Bionomics of the Gall-Parasitic Flea Weevil Rhynchaenus hustachei (Coleoptera: Curculionidae)

Kazuo YAMAZAKI¹ and Shinji SUGIURA²

¹Osaka City Institute of Public Health and Environmental Sciences, 8–34 Tojo-cho, Tennoji, Osaka, 543–0026 Japan ²Laboratory of Forest Ecology, Graduate School of Agriculture, Kyoto University, Sakyo-ku, Kyoto, 606–8502 Japan

Abstract. Field observations showed that the gall-parasitic flea weevil *Rhynchaenus hustachei* often parasitized the pouch galls of the aphid *Paracolopha morrisoni* on *Zelkova serrata* leaves in the Kinki District, Central Japan. The eggs of the weevil were laid into the gall walls and hatched larvae entered the galls. Each parasitized gall contained only one weevil. The inside of the gall wall was heavily grazed by the weevil larva, resulting in destruction of the aphid colony. These observations suggest that the weevil is an obligatory cecidophage. At three of six study sites, weevil parasitism was the greatest mortality factor for the aphids. A facultative hyperparasitoid, *Eupelmus urozonus* (Eupelmidae) and *Pteromalus* sp. (Pteromalidae) parasitized the larvae and pupae of the weevil.

Key words: Galls, host, rate of parasitism, cecidophage, Rhynchaenus hustachei, Paracolopha morrisoni.

Introduction

Galls are adaptive architecture that provides the gall-makers with nutritious tissues, mild microclimate and shelter from natural enemies (Price *et al.*, 1987). Since galls are attractive resources not only for gallmakers but also for predators, parasitoids and inquilines, diverse communities can be organized on galls (e.g., Caltagirone, 1964; Askew, 1975; Yukawa, 1983; Hawkins & Goeden, 1984; Sota, 1988). However, species interactions between gall-makers and other gall inhabitants have been poorly understood in most of the communities.

Although the gall-parasitic flea weevil *Rhynchaenus hustachei* Klima is known for a parasitic life-style on aphid galls (Kôno, 1950; Morimoto, 1984a, b), the host gall-makers have not been formally reported except for Akimoto (1995), and its biology has little been studied. We recently found that the weevil commonly parasitizes the leaf galls of the aphid *Paracolopha morrisoni* (Baker) on the keaki tree, *Zelkova serrata* (Thunberg) Makino (Ulmaceae), in the Kinki District, Central Japan. In the present paper, we report the mode of parasitism, feeding habit, rate of parasitism and natural enemies of the flea weevil based on field sampling and dissection of the galls.

Materials and Methods

The aphid *P. morrisoni* induces closed pouch galls (10 mm in height, 5–6 mm in width) on the leaves of *Z. serrata* (primary host) in spring. Several galls are frequently induced on a single leaf; one gall originates from a stem mother. Second-generation alates exit the galls through dehiscence openings and migrate to the secondary hosts, bamboo and dwarf bamboo (Yukawa & Masuda, 1996, p. 183).

We first found several larvae and pupae of R. hustachei in the aphid galls on Z. serrata leaves in mid May 2000 in Chihaya-akasaka Village, Osaka Prefecture. Field surveys of bionomics of the weevil were then undertaken at the following six sites in the Kinki District, Central Japan: (1) Michi-no-eki Parking Area $(34^{\circ}28'N, 135^{\circ}37'E, 140 \text{ m above the sea level}),$ Chihaya-akasaka Village, Osaka Prefecture, (2) a ridge of Mt. Ikoma (34°40'N, 135°40'E, 495 m a.s.l.), Higashi-osaka City, Osaka Prefecture, (3) rural residential area of Ueda (34°58'N, 135°57'E, 180 m a.s.l.), Otsu City, Shiga Prefecture, (4) Kamigamo Experimental Forest, Kyoto University (35°5'N, 135°47'E, 150 m a.s.l.), Kyoto City, Kyoto Prefecture, (5) Kibune Shrine (35°7'N, 135°46', 310 m a.s.l.), Kyoto City, Kyoto Prefecture and (6) Ashiu Experimental Forest, Kyoto University (35°18'N, 135°43', 390 m a.s.l.), Miyama-cho, Kyoto Prefecture.

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At all study sites except Mt. Ikoma, 3 to more than 50 Z. serrata trees (more than 4 m tall) were planted and grew well. At the site on Mt. Ikoma, there was only one Z. serrata tree within a radius of 50 m, and the galls on that tree were sampled. At Chihayaakasaka, the study tree had variegated leaves. We visited the study sites between mid May and mid June, 2000 and arbitrarily clipped off twigs of a Z. serrata tree at each site at a height of 50–350 cm above the ground. The sampled twigs were placed in plastic bags and transferred to our laboratories. The numbers of leaves and galls were counted. The galls were dissected with tweezers under a stereomicroscope to inspect the inside of the galls.

To estimate the impact of the gall-parasitic weevil on the aphid population, the fate of the galls were classified into the following six categories: 1) successful alate emergence, when alates emerged from the galls through dehiscence openings; 2) miscellaneous death of aphids, firstly when the stem mothers died of unknown causes before alate production, secondary when alate nymphs died of unknown factors during development, thirdly when alates died possibly due to asynchrony between alate production and dehiscence of gall walls, and so on; 3) weevil parasitism; 4) fungus infestation, when fungi thrived inside the galls and all aphids died in the galls; 5) destruction by birds and other herbivores, when the galls were pecked by birds (Sunose, 1980) or destroyed by leaf-chewing insects; 6) abortion, when the galls ceased development at immature stages, or the galls necrosed, partly because of plant resistance.

The chi-square test was used to compare the percentages of weevil parasitism among the six study sites. Then, post hoc test using the sequential Bonferroni correction (Rice, 1989; $\alpha = 0.05$) was performed between the six sites.

During dissection of the galls, some parasitoids of the weevil were found and were reared in glass vials under laboratory conditions.

Results

Mode of parasitism and feeding habit of R. hustachei

Each parasitized gall contained only one weevil larva, a pupa (Fig. 1), or a new adult and had one to three tiny holes made by the mother weevil for oviposition. The eggs were embedded into the gall walls and the hatched larvae entered the galls. The inside of the gall wall was heavily grazed by the weevil larva, resulting in the destruction of the aphid colony. The parasitized galls were filled with fecal pellets of weevil



Fig. 1. A pupa of *R. hustachei* in a pouch gall of *P. morrisoni* on a *Z. serrata* leaf (cross section). Scale bar: 5 mm.

larvae and the pellets were made of plant tissues alone, suggesting that the weevil larvae did not prey on aphids. In the galls with two or three tiny holes, no dead weevil larvae, including remains such as head capsules and mandibles, were found. This observation suggests that female adults cease laying eggs after making small holes with their rostra when they detect oviposition by other females. In the plastic bags, some adult weevils emerged from the galls through small holes that they made themselves. The new adults obtained in the field grazed on Z. serrata leaves very well when provided in the laboratory.

Fate of the aphid galls

Parasitism by the weevils varied greatly among study sites (Table 1): At Kamigamo 28.1% of galls were destroyed by weevil parasitism, while on Mt. Ikoma weevil parasitism was negligibly low (1.2%). The percentages of weevil parasitism in the total mortality of the aphid colonies differed among the six sites (df=5, x^2 =112.716, P<0.0001). At Chihaya weevil parasitism, which accounted for 76.7% of total mortality of the aphid colonies, was greatest and at Ka-

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	Chihaya, Osaka	Mt. Ikoma, Osaka	Otsu, Shiga	Kamigamo, Kyoto	Kibune, Kyoto	Ashiu, Kyoto
Successful alate emergence	2081)(82.9)	141(56.2)	96(65.8)	64(22.5)	109(38.4)	155(55.6)
Miscellaneous death of alates	1(0.4)	51(20.3)	12(8.2)	56(19.6)	92(32.4)	64(22.9)
Weevil parasitism	33(13.1)	3(1.2)	8(5.5)	80(28.1)	32(11.3)	50(17.9)
Fungue infestation	0(0)	1(0.4)	0(0)	2(0.7)	0(0)	0(0)
Destruction by birds and other herbivores	8(3.2)	20(8.0)	13(8.9)	18(6.3)	9(3.2)	3(1.1)
Abortion	1(0.4)	35(13.9)	17(11.6)	65(22.8)	42(14.8)	7(2.5)
% weevil parasitism/total mortality ²⁾	76.7a	2.7d	16.0c	36.2b	18.3c	40.3b
No. of leaves examined	69	354	111	501	549	1,039
No. of galls examined	251 '	251	146	285	284	279

Table 1. Fate of leaf pouch galls of *P. morrisoni* on *Z. serrata* trees in six study sites in the Kinki District, Central Japan. The numbers in parentheses are percentages.

¹⁾ Since the sampling date was the earliest (14 May) of six sites, there were still many alates (including nymphs) in the normal galls and no dehiscence openings on the gall walls.

²⁾ The percentages of weevil parasitism per total mortality factors differed among the six study sites (df=5, $x^2=112.716$, P<0.0001). The values with different alphabetical letters were significantly different (sequential Bonferroni test (Rice, 1989), $\alpha = 0.05$).

migamo and Ashiu weevil parasitism was about 40%. Since miscellaneous death comprised several mortality factors, weevil parasitism was the greatest mortality factor at three study sites, Chihaya, Kamigamo and Ashiu. Destruction by birds and other herbivores, though relatively minor factor, was observed at all sites. Gall abortion exceeded 10% at four sites, Mt. Ikoma, Otsu, Kamigamo and Kibune, indicating that it is a relatively important mortality factor.

Parasitoids of R. hustachei

At Kamigamo, *Eupelmus urozonus* Dalman (Eupelmidae) was observed as a larval and pupal idiobiont ectoparasitoid of *R. hustachei*, which killed 9.1% of the larvae (N=77). At Kibune, however, *Pteromalus* sp. (Pteromalidae) parasitized a pupa of the weevil externally, with the rate of parasitism being 3.3% (N=30).

Discussion

The present study indicated that *R. hustachei* usually parasitized the galls of *P. morrisoni* on *Z. serrata* leaves in the Kinki District (Table 1). At Chihaya, Kamigamo and Ashiu, weevil parasitism was the greatest mortality factor of aphids. Thus, weevil parasitism may affect aphid populations considerably. Key factor analyses based on long-term life table data of the aphid populations are needed to quantify the impact of the weevil. In the site on Mt. Ikoma, weevil parasitism was minimal, probably because the study tree was isolated.

Larvae of R. hustachei fed on gall walls inside galls

and destroyed the aphid colonies. The weevil is specific to aphid galls and seems to be an obligatory cecidophage (sensu Mani, 1964) of the aphid gall, similarly as Nola innocua (Noctuidae) found in aphid galls on Distylium racemosum trees (Itô & Hattori, 1982, 1983; Itô, 1984) and Characoma ruficirra (Noctuidae) in Trichagalma serratae (Cynipidae) galls on Quercus acutissima trees (Abe, 1995). Akimoto (1995) reported that R. hustachei parasitized the galls of the aphids Tetraneura spp. on the Japanese elm, Ulmus davidiana, in Hokkaido, northern Japan. The weevil association with host galling aphids should be studied in various sites of Japan. Among the speciose family Curculionidae, Anthonomus hematopus, Curculio parasiticus and C. koreanus have been known as cecidophages. A. hematopus and C. parasiticus feed on the galls of sawflies on willows (Caltagirone, 1964; Smith, 1970; Morimoto, 1984b), and C. koreanus feeds on the galls of Biorhiza weldi (Cynipidae) on oaks (Masuda, 1956).

Flea weevils (the subfamily Rhynchaeninae) are characterized ecologically by their leaf-mining habit (Morimoto, 1984a). Conceivably, *R. hustachei* gained its life-style as a cecidophage from a leaf-mining ancestor. The adaptive significance of leaf-mining habit is analogous to that of insect galls, since both protect their inhabitants from desiccation and provide superior nutrition (Connor & Taverner, 1997). Therefore, the leaf-mining habit of this subfamily could serve as a preadaptation for cecidophagy.

Akimoto (1996) documented that a small number of soldiers were produced in *P. morrisoni* galls and suggested that these soldiers may be effective in counterattacking small invaders which tunnel into the closed galls. Although we could not find dead weevil larvae that were attacked by the aphid soldiers, the weevil larva is a candidate to be counterattacked by the soldiers.

Although E. urozonus has been known as a facultative hyperparasitoid of various gall wasps, gall midges and lepidopterous pupae (Askew, 1975; Yasumatsu & Kamijo, 1979), our study revealed that this wasp is parasitic on the weevil inhabiting aphid galls.

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