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**PARASITISM OF *CYDIA* SPP. (LEPIDOPTERA:
TORTRICIDAE) ON *SOPHORA CHRYSOPHYLLA*
(FABACEAE) ALONG AN ELEVATION GRADIENT OF
DRY SUBALPINE FOREST ON MAUNA KEA, HAWAII**

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Abstract.—The biology and ecological importance of Hawaiian endemic *Cydia* spp. (Lepidoptera: Tortricidae) are poorly known. *Cydia* larvae are an important food to palila, an endangered Hawaiian bird that inhabits *Sophora* woodlands on Mauna Kea, Hawaii. We quantified *Cydia* larval abundance in seeds of *Sophora chrysophylla* Salisbury (Fabaceae) and larval mortality caused by parasitism. Four new host plant associations are reported: *C. crassicornis* [Walsingham], *C. falsifalcella* [Walsingham], *C. obliqua* [Walsingham], and *C. storeella* [Walsingham]. Four parasitoid wasp species were consistently reared from larval *Cydia*: *Calliephialtes grapholithae* [Cresson], *Diadegma blackburni* [Cameron], *Pristomerus hawaiiensis* Perkins (Hymenoptera: Ichneumonidae), and *Euderus metallicus* [Ashmead] (Hymenoptera: Eulophidae). The three Ichneumonidae appear to be accidental introductions, while *E. metallicus* is likely to be native to Hawaii. Parasitism rates by all four wasps combined decreased with elevation from 94% at 1800 m to 20% at 2700 m.

Key Words.—Insecta, *Cydia* spp., parasitism rates, seasonal abundance, Hawaii, alien species.

Cydia Hübner (Lepidoptera: Tortricidae) is a cosmopolitan genus of small moths. *Cydia* species include economic pests such as the codling moth, *C. pomonella* (L.) on apples and the pea moth, *C. nigricana* (Stephens) on legumes, while other *Cydia* species attack fruits, nuts, and cambium of other angiosperms and conifers (Zimmerman 1978). There are fourteen known *Cydia* species endemic to Hawaii that form a closely allied species complex (Walsingham 1907, Zimmerman 1978) with broad variations in colors and wing patterns. All endemic Hawaiian *Cydia* species, with known hosts, are found exclusively on plants in the family Fabaceae including *Acacia koa* A. Gray, *Acacia koaia* Hillebrand, *Canavalia galeata* (Gaudichaud), *Sophora chrysophylla* (Salisbury), and *Strongylodon lucidus* (Seemann). The host plants of six *Cydia* species are not known (Zimmerman 1978). On *Sophora*, three seed-feeding *Cydia* species are known; *C. latifemoris* (Walsingham), *C. montana* (Walsingham), and *C. plicata* (Walsingham) (Swezey 1954). Little is known about the ecology of Hawaiian *Cydia* species, and descriptions of their impact on seed production have been only anecdotal (Swezey, personal communication in Zimmerman 1978).

Three parasitoid species are historically known from *Cydia* larvae (Perkins 1913, Swezey 1954, Zimmerman 1978). *Eupelmus pelodes* Perkins (Hymenoptera: Eupelmidae) is an endemic parasitoid of *C. plicata*; *Trathala flavo-orbitalis* (Cameron) (Hymenoptera: Ichneumonidae) is an accidental alien parasitoid of *C. parapteryx* (Meyrick); and *Pristomerus hawaiiensis* Perkins (Ichneumonidae),

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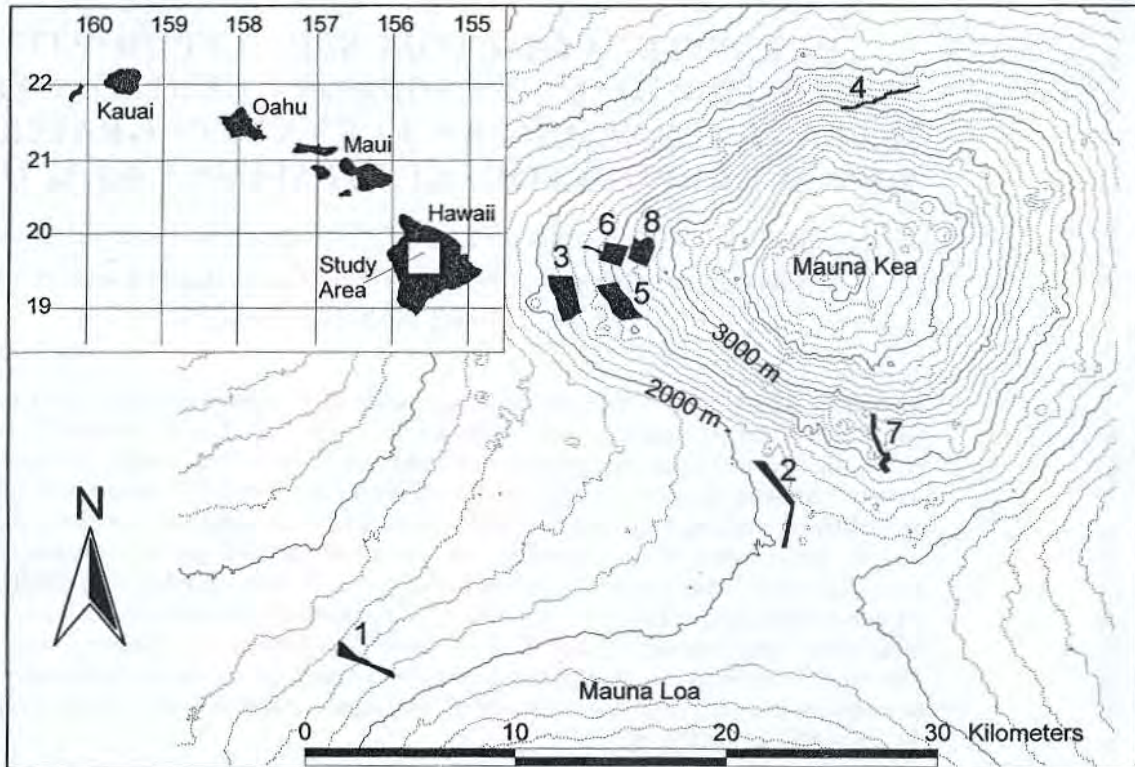


Figure 1. Location of 8 study sites on Mauna Kea and Mauna Loa volcanoes. Inset shows location of study areas on Hawaii Island, Hawaii.

place of origin uncertain, is a parasitoid of *C. conspicua* (Walsingham), *C. plicata*, and *C. walsinghamii* (Butler). The rate of parasitism by these wasps, and their impacts to ecosystems are not known.

Sophora-feeding *Cydia* are the most important insect prey of palila (*Loxioides bailleui* Oustalet), an endangered species of Hawaiian finch (Fringillidae: Drepanidinae) and may represent an important protein source for developing chicks (U.S. Geological Survey, unpublished data). Parasitism by native and alien wasps may be resulting in decreased abundance of *Cydia*. We investigated the seasonal abundance and rate of parasitism of *Sophora*-feeding *Cydia* species along an elevation gradient of dry subalpine forest on Mauna Kea, Hawaii.

MATERIALS AND METHODS

Site Description.—Eight study sites were located from 1700 m to 2850 m elevation on Mauna Kea volcano and the saddle region between Mauna Kea and Mauna Loa, Hawaii Island, Hawaii (Fig. 1). Rainfall averages 511 mm/year at 2260 m elevation on the western slope of Mauna Kea (58-year average, Juvik et al. 1993) and varies slightly with elevation and aspect. Average annual temperature at 2600 m elevation is 11° C, with mean daily maximum temperatures ranging from 15° to 17° C and mean daily minimum ranging from 4° to 9° C (Juvik et al. 1993). The dominant vegetation type at higher elevations is open *Sophora chrysophylla* forest (sites 6, 8), and at lower elevations mixed *Myoporum sandwicense* A. Gray (Myoporaceae)—*Sophora* forest (sites 1–5, 7) (see Hess et al. 1999 for more detailed descriptions). The eight sites generally follow an ele-

Table 1. Abundance, density, and activity of *Cydia* larvae in *Sophora* pods from Feb 1992 to Apr 1997 at 8 sites along an elevation gradient. *Cydia* abundance = # larvae/pod, *Cydia* density = # larvae/ha, *Cydia* activity = Ave # seeds eaten/pod, % Seeds eaten = Ave % seeds eaten/pod.

Site	Ave. elev. (m)	<i>Cydia</i> abundance	<i>Cydia</i> density	<i>Cydia</i> activity	% Seeds eaten	No. of pods (n)
1	1800	0.04	20	0.07	2.4	523
2	2015	0.02	144	0.06	2.0	2244
3	2150	0.09	475	0.20	6.8	2616
4	2325	0.22	1010	0.52	15.5	1736
5	2425	0.13	572	0.27	8.4	3166
6	2450	0.25	4584	0.57	16.4	5418
7	2650	0.23	2287	0.53	16.6	1550
8	2700	0.20	6682	0.54	15.2	5210

vation gradient (Table 1). *Sophora* trees sampled were spaced 150 m apart along transects (except sites 1 and 2, where trees were at random distances 100 to 500 m). Transects within each site were at least 200 m apart.

Cydia Abundance.—Each month from Feb 1992 to Aug 1997 two *Sophora* pods were collected haphazardly and within reach from the ground from each tree being studied. If pods were not available on a study tree, they were collected from the nearest tree with pods. The number of trees sampled varied between sites and in some months pods were not available at all sites (Table 1). Pods were dissected in the laboratory, and the number of seeds eaten and number of *Cydia* larvae present were recorded for each pod.

Parasitism.—Each month from Apr 1996 to Apr 1997 ten additional pods with external evidence of *Cydia* caterpillars inside (approximately 1 mm hole with silk cap) were selected from each study site. Pods were placed individually into 240 ml clear plastic cups and covered with mosquito netting to allow air circulation and prevent molding. Cups were checked daily for the emergence of adult moths or parasitoids. After three months, pods showing no activity were dissected to determine caterpillar occupancy. Live caterpillars were returned to their pods and wrapped with moist paper towels to finish development. Voucher specimens of parasitic Hymenoptera were sent to the Hawaii Department of Agriculture for identification. Tentative identifications were made for species of *Cydia* pending a revision of the genus, therefore, analysis considered all *Cydia* species together.

Analysis.—Parasitism rate was calculated as the percent of *Cydia* larvae that produced a parasitic wasp (*Cydia* larvae that died of unknown causes before adults emerged were not included). Linear regression was used to assess *Cydia* abundance, *Cydia* feeding activity, and parasitism over elevation.

RESULTS

We detected 3969 *Cydia* larvae during dissection of 22,463 pods from February 1992 to August 1997. *Cydia* abundance (number of larvae per pod) followed a yearly cycle, generally peaking in August through October and dropping to a low during April through June (Fig. 2). Average *Cydia* abundance reached a peak of 515 larvae per 1000 pods in October 1992 and a low of 7 larvae per 1000 pods in March 1994, for all sites combined. Peaks in *Cydia* abundance generally oc-

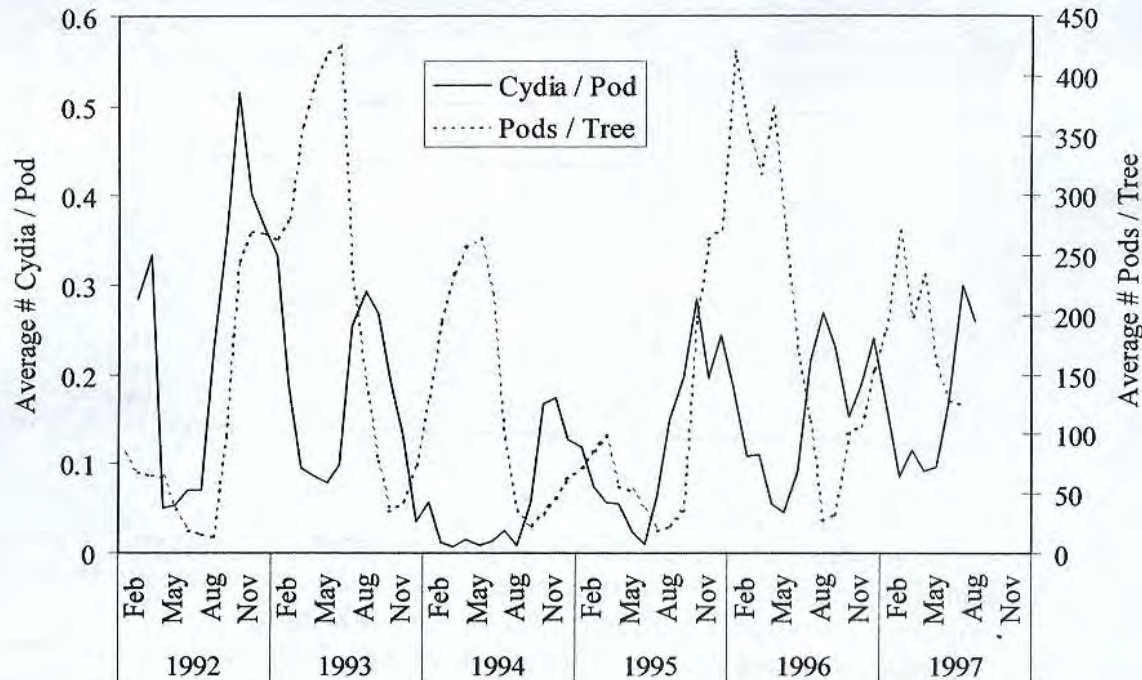


Figure 2. Average number of *Cydia* larvae per pod and average number of pods per tree from Feb 1992 to Aug 1997 for 8 study sites combined.

curred when pods were least available as caterpillars became more concentrated in the few remaining pods.

Cydia density (number of larvae per hectare) generally increased with elevation (Table 1). *Cydia* density was calculated using tree density estimates (Hess et al. 1999), average number of pods per tree (U.S. Geological Survey, unpublished data), and average *Cydia* abundance per pod. *Cydia* activity (number of seeds eaten by *Cydia* per pod) also increased with elevation (Table 1).

Seven *Cydia* species were reared from *Sophora* pods. *C. latifemoris*, *C. montana*, and *C. plicata* were previously known to feed on mamane (Zimmerman 1978), while *C. crassicornis* (Walsingham), *C. falsifalcella* (Walsingham), *C. obliqua* (Walsingham), and *C. storeella* (Walsingham) are new host records. All were previously known from Hawaii Island, except *C. storeella*, which was previously known only from Maui (Nishida 1997).

Cydia moths or their associated parasitoids emerged from 439 pods out of 616 pods collected for rearing from April 1996 to April 1997. Each pod contained one *Cydia* larva, except for 42 pods that contained two larvae, and two pods that contained three larvae. Of the 177 pods from which no insects emerged, larvae in 84 died in the laboratory (possibly from pseudoparasitism (Jones et al. 1986), desiccation, or other unknown causes) and 93 had no larvae when collected (larvae vacated pods before collection or external signs of larvae were misidentified in the field).

Four parasitoid species were reared from pods containing *Cydia* larvae (Table 2). *Pristomerus hawaiiensis* (Ichneumonidae), a solitary endoparasitoid, was the most common (98 wasps total), particularly at lower elevations. *Euderus metallicus* (Ashmead) (Eulophidae), a gregarious ectoparasitoid, was found consistently across elevations. Forty-six parasitized *Cydia* larvae produced 221 *E. metallicus*

Table 2. Parasitism of *Cydia* spp. by 4 wasp species over 8 sites along an elevation gradient (data pooled from Apr 1996 to Apr 1997). % Parasitism (of *Cydia* larvae) for each site is given for each wasp species individually. % Emergence *Cydia* spp indicates the % of *Cydia* larvae that successfully reared to an adult moth.

Site	Elevation average (m)	% Parasitism <i>P. hawaiiensis</i>	% Parasitism <i>E. metallicus</i>	% Parasitism <i>C. grapholithae</i>	% Parasitism <i>D. blackburni</i>	% Emergence <i>Cydia</i> spp.	# Larvae (n)
1	1800	64.7	5.9	23.5	0.0	5.9	17
2	2015	38.9	5.6	44.4	0.0	11.1	18
3	2150	46.9	12.5	3.1	0.0	37.5	32
4	2325	25.0	9.1	9.1	0.0	56.8	44
5	2425	28.6	9.5	9.5	2.4	50.0	84
6	2450	16.5	4.9	1.0	6.7	70.9	103
7	2650	19.1	5.9	5.9	7.3	61.8	68
8	2700	0.0	15.1	0.0	4.7	80.2	126
Total	—	19.9	9.3	6.1	4.1	60.6	492

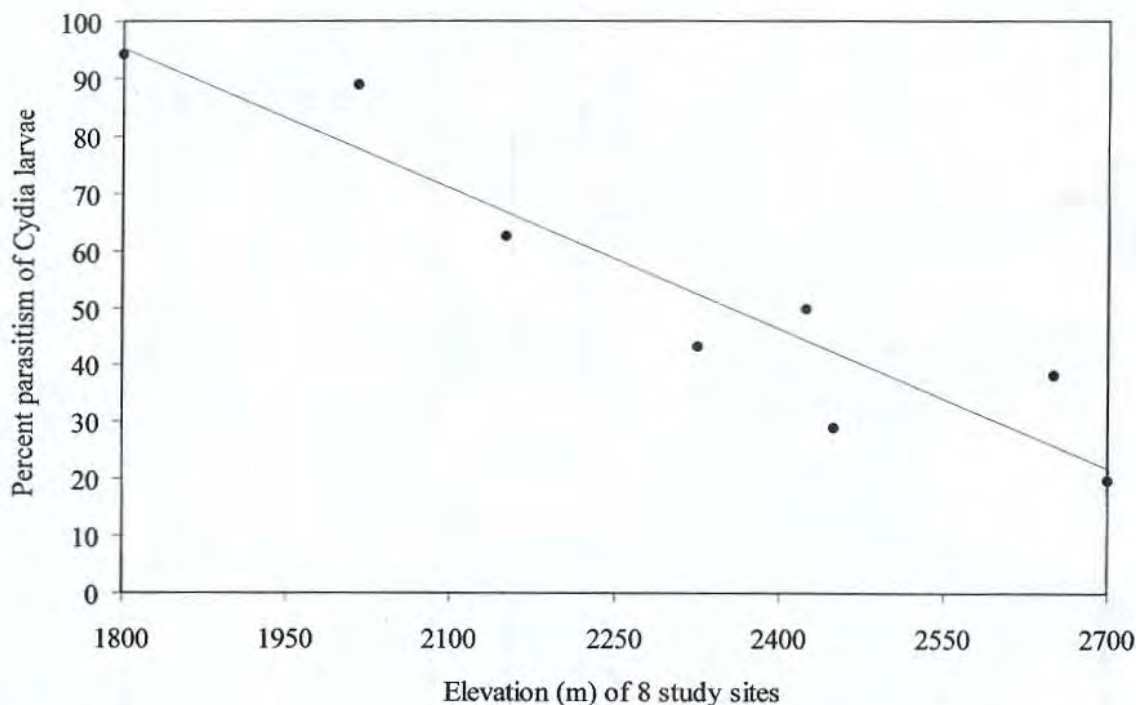


Figure 3. Percent of *Cydia* larvae parasitized by 4 wasp species combined over an elevation gradient (data pooled from Apr 1996 to Apr 1997).

wasps. *Calliephialtes grapholithae* (Cresson) and *Diadegma blackburni* (Cameron) (Ichneumonidae), both solitary endoparasitoids, were less abundant (30 and 20 wasps, respectively). Six other Hymenoptera species, including *Sierola* sp. (Bethyridae), *Anagyrus* sp. (Encyrtidae), *Brasema cushmani* (Crawford) (Eupelmidae), Unidentified sp. (Mymaridae), *Brachyserphus hawaiiensis* (Ashmead) (Proctotrupidae), Unidentified sp. (Trichogrammatidae), and unidentified species of Acari, Anthocoridae, Pseudococcidae, Hemerobiidae, Psocoptera, and Thysanoptera were also recovered from mamane pods. These species occurred infrequently and probably have little impact on *Cydia* populations.

Parasitism rate (percent of larvae parasitized) by all four parasitoid species combined decreased with increasing elevation (Fig. 3). There was strong evidence that the abundance of *Cydia* at each site was influenced by the rate of parasitism ($t = -3.0995$, $P = 0.0269$), after accounting for changes in *Cydia* abundance due to elevation (multiple $r^2 = 0.8663$):

$$\text{Abundance} = 0.8585 - 0.0052(\text{Parasitism rate}) - 0.0001(\text{Elevation}).$$

There was also strong evidence that the percent of *Sophora* seeds consumed by *Cydia* was negatively influenced by the rate of parasitism (multiple $r^2 = 0.8474$):

$$\% \text{ Seeds Eaten} = 22.0331 - 0.2289(\text{Parasitism Rate}).$$

DISCUSSION

Of the fourteen described species of Hawaiian *Cydia* several are known only from one gender and only eight have recorded host plant associations (Zimmerman 1978). One unnamed species (new species 1 in Zimmerman 1978) was witnessed to infest 50 to 75 percent of the crown of several trees of *Acacia koaia*,

boring through twigs and small branches (C. J. Davis, personal communication in Zimmerman 1978). Other species inhabiting *Acacia koa* have been reared from the bark, dead twigs, and seeds of the tree. On *Sophora chrysophylla*, *C. latifemoris* was observed to destroy nearly one-half of a season's seed crop on Maui, while *C. plicata* was found in up to 70% of seeds on Hawaii Island (O. H. Swezey, personal communication in Zimmerman 1978). Tentative identifications in this study suggest the following new associations with *Sophora*: *C. crassicornis*, *C. falsifalcella*, *C. obliqua*, and *C. storella*, with hosts previously unknown, were reared from *Sophora* seeds. It is unclear, therefore, whether the high infestation rates of *Sophora* seeds previously reported represent an attack by one species or more.

Abundance of *Sophora*-feeding *Cydia* species followed temporal and spatial patterns. Larval abundance, in most years, reached its peak within the late summer (August, September, and October), while reaching its lowest point in the spring (April, May, and June). *Sophora* pods are generally available year round with several peaks occurring throughout the year (U.S. Geological Survey, unpublished data). *Cydia* larval abundance (caterpillars/pod) is most pronounced when pods are scarce and caterpillars become more concentrated in the few remaining pods. This result suggests that larval densities (caterpillars/hectare) may change little throughout the seasons or in response to food decline. Several measures (abundance, density, and feeding activity) indicate that *Cydia* prevalence in pods increased with increasing elevation. Of the two anomalies to this pattern, one site (site 7) covers a broader elevation range than the others, while the second site (site 5) differs in dominant forest type from its neighboring sites. Increase in *Cydia* prevalence with elevation may also be confounded by increased *Sophora* tree density and decreased parasitism over the same elevation gradient.

Overall parasitism rates of *Cydia* decreased with increasing elevation, from 94% at 1800 m to 20% at 2700 m. Individually, however, the ichneumon species showed segregation relative to elevation. Parasitism at lower elevations was dominated by *Pristomerus hawaiiensis* and *Calliephialtes grapholithae*, while *Diadegma blackburni* was discovered only at higher elevation sites. In contrast, parasitism by the eulophid wasp, *Euderus metallicus*, appeared uniform across sites.

The origin of the three Ichneumonidae is under debate, though each is likely alien to Hawaii. It appears unlikely that any of these three wasps were introduced as biological control agents in Hawaii. Although congeners of *D. blackburni* and *P. hawaiiensis* were introduced into Hawaii for the control of lepidopteran pests in 1953 and 1942, respectively (Lai & Funasaki 1986), both species were already present at the turn of the 20th century (Ashmead 1901, Perkins 1910). Furthermore, although collected in Oregon in 1897 (Carlson 1979), *D. blackburni* was originally described from Mauna Kea, Hawaii (Cameron 1883), before formal biological control efforts began in Hawaii. Fullaway & Krauss (1945) suggest *P. hawaiiensis* is an immigrant from the Orient, but give no reasoning for this supposition.

C. grapholithae is an important parasitoid of *Cydia caryana* (Fitch), a major pest of pecans in the southeastern United States (Yonce et al. 1996). And although this wasp is the most common parasitoid of *Cryptophlebia illepidia* (Butler) (Lepidoptera: Tortricidae), a major pest of macadamia nuts in Hawaii (V. P. Jones, unpublished data), neither *C. grapholithae* nor any congeners have been recorded

as purposeful introductions into Hawaii (Lai & Funasaki 1986). However, records of biological control releases were incomplete in the first half of the 20th century when many new species were introduced to the islands (Swezey 1931, Howarth 1991).

The status of *E. metallicus* is also unclear (Nishida 1997). However, it has not been collected outside of the Hawaiian Islands, and may represent an endemic species (J. W. Beardsley, personal communication). Given the ubiquity of this species in our collections, it is curious that this wasp was not previously documented from *Cydia*, while *Eupelmus pelodes*, previously reared from *C. plicata* (Swezey 1954), did not occur in our study.

Sources of *Cydia* mortality, other than these four wasps, remain uncertain. An immigrant ground beetle, *Pristonychus complanatus* Dejean (Coleoptera: Carabidae), and immigrant spiders, *Cheiracanthium diversum* L. Koch (Clubionidae) and *Tegenaria domestica* (Clerck) (Agelenidae) can each be found in *Sophora* trees along with native predators (PTO, personal observation) and may prey on *Cydia* adults. Egg parasitoids, such as *Trichogramma* spp. (Hymenoptera: Trichogrammatidae), have not been investigated for most of Hawaii's native Lepidoptera and may also be a source of *Cydia* mortality.

Hawaiian *Sophora*-feeding *Cydia*, are prey to parasitoids and consumers of endemic seed crops. However, habitat associations and environmental constraints of both native and alien parasitoids require further elucidation to determine factors guiding patterns of parasitism witnessed in this study. Mortality factors, other than parasitism, and basic life histories of *Cydia* species also need to be systematically addressed. Finally, long-term viability of these endemic moth populations needs to be assessed in light of their importance as a food resource to an endangered bird species.

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