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Parasitism of Hawaiian Non-Frugivorous Fruit Flies (Diptera: Tephritidae) by an Exotic Parasitoid, *Eurytoma tephritidis* Fullaway (Hymenoptera: Eurytomidae)

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Abstract. *Eurytoma tephritidis* Fullaway (Hymenoptera: Eurytomidae) is an exotic solitary larval endoparasitoid that has been recorded to parasitize gall-forming tephritids in Hawaii. We surveyed *E. tephritidis* parasitism of *Tetreuaresta obscuriventris* (Loew.), *Ensina sonchi* (L.), *Acinia picturata* (Snow), *Procecidochares utilis* Stone, *P. alani* Steyskal, *Trupanea* sp. nr. *cratericola*, and *T. dubautiae* (Bryan) (Diptera: Tephritidae) on four major Hawaiian islands. No wasps emerged from *T. obscuriventris* and *E. sonchi*. Among other species, percent parasitism ranged from less than 1% to over 67%, depending on fly species and sampling location. Overall, *E. tephritidis* showed higher affinity for gall-forming tephritids than flowerhead-feeders, although it parasitized substantial numbers of the native flower-infesting *T.* sp. nr. *cratericola*. The implications of our findings for a more accurate estimation of the risks posed by biological control programs to non-target fruit flies in Hawaii are discussed.

Key words: parasitism, exotic species, host range, insect conservation

Introduction

Invasion by non-indigenous insect species is an important factor affecting island ecosystems (Simberloff 1986). Funasaki et al. (1988) estimated that, on average, 17 immigrant species of insects and related arthropods become established in Hawaii every year. Currently, introduced species constitute approximately 35% of all Hawaiian terrestrial arthropods (Nishida 1997). In addition to addressing conservation concerns, investigating invasion biology is important for a better understanding of many fundamental issues in community ecology, such as species diversity, niche overlap, limiting similarity, and community change (Moulton and Pimm 1986). It is also essential for improving predictability of biological control programs. However, invading insect species usually attract public attention only when they are highly visible (e.g. large butterflies), or when they become pests (Simberloff 1986, Simberloff and Stiling 1996). Less conspicuous organisms are often ignored not only by the general public, but also by the scientific community.

Fruit flies in the family Tephritidae include some of the most severe horticultural pests in many regions of the world. However, the majority of them are non-frugivorous species that are either beneficial (mainly as weed biocontrol agents), or benign (Headrick and Goeden 1994, Duan et al. 1996). In Hawaii, there are 33 species of non-pest tephritids. This includes 26 endemic species, as well as 5 deliberately introduced and 2 inadvertently introduced weed control agents (Hardy and Delfinado 1980). Most of these species are seed feeders living in the flowerheads of plants in the family Compositae; some are gall-formers and stem-miners. At least some of these flies are potentially at risk of being attacked by the hymenopterous parasitoids deliberately introduced to control their frugivorous relatives

(Howarth 1991, Follett 2000). Therefore, ecologically sound utilization of biological control agents to control pest fruit flies in Hawaii requires a better understanding of their possible impact on both native and beneficial tephritids.

Accurate estimation of the risks posed by biological control programs to non-target fruit flies in Hawaii is impossible without a more comprehensive knowledge on the extant parasitoids already attacking them in a variety of island habitats. Recent surveys indicate that parasitism by inadvertently introduced parasitoids might be a greater threat to non-target tephritids than deliberately introduced parasitoids (Duan et al. 1996). However, the host ranges of most of these vagrant species have never been thoroughly investigated, nor their impacts on non-target populations quantified.

Parasitoid wasps of the genus *Eurytoma* Illiger are common parasitoids of tephritid flies in a wide variety of geographical areas. Under certain circumstances, they can have a profound effect on the populations of their hosts, including extinction of local fly subpopulations (Eber and Brandl 1994) and fly shifts to different host plants in pursuit of enemy-free space (Abrahamson et al. 1989, Brown et al. 1995). Therefore, invasion of these wasps to Hawaii may have far-reaching consequences for local ecosystems. One eurytomid species, an exotic solitary larval endoparasitoid, *Eurytoma tephritidis* Fullaway, has already been documented to parasitize the gall-forming beneficial weed biocontrol agents *Procecidochares alani* Steyskal and *Eutreta xanthochaeta* Aldrich on several major Hawaiian islands (Bess and Haramoto 1959, 1972, Duan et al. 1996, 1998). Furthermore, it was responsible for the most parasitoid-related mortality in *P. alani* (Duan et al. 1996). However, little is known about the propensity of *E. tephritidis* to attack other tephritid species that are currently present on the islands. In the present study, we investigated the incidence of *E. tephritidis* parasitizing several species of non-frugivorous tephritids in Hawaii.

Materials and Methods

Fly species. Five exotic and two endemic tephritid species were surveyed to determine the extent of *E. tephritidis* parasitism. Exotic species included *Tetreuaresta obscuriventris* (Loew.), *Ensina sonchi* (L.), *Acinia picturata* (Snow), *Procecidochares utilis* Stone, and *P. alani* Steyskal. Native Hawaiian species included *Trupanea* sp. nr. *cratericola* and *T. dubautiae* (Bryan). Fly origin and host plant associations for all 7 species are shown in Table 1. Among the exotic species, *T. obscuriventris*, *A. picturata*, *P. utilis*, and *P. alani* were deliberately introduced to Hawaii as weed biocontrol agents. *E. sonchi* was an accidental introduction recorded on the islands for the first time in 1968 (Hardy and Delfinado 1980).

Parasitism survey. Host substrates (flowerheads or stem galls) were sampled by excising randomly selected plant stems at approximately bi-weekly intervals between February, 1999 and April, 2000 at a number of different sites on the islands of Hawaii, Kauai, Maui, and Oahu. Flowerheads of *D. laxa*, which flowers during a relatively short period of time, were collected weekly. The exact quantity of sampled material, as well as the location and time of sampling varied depending on plant abundance, distribution and flowering phenology (Tables 2 and 3). Excised stems bearing inflorescences or galls were brought to the laboratory, where they were incubated at 24±2°C under natural lighting as described by Duan et al. (1996). Emergence of adult flies and parasitoids was recorded every 3 to 5 days.

Insect identification. Insects were identified using the keys developed by Hardy and Delfinado (1980) and by comparing our specimens to voucher specimens identified by Dr. John Beardsley (University of Hawaii, Manoa). The identity of *Trupanea* spp. was confirmed by Dr. Elmo Hardy (University of Hawaii, Manoa). Voucher specimens of all species are stored in the Entomology Museum of the University of Hawaii at Manoa.

Table 1. Geographical origin and host plant associations of surveyed tepritid fly species (Hardy and Delfinado 1980).

Fly species	**Fly origin**	**Host plant species**	**Pattern of host utilization**
Tetrauresta obscuriventris	tropical America	*Elephantopus mollis* Kunth	flowerhead-feeder
Ensina sonchi	Europe	*Sonchus oleraceus* L.	flowerhead-feeder
Acinia picturata	tropical America	*Pluchea odorata* L.	flowerhead-feeder
Procecidochares utilis	Mexico	*Ageratina adenophorum* (Spreng.)	gall-former
Procecidochares alani	Mexico	*Ageratina riparia* (Regel)	gall-former
Trupanea sp. nr. *matericola*	Hawaii	*Dubautia ciliolata* Keck	flowerhead-feeder
Trupanea dubautia	Hawaii	*Dubautia laxa* Hooker and Arnott	flowerhead-feeder

Statistical analysis. Percent parasitism was calculated for each fly species as 100 × number of *E. tephritidis* emerging from collected samples / total number of insects (flies and parasitoids) emerging from collected samples. Even though this method might not accurately reflect levels of field parasitism, it provides a good estimate of host mortality due to parasitization (Duan et al. 1996), and has been traditionally used by many researchers (e.g. Bess and Haramoto 1959, 1972, Wong et al. 1991). The differences among various fly species and sampling locations were analyzed using Chi-square tests (Analytical Software 1994).

Results and Discussion

E. tephritidis adults were reared from five out of seven surveyed fly species (Table 3). No *E. tephritidis* emerged from flowerheads containing *T. obscuriventris* and *E. sonchi*. The latter is consistent with the findings by Duan and Messing (1998) who surveyed abundance and distribution of *E. sonchi* and its parasitoids inhabiting *S. oleraceous* flowerheads in the Wailua district of Kauai. Among parasitized species, percent parasitism varied widely, ranging from less than 2% for *A. picturata* to over 67% for *P.utilis* (Table 3). The observed difference was statistically highly significant (Chi-square test, df=4, c^2=234.65, P<0.0001).

T. dubautia flies inhabiting *D. laxa* flowerheads in our survey suffered low levels (^{a}2%) parasitism by *E. tephritidis* (Table 3). In contrast, Duan et al. (1996) reared no *E. tephritidis* from *T. dubautia* inhabiting *D. raillardioides* flowerheads in Kokee State Park on Kauai. Environmental conditions between the two study sites were fairly similar (Table 2); therefore, it is likely that the observed difference was due to the wasp's preference towards searching on *D. laxa*. Likewise, *E. obtusiventris*, a congener of *E. tephritidis*, has been shown to display a bias towards parasitizing a tephritid fly *Eurosta solidaginis* Fitch when it inhabits the goldenrod species *Solidago altissima* L., but not the taxonomically close

Table 2. Sites of *Eurytoma tephritidis* surveys, 1999-2000.

Island	**District**	**Location (N lat., W long.)**	**Elevation (m)**	**Mean annual precipitation[1] (mm)**	**Vegetation cover[2]**
Hawaii	Kau	Hawaii Volcanoes National Park (19°25′, 155°15′)	1000–1150	2000–2500	Mixed closed forest with native shrub understory
		Pahala (19°12′, 155°29′)	130	1000	Former sugarcane plantation divided into a number of small vegetable farms
	South Hilo	Waiakea Forest Reserve (19°37′, 155°08′)	240–260	5000	Alien closed forest with uluhe-*Rubus* spp. understory
	North Hilo	Hamakua Coast (19°48′, 155°06′)	67	3000	Edge of unused pasture land
Kauai	Hanalei	Anini, (22°13′, 159°27′)	1–5	1250	Roadside alien weeds
	Kawaihau	Kauai Agricultural Research Center (22°04′, 159°24′)	180	1875	Unmanaged open grassland
	Waimea	Kokee State Park (22°08′, 159°39′)	1200	1765	Mixed open forest with uluhe-*Rubus* spp. understory
		Waimea Canyon State Park (22°02′, 159°40′)	1000	1300	Alien closed forest with guava-lantana understory

Maui	Makawao	Waipoli Rd. (20°43′, 156°18′)	1720	1000	Upland open shrub
Oahu	Koolaupoko	Old Pali Rd. (21°22′, 157°47′)	365	3000	Scattered weeds overgrowing abandoned paved road
	Koolaupoko	Maunawili trail (21°22′, 157°47′)	244	3000	Tropical rainforest
	Waianae	Kaala Natural Area Reserve (21°30′, 158°10′)	1100–1200	2000	Open native forest

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[1] Precipitation figures were interpolated from published isohyets based on 67-year rainfall data (Giambelluca *et al*. 1986).

[2] Types of plant communities were determined using descriptions and vegetation maps developed by Ripperton and Hosaka (1942), Mueller-Dombois

Table 3. Parasitism of adventive and endemic non-pest tephritid flies by *Eurytoma tephritidis*.

Fly species collected	Location	Time period	No. plant substrates	No. flies emerging	*E. tephritidis* parasitism (%)
Tetraruesta obscuriventris	Anini	Feb–June 1999	4463	4448	0
	KARC	Jan.–June 1999	9227	6670	0
	TOTAL for *E. mollis*		**13690**	**11118**	**0**
Acinia picturata	HAVO	April–Oct.1999	9721	98	0.90
	HAVO	March–April 2000	6013	25	0
	Pahala	April–Aug. 1999	8755	212	5.17
	Pahala	March–April 2000	13500	215	0.42
	Waiakea	March–April 2000	3343	89	0
	Kokee	March 1999	492	17	0
	Anini	Feb.–May 1999	5174	16	0
	KARC	Feb.–June 1999	7760	82	0
	Waimea Canyon	Feb.–March 1999	3361	7	0
	Old Pali Rd.	Feb.–March 2000	1768	56	0
	TOTAL for *P. odorata*		**59886**	**817**	**1.36**
Ensina sonchi	Anini	March–June 1999	2456	616	0
	KARC	April–June 1999	1078	225	0
	TOTAL for *S. oleraceous*		**3534**	**841**	**0**
Procecidochares utilis	Waipoli Rd.		240	16	20.34
	Maunawili Trail		175	5	26.92
	TOTAL for *P. utilis*		**415**	**21**	**22.35**
Procecidochares alani	Hamakua Coast		130	12	76.79
	HAVO		360	19	70.51
	Old Pali Rd.		281	33	55.97
	TOTAL for *P. alani*		**771**	**64**	**67.67**
Trupanea sp. nr. *cratericola*	HAVO	April–Sept. 1999	15692	228	39.76
Trupanea dubautia	Kaala	Oct. 1999	5215	2019	2.22

goldenrod species *Solidago gigantea* Ait (Brown et al. 1995). Also, an unidentified *Eurytoma* sp. was reared from *Procecidochares flavipes* Aldrich residing in *Brickelia oblongifolia* Nuttall flowerheads, but was absent from the same fly inhabiting *B. californica* (Torrey and Gray) Gray flowerheads (Goeden et al. 1994).

With the notable exception of *T. dubautia*, gall-formers suffered much heavier parasitism than flowerhead-feeders. The percent parasitism by *E. tephritidis* recorded for *P. utilis* in our survey (^{a}20 – 25%) is comparable to the earlier reports by Bess and Haramoto (1959, 1972). At the same time, samples of *P. alani* collected in our study revealed higher parasitism rates than were reported for this species by Duan et al. (1996).

Sampling site had a highly significant effect on *E. tephritidis* parasitism of *P. alani* (Chi-square test, df=2, c^2=9.74, P=0.0077). A high degree of geographic variation in parasitism rates has also been reported for the congener *E. obtusiventris* attacking *E. solidaginis* in the continental U.S. (Brown et al. 1995, Sumerford and Abrahamson 1995), as well as for *E. tephritidis* attacking *P. utilis* in Hawaii (Bess and Haramoto 1972). At the same time, we detected no significant differences among sampling sites in the rates of *E. tephritidis* parasitism of either *P. utilis* (Chi-square test, df=1, c^2=1.36, P=0.2431) or *A. picturata* (Chi-square test, df=2, c^2=4.68, P=0.0963). Since percent parasitism is determined by numerous biotic and abiotic factors, the relative importance of which varies widely among different species and different geographic locations (Goeden and Louda 1976), it was difficult to pinpoint exact causes of the observed differences.

Overall, it appears that the accidental introduction of *E. tephritidis* to Hawaii represents a negligible to moderate threat to the majority of surveyed tephritid species. Numerically, the percent parasitism recorded for *P. alani* and *P. utilis* was fairly high. However, extensive studies by Bess and Haramoto (1959, 1972) revealed that even such substantial parasitoid pressure did not compromise the fly's ability to control the target weeds. The recovery of *E. tephritidis* from *T.* sp. nr. *cratericola* is more worrisome. Very little is known about the current abundance and distribution of this fly, which has not even been taxonomically described yet. With the high degree of endemism typical of many Hawaiian insects, it is not unlikely that this species is fairly rare, and parasitoid-induced mortality by an invasive exotic wasp is highly undesirable. More detailed life table or recruitment studies are required to accurately quantify the full extent of the impact of this adventive wasp on endemic flies.

The somewhat disjunct host range of *E. tephritidis* illustrates the difficulties inherent in trying to predict host range of exotic parasitoids based strictly on the hosts' taxonomic affinities (an approach common in classical biological control under the precept of "centrifugal phylogeny") (Wapshere 1974). While the adventive wasp was largely absent in our study from the endemic tephritid *T. dubautia*, it killed almost 40% of the larvae of the congeneric fly *T.* sp. nr. *cratericola* on a closely related *Dubautia* host plant. It also appeared to show a strong affinity for gall-forming flies, but moved readily onto *T.* sp. nr. *cratericola* in the dissimilar flower-head habitat (an acceptance of host-habitat diversity not usually seen in other exotic parasitoids of tephritids in the Braconidae and Eulophidae) (Duan and Messing 1997, 1998, 2000).

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