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# Surveys for Stenoma catenifer (Lepidoptera: Elachistidae) and Associated Parasitoids Infesting Avocados in Perú

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ABSTRACT Surveys for Stenoma catenifer Walsingham, the avocado seed moth, and its associated larval parasitoids were conducted in the Departments of Junín, Huánuco, Cusco, and Madre de Dios in Perú. Fruit infestation levels in some areas ranged from 0 to 58%, and parasitism of S. catenifer larvae in Junín and Huánuco was 23%. Five species of hymenopteran parasitoid in two families, Braconidae (Apanteles sp., Hypomicrogaster sp., and Chelonus sp.) and Ichneumonidae (Pristeromerus sp. and Xiphosomella sp.), were reared from larvae, and one species of tachinid fly (Chrysodoria sp.) emerged from pupae. The dominant larval parasitoid, a gregarious Apanteles sp., accounted for 55% of parasitized hosts. Branch and twig tunneling by S. catenifer larvae in a commercial Hass avocado orchard was observed in Cusco. The field attractiveness of the sex pheromone of S. catenifer was demonstrated with 73% of monitoring traps deployed in three departments (Junín, Huánuco, and Cusco) catching male moths. Approximately 55% of avocado fruit sourced from the Province of Chanchamayo (Junín) and purchased at the Mercado Modelo de Frutas in La Victoria, in central Lima were infested with larvae of S. catenifer. Infested avocado fruit sold at this market could represent a potential incursion threat to coastal Hass avocado production regions in Perú that are reportedly free of this pest.

KEY WORDS avocado, life table, Perú, sex pheromone, Stenoma catenifer

Exports of fresh avocados (Persea americana Miller [Lauraceae]) from countries where this plant is native (i.e., México, Central and South America; Knight 2002) are rapidly increasing as international trade agreements are brokered to satisfy consumer demand for year round supplies of this fruit (Hoddle et al., 2009-2010). A risk associated with fresh fruit exports from countries in the native range of this plant into countries with domestic avocado production outside of the native range (e.g., California) is accidental contamination with coevolved pest species that could be injurious to the receiving country (Hoddle et al., 2009-2010, Morse et al. 2009). In 2008, the United States was the world's largest importer of avocados at  $\approx$ 315,000 tonnes and these fresh fruit imports had an estimated value of around \$600 million (FAOSTAT 2011). Most of this imported fruit originates from México the largest exporter of avocados to the U.S. (Pollack et al. 2010) and is destined for sale in southern California, an area with the largest domestic avocado industry in the United States. To help meet this domestic demand for fresh avocados over August through October 2011, Péru exported 8,890 tonnes of fruit to the United States, of which  $\approx$ 80% was shipped to California.

In California, avocados are grown by  $\approx$ 6,000 growers on  $\approx$ 24,000 ha, and the 'Hass' cultivar accounts for 95% of production. In 2010, this crop was worth \$403 million (California Avocado Commission 2009–2010). Notably in California, there is a pronounced absence of specialist coevolved fruit feeding pests (i.e., fruit flies, moths, and weevils; Hoddle 2004) that adversely affect commercial production in areas where this plant is native. This absence of frugivorous insects has been attributed, in part, to a Federal ban on fruit imports that was established in 1914 to protect the U.S. industry from these pests. However, commencing in 1998 imports of fresh fruit from countries with this coevolved frugivorous pest fauna underwent gradual legalization (California Avocado Commission 2004).

Stenoma catenifer Walsingham (Lepidoptera: Elachistidae), the avocado seed moth, is a specialist herbivore of Lauraceae and a notorious fruit pest in countries where avocados are native. It is widely distributed from México through Central America into South America (Wysocki et al. 2002). In some areas where *S. catenifer* is native, it is the major limiting factor to commercial production, and in parts of Venezuela (Boscán de Martínez and Godoy 1982) and Brazil (Nava et al. 2005a) fruit infested with feeding larvae can reach 80% or higher. Adult *S. catenifer* are nocturnal, and female moths lay eggs on or near fruit. Larvae bore into fruit to feed on the pulp and seed that results in economic loses (Hoddle and Hoddle 2008a). Fruit with advanced stages of infestation commonly

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exhibit holes with frass accumulating at the openings, and often white perseitol residues stain the fruit below these holes (Hoddle and Hoddle 2008a). *S. catenifer* has demonstrated an ability to establish in areas outside of its native range via the accidental importation of infested fruit. This occurred in 2000, when *S. catenifer* established in the Galápagos Islands after its likely introduction with infested avocados from Ecuador (Landry and Roque-Albelo 2003).

One sensitive and highly specific tool for monitoring and detecting invasive pests are sex pheromones. Traps baited with sex pheromone can be used to monitor export orchards to demonstrate that they are pest free and traps can also be used for incursion monitoring in countries receiving imports from high risk areas (Hoddle et al. 2011). The sex pheromone of S. *catenifer* has been identified (Millar et al. 2008), protocols for its synthesis have been developed (Hoddle et al. 2009), and improved (Zou and Millar 2010), use under field conditions has been optimized (Hoddle et al. 2011), field longevity is  $\approx 4-6$  wk (Hoddle et al. 2009), and the pheromone is commercially available (www.iscatech.com). The attractiveness of the S. catenifer sex pheromone has been demonstrated in México, Guatemala, and Brazil. These results suggest that it is unlikely that widely separated populations of S. catenifer use different sex pheromones (Hoddle et al. 2011). Despite the commercial availability of the pheromone and its demonstrated utility, exporters shipping fruit to the United States from areas with S. catenifer are not required to monitor export-certified orchards with the sex pheromone to verify the absence of this pest.

Despite the widely acknowledged pestiferousness of S. catenifer and its propensity to invade new areas, relatively little is known about this moth in most of its native range, especially in countries that export large volumes of fruit internationally (e.g., México). One country with an emerging Hass avocado export industry to the United States is Perú and production is concentrated in desert areas along the west coast and includes the Departments of La Libertad, Lima, Ica, and Arequipa (Hoddle et al. 2009–2010). Outside of these coastal production zones, S. catenifer is considered to be the most serious pest attacking avocados (Wille 1952) and is recorded as being restricted to the Departments of Junín and Pasco (Núñez 2008, SENASA 2006). S. catenifer is especially problematic in the Provinces of Chanchamayo and Satipo (Junín) (Cruz 1998), areas with the largest production of avocados in Perú (SENASA 2006). In Perú, larvae have been reported to damage maturing fruit, and attacks on immature fruit <5 cm in length results in premature fruit drop (Wille 1952). Larval tunneling inside twigs and branches causes branch and shoot mortality, and young trees can be killed by internally feeding larvae (Wille 1952). Similar observations on twig boring by S. catenifer larvae have been made in México (Wolfenbarger and Colburn 1979). In an attempt to better understand the bioecology and distribution of S. catenifer in Perú, a joint project was initiated by SENASA (Servicio Nacional de Sanidad Agraria del Perú) with the authors. The project had four major objectives: 1) to document the parasitoid fauna associated with *S. catenifer* larvae and pupae in the Departments of Junín and Huánuco, 2) to survey for *S. catenifer* in the Departments of Cusco and Madre de Dios, areas not officially known to have this pest, 3) to verify the twig infesting habit of *S. catenifer* larvae, and 4) to ascertain whether the sex pheromone is attractive to *S. catenifer* in different areas of Perú. The results of this work conducted in Perú over the period 1 May 2010 through 27 July 2010 are presented here.

## Materials and Methods

Fruit Collections and Insect Rearing in the Laboratory. In total, 405 avocado fruit exhibiting symptoms suggestive of being infested with *S. catenifer* were collected over the period 27 May 2010 through 30 June 2011 from two departments (Junín and Huánuco) and at least four districts within these departments. Damaged fruit were collected from farms, packing houses, and fruit markets (Table 1). Fruit were kept in collapsible ventilated insect rearing cages (Bug-Dorm-2120,  $[60 \times 60 \times 60 \text{ cm}]$ , MegaView Science Education Services, Taiwan) that were labeled by location and collecting date. Cages were held in a well lit and ventilated room at the SEANSA Offices in San Ramón, Junín under natural daylight and lengths ( $\approx$ 12 h) at 25.29°C ± 1.32 and RH 72.12% ± 5.76.

Fruit were inspected regularly, 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 a 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. Immature larvae feeding on pulp were removed from fruit and used to inoculate clean uninfested avocado seeds. A number two cork borer (4.0 mm 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 larvae readily entered seeds in this manner. Inoculated avocado seeds supported the complete development of S. catenifer larvae. The fate of all S. catenifer larvae reared from these fruit was recorded as having pupated, died from parasitism or unknown causes. Survivorship and mortality data for 298 S. catenifer larvae reared from infested avocados were used to construct a partial life table for this pest.

An additional 110 fruit sourced from the Province of Chanchamayo (Junín) were purchased from vendors at the Mercado Modelo de Frutas in La Victoria, Lima Perú on 14 July 2010. These fruit were held until 26 July 2010 in ventilated collapsible cages at  $24.34^{\circ}$ C  $\pm$  0.83 and RH 53.39%  $\pm$  2.56 under natural light and daylength of  $\approx$ 12 h. The percentage of fruit infested was calculated, and *S. catenifer* larvae were managed in the same manner as described above so as to determine their developmental fate and associated parasitoid fauna.

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GPS Elevation No. fruit Collection date Department Province District Fruit source collected coordinates (m) 27 May 2010 [June 14 2010]<sup>a</sup> 11°10.781'S  $22 [17]^a$ Junín Chanchamayo San Ramón Orchard 1,398 75°21.862'W 28 May 2010 [15 June 2010]<sup>a</sup> Junín Chanchamayo Perené Orchard  $10^{\circ}56.443$ 'S 906 22 [36]<sup>a</sup> 75°09.621'W 10 June 2010 27 Huánuco Leoncio Prado Pumahuasi Orchard 09°11.035'S 707 75°57.925'W 10 June 2010 Huánuco Leoncio Prado Rupa Rupa Orchard 09°16.727'S 706 40 75°59 418'W Tingo María fruit 11 June 2010 Huánuco Leoncio Prado Rupa Rupa 9 market 13 June 2010 [15 June 2010]<sup>a</sup> Junín Chanchamayo San Ramón La Merced fruit 25 [19]<sup>a</sup> market<sup>4</sup> Packinghouse<sup>b</sup> 14 June 2010 Junín Chanchamayo Perené 20 15 June 2010 [30 June 2010]<sup>a</sup> Iunín Chanchamavo San Ramón San Ramón fruit 33 [135]<sup>a</sup> market<sup>b</sup>

Table 1. In total, 405 avocado fruit exhibiting symptoms of potential infestation by *S. catenifer* were collected from orchards and packinghouses, or purchased from vendors in fruit markets in the Departments of Junín and Huánuco, Perú. *S. catenifer* larvae reared from these fruit were used to construct a partial life table (Table 4)

<sup>a</sup> Second collection made on a different date at the same site.

<sup>b</sup> The origin of infested fruit purchased at fruit markets or collected from discard piles or unsorted deliveries in packinghouses was undeterminable because fruit from different orchards was commingled by delivery agents and then again for redistribution after delivery and subsequent sale.

Surveys for S. catenifer in Avocado Fruit in Cusco and Madre de Dios and Branches in Cusco. The presence of S. catenifer in fruit was investigated by visiting three and four avocado orchards in the Departments of Cusco and Madre De Dios, respectively (Table 2). In total, 53 and 95 fruit exhibiting damage symptoms indicative of S. catenifer infestation were cut open and examined for this pest in Cusco and Madre de Dios, respectively (Table 2). In Cusco, 11 avocado branches on one small ( $\approx 1.0$  m in height) and eight mature trees exhibiting exit holes with frass or white perseitol exudates were cut from these trees, diameter and length of cut branches were recorded, and opened longitudinally with a pocket knife and examined for the presence of S. catenifer larvae feeding internally (Table 2).

Pheromone Trap Deployment. The attraction of male S. catenifer to its sex pheromone in Perú was evaluated by deploying a total of 11 pheromone traps in 11 different avocado orchards in three departments (Huánuco, Junín, and Cusco; Table 3). The sex pheromone, synthesized specifically for these surveys (Hoddle et al. 2009, Zou and Millar 2010), was dissolved in hexane (Optima grade, Fisher, MO) and loaded on 11 mm gray silicon rubber septa (West Pharmaceutical Services Inc., Lionville PA) as a hexane solution at 1,000  $\mu$ g/septum. Lures were placed in Pherocon 1C wing traps (Trécé Incorporated, Adair, OK) and traps were hung inside the canopy of randomly selected trees  $\approx 1.75$  m above the ground at survey sites. Traps were deployed for 15 (five traps), 17 (two traps), 18 (three traps), or 28

Table 2. Collection data for avocado fruit and branches examined for S. catenifer in the Departments of Cusco and Madre de Dios, Perú

Sampling date	Department	Province	District	Fruit and/or branch source	GPS coordinates	Elevation (m)	No. damaged fruit examined (% infested with S. catenifer)	Branches infested with <i>S. catenifer</i> ?
5 July 2010	Cusco	La Convención	Huayopta	Non Hass trees	12° 59.368'S 72° 31.834'W	1,803	15 (40%)	No
	Cusco	La Convención	Huayopta	Non Hass trees	12° 59.760'S 72° 32.083'W	1,728	12 (25%)	Yes $(n = 3)$
	Cusco	La Convención	Huayopta	Commercial Hass orchard	13°00.641'S 72°35.462'W	1,357	26 (58%)	Yes $(n = 8)$
7 July 2010	Madre de Dios	Tambopata	Tampopata	Non Hass trees	12°43.505'S 69°12.916'W	195	18 (6%)	$\mathbf{N}/\mathbf{A}^{a}$
	Madre de Dios	Tambopata	Las Piedras	Non Hass trees	12°13.272'S 69°08.181'W	277	27 (7%)	N/A
	Madre de Dios	Tahuamanu	Tahuamanu	Non Hass trees	11°27.198'S 69°19.432'W	283	38 (45%)	N/A
	Madre de Dios	Tahuamanu	Iñapari	Non Hass trees	10°57.179'S 69°34.855'W	244	22 (50%)	N/A

<sup>a</sup> N/A, not applicable as branch infestation surveys were not conducted.

Date trap deployed [taken down]	Department	Province	District	GPS coordinates	Elevation (m)	No. male S. <i>catenifer</i> caught
25 May 2010 [9 June 2010]	Huánuco	Ambo	Huacar	10°11.105'S 76°13.939'W	2,166	0
25 May 2010 [9 June 2010]	Huánuco	Ambo	Huacar	10°12.535'S 76°14.609'W	2,167	0
26 May 2010 [10 June 2010]	Huánuco	Leoncio Prado	Rupa Rupa	09°16.727'S 75°59.418'W	706	3
26 May 2010 [10 June 2010]	Huánuco	Leoncio Prado	Pumahuasi	09°11.035'S 75°57.925'W	707	3
26 May 2010 [10 June 2010]	Huánuco	Leoncio Prado	Aucayacu	09°09.091'S 75°59.961'W	630	7
27 May 2010 [14 June 2010]	Junín	Chanchamayo	San Ramón	11°05.604'S 75°23.719'W	941	1
27 May 2010 [14 June 2010]	Junín	Chanchamayo	San Ramón	11°10.873'S 75°21.750'W	1,407	0
27 May 2010 [14 June 2010]	Junín	Chanchamayo	San Ramón	11°10.781'S 75°21.862'W	1,398	2
28 May 2010 [14 June 2010]	Junín	Chanchamayo	La Merced	10°59.242'S 75°18.569'W	711	1
28 May 2010 [14 June 2010]	Junín	Chanchamayo	Perené	10°56.443'S 75°09.621'W	906	2
30 Aug 2010 [27 Sept 2010] <sup>a</sup>	Cusco	La Convención	Huayopta	13°00.641'S 72°35.462'W	1,357	32

Table 3. S. catenifer sex pheromone trap deployment schedule and capture data

<sup>*a*</sup> Cooperators with SENASA deployed this trap in a commercial Hass avocado orchard, pulled it down, and the Laboratorio de Entomología del SENASA Lima confirmed the presence of *S. catenifer* in the trap. The authors were provided photographs of trap contents and the no. male *S. catenifer* unambiguously photographed in this trap were counted and reported here.

(one trap) nights before being inspected for captured male *S. catenifer*. The number of male *S. catenifer* caught per trap per site was recorded (Table 3).

#### Results

Parasitism Studies and Partial Life Table for S. catenifer. Five species of hymenopteran parasitoid in two families, Braconidae (three genera; two Microgastrinae [Apanteles sp. and Hypomicrogaster sp.] and one Cheloninae [Chelonus sp.]) and Ichneumonidae (two genera [*Pristeromerus* sp. and *Xiphosomella* sp.] both Cremastinae) were reared from S. catenifer larvae in fruit collected from Junín and Huánuco (Table 4). The dominant larval parasitoid, a gregarious Apanteles sp. (Braconidae), accounted for 55% of parasitized hosts (Table 4). The mean number of Apanteles sp. cocoons per S. catenifer host was  $5.89 \pm 0.59$  (SE) (range of cocoons per host 2-13) and 47% of adult parasitoids were female. One species of tachinid fly, Chrysodoria sp., emerged from S. catenifer pupae that had been reared in the laboratory from field collected larvae indicating it is a larval-pupal parasitoid. Death of S. catenifer from unknown causes in the larval and pupal stages was 26 and 53%, respectively. Species of unidentified entomopathogenic fungi were suspected of being the causal agents of unknown mortality because fungal growth on larvae (either inside fruit or on emerged larvae searching for pupation sites) and pupae (outside of fruit) was evident and was likely promoted by high humidity and accumulation of water released from fruit inside rearing cages.

Of the 110 fruit that originated from Chanchamayo and purchased at the Mercado Modelo de Frutas in La Victoria in Lima, 55% were infested with at least one *S. catenifer* larva, and a total of 61 larvae were counted in fruit. Over the 12-d period these fruit were held, the tachinid fly, *Chrysodoria* sp. emerged from three *S. catenifer* pupae; seven and three larvae were parasitized by *Apanteles* sp. and unidentified ichneumonids (adults failed to emerge because of insufficient rearing time), respectively. Additionally, 2 larvae and 15 pupae died from unknown causes and 31 larvae were still alive at the time rearing was terminated 12 d postpur-

Table 4. Partial life table for *S. catenifer* reared from 405 avocados showing external symptoms of infestation that were collected from 5 May 2010 through 30 June 2010 from the Departments of Junín (329 fruit) and Huánuco (76 fruit) in Perú

No. Life stage entering stage		Cause of mortality	No. dying in stage	
Larva	299	Braconidae		
		Parasitism:	37	
		Apanteles sp.		
		Parasitism:	8	
		Chelonus sp.		
		Parasitism:	1	
		Hypomicrogaster		
		sp.		
		Ichneumonidae		
		Parasitism:	8	
		Pristeromerus sp.		
		Parasitism:	6	
		Xiphosomella sp.		
		Unknown causes	76	
Pupa	163	Tachinidae		
-		Chrysodoria sp.	9	
		Unknown causes	87	
Adult	67			

Larval to adult survivorship, 22%; parasitism, 23%; mortality from unknown causes, 55%, and 54% of reared adults were female.

chase. No *S. catenifer* larvae were reared to adults because there was insufficient time before terminating this study.

S. catenifer Infestation of Fruit and Twigs, and Male Attraction to the Sex Pheromone. In Madre de Dios and Cusco, S. catenifer larvae were found infesting non-Hass and Hass fruit. Infestation rates ranged from 6 to 58% and these data appear to be the first records of S. catenifer activity in avocado orchards outside of the Districts of Junín and Pasco in Perú (Núñez 2008, SENASA 2006; Table 2).

In Cusco, S. catenifer larvae were found tunneling small green twigs on immature non-Hass avocado trees (<1 m in height) and in green stems and woody branches in a commercial Hass avocado orchard (Table 3). Tunneling activity was readily obvious from twig die back, accumulations of frass at tunnel openings (often seen at an internode) and white perseitol residues dripping from infested branches (for colored photos see Hoddle 2011). The average diameter of tunneled stems was 8.18 mm  $\pm$  1.42 (SE) and the average tunnel length was 121 mm  $\pm$  14.44 (SE) (range of tunnel length 65-200 mm). In one instance, two S. catenifer larvae were found in one wooden branch (19 mm diameter) and they had constructed parallel but separate tunnels. Tunnels were occasionally full of a clear viscous fluid that completely submerged live motile larvae. Submergence of live larvae inside avocado twigs was first reported by Wille (1952).

In total, 51 male S. catenifer were captured in 73% of traps that were deployed for an average of  $17.36 \pm 1.14$  (SE) nights in three different departments (Table 3). Nightly trap capture rates ranged from 0 to 1.14 males per night, with an average nightly capture rate of 0.21  $\pm$  0.10 (SE) males (Table 3).

#### Discussion

In Perú, S. catenifer was a commonly encountered avocado pest in the Departments of Junín, Huánuco, Cusco, and Madre de Dios. This moth was previously known from Junín (Cruz 1998, SENASA 2006) and Pasco (Núñez 2008, SENASA 2006) but appears to have been unrecorded from Huánuco, Cusco, and Madre de Dios (Núñez 2008, SENASA 2006). It is likely that S. catenifer populations exist in other departments in Perú and would be detected if sampled for. Larvae were found tunneling in fruit and branches of Hass and non-Hass avocados, and male moths were caught in pheromone traps in 73% of sampled orchards. Further, S. catenifer was recorded from 55% of fruit that had been sourced from Chanchamayo (Junín) and purchased at the Mercado Modelo de Frutas in La Victoria, Lima. Importation of avocados infested with S. catenifer into Lima for subsequent sale and redistribution may pose a significant incursion threat to coastal Hass avocado orchards that export fruit internationally. Lima is within ≈150 km of desert production areas and residential avocados are common in Lima and many small towns along the coast that are interspersed between commercial Hass avocado orchards. These backyard plants could act as reservoirs for this pest from which they could threaten commercial production areas. The unregulated movement of avocado plants out of zones with *S. catenifer* may also present a previously unrecognized incursion threat as hidden larvae feeding inside stems and branches may be inadvertently moved into new areas.

Other native pest Lepidoptera, notably Oiketicus kirbyi Guilding (Psychidae), a key pest in commercial Hass avocado orchard in Perú, have successfully established populations in these isolated desert orchards (Rhainds and Cabrera-La Rosa 2010). Pesticide applications for O. kirbyi and other pests (e.g., whiteflies, mites, and thrips) may help prevent infiltration by S. catenifer into export-certified zones. Temperatures in coastal zones do not appear to be unsuitable for S. catenifer development and reproduction when compared with production areas in Junín (e.g., La Merced) where this pest is problematic. Laboratory rearing studies that investigated the effects of temperature on the development of S. catenifer also support this observation (Nava et al. 2005b; Fig. 1). The effect of humidity on S. catenifer egg hatch rates is not known and these data could be useful for understanding the potential invasion threat by this pest into desert zones.

Deployment of pheromone traps in commercial Peruvian Hass avocado orchards could be incorporated into existing and well established Mediterranean fruit fly (*Ceratitis capitata* (Weidemann) Diptera: Tephritidae) monitoring programs to demonstrate that export certified production zones are free of *S. catenifer*. This dual-pest monitoring approach using an existing trapping program in Hass orchards to simultaneously monitor for *C. capitata* and *S. catenifer* was employed by the authors with SENASA colleagues in the Departments of Arequipa, Ica, Huacho, Huaral, and Trujillo, and would appear feasible and easy to implement quickly, and would require little extra work with both traps hanging on opposite sides of one tree.

The results of this study support earlier findings by Wille (1952) and Cruz (1998) that infestation of avocado fruit by S. catenifer can be significant in some areas of Perú. Fruit infestation rates of 0-58% were recorded here, and Cruz (1998) reported infestation rates ranging from 0 to 54% for eight avocado cultivars in Chanchamayo (Junín). Wille (1952) stated that larval tunneling can be a significant source of branch mortality on fruit bearing trees, and it can occasionally kill young trees. Stem boring damage of this nature was observed on Hass and non-Hass avocados in Cusco. A conversation with the owner of one nursery in Cusco that produced trees from avocado seeds to be used as rootstocks, indicated that larval S. catenifer infestations of young rootstock plants was severe and predictable enough to warrant its own pest "season" and the need for control with pesticides.

In Junín and Huánuco, over the period 5 May 2010 through 30 June 2010, *S. catenifer* larvae were attacked by three species of braconid, two species of ichnuemonid, one species of tachinid fly, and combined larval mortality from all sources of parasitism was 23%. The dominant parasitoid detected during this time was a

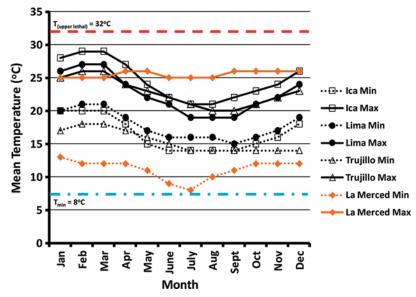


Fig. 1. Mean monthly minimum and maximum temperatures for areas of Perú with commercial avocado production. Trujillo (Department La Libertad, northern Perú), Lima (Department Lima, central Perú), and Ica (Department Ica, southern Perú) are within coastal desert production areas with commercial Hass production. La Merced (Department Junín) is in the Province of Chanchamayo, the largest avocado (Hass and non-Hass) production area in Perú with native *S. catenifer* populations. In the laboratory under constant temperatures, the lower developmental temperature for *S. catenifer* is 8°C, the upper lethal temperature is 32°C, and the optimal developmental and reproductive temperature range is 18–28°C (Nava et al. 2005b). Ica climate data were sourced from www.worldweatheronline.com; Lima, www.weather.com; Trujillo, www.weather.com; and La Merced, www.meoweather.com. (Online figure in color.)

gregarious *Apanteles* sp. In the same general area this survey was conducted, Cruz (1998) reported that five species of Hymenoptera comprised of two species of gregarious *Apanteles*, one unidentified species each of cynipid, ichneumonid, braconid, and two unidentified species of tachinid attacked *S. catenifer* larvae. Cruz (1998) reported that combined parasitism by the two *Apanteles* spp. ranged 60–81% and averaged 70% across two orchards over the survey period September 1985 to August 1987. Combined parasitism from non-*Apanteles* spp. parasitoids was <10% during this period (Cruz 1998).

Apanteles spp. have been recorded as the dominant larval parasitoids of S. catenifer in Guatemala, Venezuela, and Perú, and members of this genus are second in importance after another braconid, Dolichogenidea sp. in Brazil (Table 5). It appears that *Apanteles* sp. reared from S. catenifer larvae in Guatemala and Perú are different from each other and from A. stenomae described from Venezuela (J. Whitfield, personal communication). This would suggest that there is a complex of Apanteles spp. attacking S. catenifer and that species identity and impact varies by locality. A review of the natural enemy fauna associated with eggs and larvae of S. catenifer from ≈6 countries comprising its home range suggests that a rich parasitoid guild exists and is comprised of  $\approx 20$  species that attack eggs (three species of trichogrammatids), and larvae ( $\approx 10$  species of braconid, 5 species of ichneumonid, and  $\approx 1-2$  species of tachinid; Table 5). Braconids are the dominant parasitoid group attacking S. catenifer larvae (Table 5) and in Guatemala <5% of braconids may be hyperparasitized by a *Perilampus* sp. (Hymenoptera: Perilampidae) (Hoddle and Hoddle 2008b). Tachinids have only been recorded from *S. catenifer* in Perú. Published natural enemy records and their impacts on this pest in México are very sparse (Table 5).

It is likely that additional species of egg parasitoids, in particular trichogramatids, attack S. catenifer eggs in countries outside of Brazil and these are currently unknown because they have not been surveyed for. No true pupal parasitoids of S. catenifer are known, and this shortcoming may be because of the absence of studies on the pupation biology of this pest in the field. In the field, S. *catenifer* abandon food substrates and pupate in the top 0.5-2 cm of soil (Boscán de Martínez and Godoy 1984). Consequently, the discovery of pupal parasitoids would require focusing on field collections of pupae excavated from soil samples, or perhaps more easily, the deployment and subsequent retrieval of laboratory reared S. catenifer pupae at field sites with resident pest infestations. Projects aimed at identifying parasitoids and quantifying their impacts on the eggs and pupae of S. catenifer are recommended for countries where this has not been done but surveys on larval parasitoids have been completed (e.g., Guatemala and Perú). A thorough set of studies on the distribution and the natural enemy fauna associated with S. catenifer in México, the world's largest exporter of avocado fruit, needs to be executed and published.

Table 5. Parasitoid species associated with the eggs and larvae of S. catenifer

Parasitoid species	Country	% parasitism	Reference		
Diptera <sup>a</sup>					
Tachinidae					
Chrysodoria sp.	Perú	3%	This study		
Hymenoptera Braconidae <sup>b</sup>					
Apanteles sp.	Venezuela	31-33%	Boscán de Martínez and Godoy (1982)		
Apanteles sp.	Guatemala	22-52%	Hoddle and Hoddle (2008a,b,c), Hoddle et al. (2011)		
Apanteles sp.	Perú	12%	This study		
Apanteles sp.	Brazil	13-18%	Nava et al. (2005a)		
Apanteles sp.	Galápagos Islands, Ecuador	5%	Hoddle (2011)		
Apanteles stenomae	Venezuela	?	Muesebeck (1958)		
Chelonus sp.	Brazil, Guyana, Perú	3%	Nava et al. (2005a), Cervantes Peredo et al. (1999), this study		
Dolichogenidea sp.	Brazil	39-77%	Nava et al. (2005a)		
Hymenochaonia sp.	Brazil	2%	Nava et al. (2005a)		
Hypomicrogaster sp.	Brazil, <sup>a</sup> Perú <sup>b</sup>	$9-35\%^{a}; 0.3\%^{b}$	Nava et al. $(2005a)$ , <sup><i>a</i></sup> this study <sup><i>b</i></sup>		
Macrocentrus sp.	Guatemala	0.2 - 15%	Hoddle and Hoddle (2008a,b,c), Hoddle et al. (2011)		
Ichneumonidae <sup>b</sup>					
Brachycyrtus sp.	Guatemala	0.05%	Hoddle and Hoddle (2008a)		
Eudeleboea sp.	Brazil, Guyana	1-2%	Nava et al. (2005a), Cervantes Peredo et al. (1999)		
Pristomerus sp.	Brazil, Guatemala Perú	0.2–3%	Hoddle and Hoddle (2008a), Nava et al. (2005a), this study		
Xiphosomella sp.	Perú	2%	This study		
Xiphosomella stenomae Trichogrammatidae <sup>c</sup>	Panama	5	Cushman (1924)		
Trichogramma bruni	Brazil	5	Hohmann et al. (2003)		
Trichogramma pretiosum	Brazil	?	Hohmann et al. (2003)		
Trichogrammatoidea annulata <sup>d</sup>	Brazil	15-65(?)%	Hohmann et al. (2003)		

<sup>*a*</sup> larval-pupal parasitoid; <sup>*b*</sup> larval parasitoids; <sup>*c*</sup> egg parasitoids; <sup>*d*</sup> dominant egg parasitoid reared from S. catenifer eggs in Brazil (Hohmann et al. 2003).

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