Apanteles* sp. that are provided access to a nutritive resource (i.e., honey) can live for around 5–7 d, and when denied food longevity is  $\approx 1.5$  d. A parasitized *S. catenifer* larva, on average, yields sufficient larvae to produce approximately eight to nine *Apanteles* sp. cocoons, of which 87% will emerge successfully and 47% will be female. Interestingly, it was observed that  $\approx 42\%$  of emerged parasitoid larvae failed to spin cocoons, and these larvae subsequently died of desiccation. It is not known whether this observation was an artifact of rearing conditions in the laboratory or possible malnutrition, but lack of cocoon spinning has been observed in other species of *Apanteles* (Calkins 1977). For *Apanteles* sp., failing to spin cocoons may not be as maladaptive as it would seem. Rearing studies indicated that  $\approx 35\%$  of parasitized *S. catenifer* larvae die within the protective confines of the avocado seed which could mitigate potential adverse effects (e.g., low humidity) of attempting to pupate without a protective cocoon.

No relationships were observed between parasitism rates and the number of cocoons produced per host as a function of the number of *S. catenifer* larvae inhabiting a seed. This result suggests that the size of the larval host clutch discovered by an ovipositing *Apanteles* sp. female does not affect her immediate reproductive output as most braconid parasitoids are thought to be time rather than egg limited when processing host patches (Dorn and Beckage 2007).

However, what was not studied and would be of interest are the fitness consequences to *Apanteles* sp. progeny that have developed on hosts that are members of a "family" of more than two larvae that inhabit seeds and are simultaneously competing for food. With increasing numbers of *S. catenifer* larvae feeding in seeds the amount of food available per individual declines, observed aggression between larvae is elevated, the rate of cloistering in guarded serpentine feeding chambers increases, and mature larvae are appreciably smaller in size than conspecifics that led a solitary larval existence. These observations would suggest that parasitoid progeny fitness could be affected by lower host quality resulting from resource competition in avocado seeds.

In the laboratory, ovipositing *S. catenifer* females showed clear preferences for certain avocado substrates. Avocado branches to which fruit pedicels were attached were most heavily laid on, especially the cut ends of branches. Hohmann et al. (2003) reported that field harvested avocados examined in the laboratory had the majority of eggs laid on the pedicel. Because the branch to which the pedicel was attached was not returned to the laboratory for examination, it is pos-

sible the use of this potential oviposition site was overlooked by Hohmann et al. (2003). It is curious that *S. catenifer* females lay eggs on substrates at some considerable distance from the fruit upon which neonate larvae feed. It is unknown how larvae upon hatching from eggs laid on branches locate fruit. Larvae emerging from eggs laid on pedicels could exhibit positive geotaxis to locate fruit, but this may not be possible for larvae emerging from eggs laid on branches which could have a more horizontal aspect.

Furthermore, the length of time taken by larvae emerging onto branches, and possibly pedicels, to locate fruit, crawl to the bottom of fruit, and commence boring at suitable entrance sites would seem to put exposed progeny at high risk from natural enemy attack. All microgastrine braconids are larval–larval parasitoids (Pennacchio and Strand 2006), and this attack scenario on young exposed larvae wandering in search of food substrates may occur in the field given the high parasitism rates (53%) that were observed for *Apanteles* sp. in this study. This window of larval exposure to parasitoids could be significantly reduced if the majority of *S. catenifer* eggs were laid directly on fruit. However, results reported here, and those of Hohmann et al. (2003) suggest that avocado fruit, although used by females, are not as preferred for oviposition by *S. catenifer* when other substrates (e.g., fruit pedicels or branches) close to fruit are available for egg laying. The factors affecting oviposition site selection by *S. catenifer* are unknown, but could simply be related to texture, with female moths having being stimulated by contact with avocado fruit preferring to oviposit on rough substrates. The effect of rough textures on oviposition preferences for *S. catenifer* has been demonstrated in the laboratory (Nava et al. 2005b).

Hass fruit were significantly preferred over non-Hass avocados for oviposition by *S. catenifer* females in oviposition choice tests conducted in the laboratory. Given the high oil content of Hass fruit (a quality that makes this cultivar popular with human consumers) it is possible that ovipositing *S. catenifer* females are choosy and can discriminate between resources of varying quality for offspring. Alternatively, the bumpy skin on Hass may be of sufficiently rough texture to induce females to lay preferentially on this cultivar in comparison with the smoother skinned non-Hass fruit that were used in choice tests. Regardless of the stimulus involved, this choice preference is of high significance because this result has demonstrated that Hass is an avocado cultivar preferred by *S. catenifer*. Attack rates of 45% in a Guatemalan Hass orchard treated regularly with insecticides and an oviposition preference for Hass fruit, strongly suggest that *S. catenifer*, should it establish in California, will quickly become a very serious pest of Hass avocados, the dominant avocado cultivar grown in that state.

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### References Cited

- Arellano, P. G. 1975. Key for the identification of larvae of avocado stone borers in Mexico. *Folia Entomol. Mex.* 31-32: 127-131.
- Boscán de Martínez, N., and F. J. Godoy. 1982. *Apanteles* sp. (Hymenoptera: Braconidae) parasito del taladrador del aguacate *Stenoma catenifer* Walsingham (Lepidoptera: Stenomatidae) en Venezuela. *Agron. Trop.* 32: 205-208.
- Boscán de Martínez, N., and F. J. Godoy. 1984. Observaciones preliminares sobre la biología de *Stenoma catenifer* Walsingham (Lepidoptera: Stenomidae) taladrador del aguacate (*Persea americana* Mill.). *Agron. Trop.* 34: 205-208.
- [CAC] California Avocado Commission. 2007. Mexican avocados in California: the epic battle to protect California growers. California Avocado Commission, Irvine, CA.
- Cervantes Peredo, L., C.H.C. Lyal, and V. K. Brown. 1999. The stenomatine moth, *Stenoma catenifer* Walsingham: a pre-dispersal seed predator of Greenheart (*Chlorocardium rodiei* [Schomb.] Rohwer, Richter and van de Werff) in Guyana. *J. Nat. Hist.* 33: 531-542.
- Calkins, C. O. 1977. Notes on the cocoon construction behavior of *Apanteles militaris*. *Fla Entomol.* 60: 65.
- Dorn, S., and N. E. Beckage. 2007. Superparasitism in gregarious hymenopteran parasitoids: ecological, behavioural and physiological perspectives. *Physiol. Entomol.* 32: 199-211.
- Hoddle, M. S. 2004. Invasions of leaf feeding arthropods: why are so many new pests attacking California-grown avocados? *Calif. Avoc. Soc. Yrbk.* 87: 65-81.
- Hoddle, M. S. 2007. The avocado seed moth, *Stenoma catenifer* Walsingham (Lepidoptera: Elachistidae). (<http://www.biocontrol.ucr.edu/Stenoma/Stenoma.html>).
- Hoddle, M. S., and C. D. Hoddle. 2008. Survey results for Lepidoptera and associated parasitoids attacking Hass and non-Hass avocados in Guatemala. *J. Econ. Entomol.* (in press).
- Hoddle, M. S., K. M. Jetter, and J. G. Morse. 2003. The economic impact of *Scirtothrips perseae* Nakahara (Thysanoptera: Thripidae) on California avocado production. *Crop Prot.* 22: 485-493.
- Hohmann, C. L., W. J. Dos Santos, and M. Meneguim. 2000. Avaliação de técnicas de manejo para o controle da broca-do-abacate, *Stenoma catenifer* (Wals.) (Lepidoptera: Oecophoridae). *Rev. Bras. Frutic. Jaboticabal* 22: 359-363.
- Hohmann, C. L., A. M. Meneguim, E. A. Andrade, T. Garcia de Novaes, and C. Zandona. 2003. The avocado fruit borer, *Stenoma catenifer* (Wals.) (Lepidoptera: Elachistidae): egg and damage distribution and parasitism. *Rev. Bras. Frutic. Jaboticabal* 25: 432-435.
- Mendez Villa, M. 1961. Medidas practicas para combater los barrenadores del hueso del aguacate. *Fitofilo* 14: 4-7.
- Muniz Velez, R. 1958. La oruga barrenadora del hueso del aguacate, *Stenoma catenifer* Walsingham (Lepidoptera: Stenomatidae), pp. 170-174. Memoria del Primer Congreso Nac. Entomol. Fitopatol.
- Nava, D. E., J.R.P. Parra, V. A. Costa, T. M. Guerra, and F. L. Cônsoli. 2005a. Population dynamics of *Stenoma catenifer* (Lepidoptera: Elachistidae) and related larval parasitoids in Minas Gerais, Brazil. *Fla Entomol.* 88: 441-446.
- Nava, D. E., J.R.P. Parra, G. I. Diez-Rodriguez, and J.M.S. Bento. 2005b. Oviposition behavior of *Stenoma catenifer* (Lepidoptera: Elachistidae): chemical and physical stimuli and diel pattern of egg laying. *Ann. Entomol. Soc. Am.* 98: 409-414.
- Nava, D. E., J.R.P. Parra, J.M.A. Bento, G. I. Diez-Rodriguez, and M. L. Haddad. 2006. Distribuição vertical, danos e controle cultural de *Stenoma catenifer* Walsingham (Lepidoptera: Elachistidae) em pomar de abacate. *Neotrop. Entomol.* 35: 516-522.
- Nava, D. E., K. M. Takahashi, and J.R.P. Para. 2007. Linhagens de *Trichogramma* e *Trichogrammatoidea* para controle de *Stenoma catenifer*. *Pesq Agropec. Bras. Brasília* 42: 9-16.
- Pennacchio, F., and M. R. Strand. 2006. Evolution of developmental strategies in parasitic Hymenoptera. *Annu. Rev. Entomol.* 51: 233-258.
- Poppenoe, W. 1919. The avocado in Guatemala. *U.S. Dep. Agric. Bull.* No. 743.
- SAS Institute. 1990. SAS/STAT user's guide, version 6, 4th Edition. SAS Institute, Cary, NC.
- Sasscer, E. R. 1921. Important insects collected on imported nursery stock in 1920. *J. Econ. Entomol.* 14: 353-355.
- Ventura, M. U., D. Destro, E.C.A. Lopes, and R. Montalvan. 1999. Avocado moth (Lepidoptera: Stenomatidae) damage in two avocado cultivars. *Fla Entomol.* 82: 625-631.
- Wolfenbarger, D. O., and B. Colburn. 1966. Recent observations on some avocado pests in Mexico and El Salvador. *Proc. Fla State Hortic. Soc.* 79: 335-337.
- Wolfenbarger, D. O., and B. Colburn. 1979. The *Stenoma catenifer*, a serious avocado pest. *Proc. Fla. State Hortic. Soc.* 92: 275.
- Wysoki, M., M. A. van den Berg, G. Ish-Am, S. Gazit, J. E. Peña, and G. K. Waite. 2002. Pests and pollinators of avocado, pp. 223-293. In J. E. Peña, J. L. Sharp, and M. Wysoki [eds.], *Tropical fruit pests and pollinators, biology, economic importance, natural enemies and control*. CABI Publishing, Wallingford, Oxfordshire, United Kingdom.

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