Spatial density-independent parasitism of the inquiline, *Diomorus aiolomorphi* (Hymenoptera: Torymidae), on the bamboo gall maker, *Aiolomorphus rhopaloides* (Hymenoptera: Eurytomidae)

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Abstract

Diomorus aiolomorphi Kamijo (Hymenoptera: Torymidae) is an inquiline on bamboo galls formed by the bamboo gall maker *Aiolomorphus rhopaloides* Walker (Hymenoptera: Eurytomidae). I examined (1) the spatial and vertical distribution of galls and galls from which *D. aiolomorphi* emerged, and (2) the spatial density-dependent parasitism of *D. aiolomorphi* in a stand of *Phyllostachys heterocyclus*. The percentages of galls from which *D. aiolomorphi* emerged tended to be higher than those from which *A. rhopaloides* emerged and ranged from 21.5% to 45.6%. Bamboo galls and galls from which *D. aiolomorphi* emerged were distributed contagiously on bamboo culms and branches. The attack of *D. aiolomorphi* was not dependent on gall density on culms and branches. *D. aiolomorphi* is synovigenic; females have no eggs in their ovaries when they emerge but develop eggs continuously as adults age. Thus, *D. aiolomorphi* females cannot lay eggs on freshly initiated galls aggregatively and successively, suggesting that *D. aiolomorphi* attacks regardless of gall density.

Key words: *Aiolomorphus rhopaloides*; bamboo gall maker; density-independent parasitism; *Diomorus aiolomorphi*; inquiline

INTRODUCTION

The spatial patterns of parasitism by insect parasitoids are important for the dynamics of host-parasitoid interactions (Hassell et al., 1991). In gall insects, there are many studies on detection of the spatial density-dependent parasitism; the hackberry nipplegall maker *Pachypsylla celtidismamma* (Homoptera: Psyllidae) (Lill, 1998), the galling sawfly *Euura amerinae* (Hymenoptera: Tenthredinidae) on *Salix pentandra* (Roininen et al., 1996), and the cynipid gall-former *Andricus quercuscalicis* (Hymenoptera: Cynipidae) on *Quercus cerris* (Hails and Crawley, 1992).

Adults of *Diomorus aiolomorphi* Kamijo (Hymenoptera: Torymidae) oviposit on young bamboo galls developed on young branchlets by the bamboo gall maker, *Aiolomorphus rhopaloides* Walker (Hymenoptera: Eurytomidae) (Takahashi and

Mizuta, 1971). *D. aiolomorphi* is univoltine. This species is known to be an inquiline (Takahashi and Mizuta, 1971), that is, a phytophagous insect that cannot make its own galls but feeds on gall tissues induced by a gall maker (Askew, 1961). Although inquilines are very common to many gall makers, they have received very little attention (Sanver and Hawkins, 2000).

The bamboo gall maker, *A. rhopaloides*, causes galls on two species of bamboo, *Phyllostachys heterocyclus* Matsumura and *P. bambusoides* Siebold and Zuccarini (Monocotyledoneae: Gramineae) in Japan (Takahashi and Mizuta, 1971; Kobayashi, 1994; Yukawa and Masuda, 1996). *A. rhopaloides* is also univoltine; adult females emerge from galls from mid-April to early May (Shibata, 2001; Shibata and Ito, 2005) and oviposit in the young buds of bamboo branchlets, which develop into unitary galls (length: 20–30 mm, width: 2–4 mm) (Taka-

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hashi and Mizuta, 1971). Outbreaks of *A. rhopaloides* occur occasionally in stands of *P. heterocycla* in west Japan (Kobayashi, 1994).

It is known that bamboo galls are distributed contagiously both on bamboo culms and branches in a bamboo stand (Shibata, 2003, 2005). The attack pattern of *D. aiolomorphi* on bamboo galls is important in evaluating the regulation of *A. rhopaloides* population density. This study examines (1) the spatial and vertical distribution of galls and galls from which *D. aiolomorphi* emerged, and (2) the spatial density-dependent parasitism of *D. aiolomorphi*.

MATERIALS AND METHODS

Study stand. This study was conducted in an approx. 400-m² stand of *P. heterocycla* in Nagoya City, central Japan. This stand was by the road and had not been managed. The nearest bamboo stand was apart from 1.2 km.

Methods. In late March 1999, 2000 and 2001, five to eight bamboo culms were cut at random just before *A. rhopaloides* and *D. aiolomorphi* emergence. Culm height and diameter at breast height (dbh) of each bamboo were measured. All branches were clipped from each culm after measuring the height of the base of each branch from the ground. After the branch lengths had been measured and the number of galls on each branch counted, the individual galls were collected and put in individual test tubes (diameter: 1 cm, length: 7 cm) kept outdoors at ambient temperatures. Emerged *A. rhopaloides* and *D. aiolomorphi* were counted every 2 or 3 days until mid-July.

Statistical analyses. Statistical analyses were performed using the SPSS computer program (Norussis, 1993). Differences in mean bamboo heights and mean dbh among 3 years were tested by one-way ANOVA with Tukey's HSD multiple

comparison test. One-way ANOVA was used to detect significant differences in gall numbers per culm (transformed to $\log [x+0.5]$ according to Yamamura (1999)), and percentages (transformed to arcsine-root) of galls from which *A. rhopaloides* emerged (%GM) and galls from which *D. aiolomorphi* emerged (%INQ) among 3 years. Differences in gall number per 10-cm branch length (transformed to $\log [x+0.5]$), and %GM and %INQ (both transformed to arcsine-root) in each year among height classes were tested by one-way ANOVA with Tukey's HSD multiple comparison test. One-way ANOVA was used to test significant differences in gall numbers (transformed to $\log [x+0.5]$), and the %INQ (transformed to arcsine-root) among branch length classes. Coefficient of determination (r^2) was applied to the relationships between numbers of galls and galls from which *D. aiolomorphi* emerged per culm. %INQ (transformed to arcsine-root) between the number of galls per 10-cm branch length in each year were tested by one-way ANOVA with Tukey's HSD multiple comparison test. The spatial distribution patterns of galls and galls from which *D. aiolomorphi* emerged on bamboo culms and branches were analyzed using Morisita's I_δ index (Morisita, 1959), with χ^2 -test to test the null hypothesis of randomness (Krebs, 1998).

RESULTS

Culm height and dbh

There were no significant differences in culm height and dbh among 3 years (height: $F=0.098$, $df=2$, $p=0.907$; dbh: $F=0.729$, $df=2$, $p=0.498$) (Table 1).

Number of galls, %GM and %INQ

There were no significant differences in the mean numbers of galls per culm, %GM and %INQ

Table 1. Number of culms examined, mean height and diameter at breast height (dbh) of culms and number of galls examined

Year	Number of culms	Height (m)	dbh (cm)	Number of galls
1999	5	7.2 $\pm$ 1.0 a	4.5 $\pm$ 0.9 a	3,952
2000	8	7.4 $\pm$ 0.8 a	5.2 $\pm$ 1.3 a	943
2001	6	7.2 $\pm$ 0.4 a	5.0 $\pm$ 0.7 a	1,430

Mean $\pm$ SD.

Same letters in each column indicate no significant differences ($p>0.05$).

Table 2. Mean number of galls, mean percentage of galls from which *A. rhopaloides* emerged and of galls from which *D. aiolomorphi* emerged

Year	Number of galls per culm	Percentage of galls from which <i>A. rhopaloides</i> emerged (%)	Percentage of galls from which <i>D. aiolomorphi</i> emerged (%)
1999	790.4±729.8 a	1.5±1.0 a	45.6± 5.7 a
2000	117.9± 72.5 a	2.0±2.1 a	47.7±18.6 a
2001	240.0±321.2 a	1.1±1.0 a	21.5±13.6 a

Mean±SD.

Same letters in each column indicate no significant differences ($p>0.05$).

among the 3 years (number: $F=1.777$, $df=2$, $p=0.201$; %GM: $F=0.507$, $df=2$, $p=0.612$; %INQ: $F=0.674$, $df=2$, $p=0.524$) (Table 2). The %INQ tended to be higher than %GM. The %INQ ranged from 21.5% to 45.6% (Table 2).

Spatial distribution pattern on bamboo culms and branches

Based on the bamboo culms, the indices of spatial distribution, I_δ , indicate that bamboo galls were distributed contagiously in 3 years (1999: $I_\delta=1.68$, $\chi^2=2,695.7$, $df=4$, $p<0.01$; 2000: $I_\delta=1.32$, $\chi^2=312.3$, $df=7$, $p<0.01$; 2001: $I_\delta=3.27$, $\chi^2=2,731.5$, $df=5$, $p<0.01$). The bamboo galls from which *D. aiolomorphi* emerged were distributed contagiously on the bamboo culms in 1999 and 2001 (1999: $I_\delta=1.70$, $\chi^2=1,250.5$, $df=4$, $p<0.01$; 2000: $I_\delta=1.04$, $\chi^2=21.6$, $df=7$, $p>0.05$; 2001: $I_\delta=2.81$, $\chi^2=805.1$, $df=5$, $p<0.01$).

Based on the bamboo branches, the indices of spatial distribution indicate that bamboo galls were distributed contagiously in 3 years (1999: $I_\delta=2.54$, $\chi^2=6,343.0$, $df=274$, $p<0.01$; 2000: $I_\delta=3.19$, $\chi^2=2,530.0$, $df=466$, $p<0.01$; 2001: $I_\delta=4.34$, $\chi^2=5,208.1$, $df=296$, $p<0.01$). The bamboo galls from which *D. aiolomorphi* emerged were distributed contagiously on the bamboo branches in 3 years (1999: $I_\delta=2.64$, $\chi^2=3,209.0$, $df=274$, $p<0.01$; 2000: $I_\delta=3.24$, $\chi^2=1,301.7$, $df=466$, $p<0.01$; 2001: $I_\delta=5.26$, $\chi^2=2,273.8$, $df=397$, $p<0.01$). These results suggest that the galls and galls from which *D. aiolomorphi* emerged on branches are distributed contagiously.

The indices of spatial distribution, I_δ , of galls and galls from which *D. aiolomorphi* emerged tended to be very similar to those of overall galls on both bamboo culms and branches (Fig. 1).

Fig. 1. Relationships between the indices of spatial distribution, I_δ , of galls and galls from which *D. aiolomorphi* emerged on bamboo culms (a) and branches (b). Straight lines indicate the relationship of $Y=X$.

Vertical distribution

There was a significant difference in the mean number of galls per 10-cm branch length among height classes in every year (1999: $F=6.331$, $df=5,200$, $p<0.001$; 2000: $F=1.287$, $df=5,242$, $p=0.270$; 2001: $F=0.912$, $df=5,242$, $p=0.612$) with more galls at middle parts in 1999 and 2000 and at lower parts in 2001 (Fig. 2a). However, there were no significant differences in the %GM for height classes in each year (1999: $F=1.355$, $df=5,201$, $p=0.243$; 2000: $F=2.322$, $df=2,238$, $p=0.054$; 2001: $F=1.234$, $df=3,191$, $p=0.295$) (Fig. 2b). The %INQ did not differ significantly between height classes in each year (1999: $F=0.526$, $df=5,201$, $p=0.756$; 2000: $F=2.435$, $df=5,242$,

Fig. 2. Mean number of galls per 10-cm branch length (a), and percentages of galls from which *A. rhopaloides* emerged (%GM) (b) and galls from which *D. aiolomorpha* emerged (%INQ) (c) at each bamboo height class. Horizontal lines indicate +SE. Different letters indicate significant differences ($p < 0.05$).

$p = 0.055$; 2001: $F = 0.927$, $df = 5, 191$, $p = 0.612$) (Fig. 2c).

Detection of density dependence

Significant positive linear correlations were found between gall number and gall number from which *D. aiolomorpha* emerged in 1999 and 2001 on bamboo culms (Fig. 3). There were no significant differences between the number of galls per 10-cm branch length and %INQ in each year (1999: $F = 0.232$, $df = 4$, $p = 0.920$; 2000: $F = 0.568$, $df = 1$, $p = 0.452$; 2001: $F = 1.001$, $df = 2$, $p = 0.318$) (Fig. 4). These results suggest that mortality due to *D. aiolomorpha* did not occur through gall density dependence on culms and branches.

DISCUSSION

Shibata (2001) pointed out that phenological

Fig. 3. Relationships between the number of galls and the number of galls from which *D. aiolomorpha* emerged in 3 years.

asynchrony between adult emergence and bud burst as a bottom-up effect may have large effects on the population fluctuation of *A. rhopaloides*. Furthermore, since the percentage of *D. aiolomorpha* emerging from overwintering galls was relatively high during 3 years (Table 2), parasitism of *D. aiolomorpha* as a top-down force (Shibata, 2006) might be also a main mortality factor of bamboo galls.

Takahashi and Mizuta (1971) showed that when larvae of *A. rhopaloides* and *D. aiolomorpha* live in the same gall in June and July, the latter usurps the gall because of faster growth and harder body surface. The percentage of larvae of *D. aiolomorpha* in galls from July to March tended to be constant (Shibata and Ito, 2005) and larval development is completed by August of the same year (Takahashi and Mizuta, 1971). These findings suggest that once a larva of *D. aiolomorpha* usurps a gall, the number of *D. aiolomorpha* larvae tends to be stable due to the low parasitism of the facultative hyperparasitoid (Shibata and Ito, 2005), and allowing us to evaluate the density-dependent parasitism of *D. aiolomorpha* by counting the number of galls from

Fig. 4. Percentages of galls from which *D. aiolomorpha* emerged (%INQ) in each class of the number of galls per 10-cm branch-length. Vertical lines indicate $\pm$ SE. Different letters indicate significant differences ($p < 0.05$).

which adult *D. aiolomorpha* emerge.

In this study, bamboo galls were distributed contagiously on both bamboo culms and branches. Kuno (1986) noted that the spatial distribution of insects is not usually random, but is often contagious due to oviposition behavior. *A. rhopaloides* is pro-ovigenic; emerging females have ca. 80 eggs in their ovaries, suggesting that they can oviposit soon after emergence (Shibata, 2002). Consequently, the difference in culm and branch phenology, that is, asynchronism of adult emergence of *A. rhopaloides* and bud-burst of branches where females lay eggs (Shibata, 2003), might affect the contagious distribution pattern of galls (Shibata, 2005). The contagious spatial distribution is also due to the uneven quality of habitats (Kuno, 1986). More bamboo galls are formed on longer branches, so galls are distributed contagiously on branches because longer branches with more buds allow more effective oviposition (Shibata, 2005).

If *D. aiolomorpha* lays eggs on fresh galls ag-

gregatively, the index of spatial distribution of galls on culms and branches from which *D. aiolomorpha* emerged should be higher than that of overall galls; bias in the distribution pattern of galls from which *D. aiolomorpha* emerged might be higher than that of galls. However, there was no clear difference in indices of spatial distribution between galls from which *D. aiolomorpha* emerged and overall galls (Fig. 1), suggesting that *D. aiolomorpha* does not attack galls aggregatively on particular culms and branches.

The effect of measurement scale for the spatial density-dependent parasitism is important for detecting aggregative responses in parasitoids (Force and Moriarty, 1988; Rothman and Darling, 1990; Lill, 1998). Gall density-dependent mortality of *A. rhopaloides* by *D. aiolomorpha* was not observed on two scales: culms and branches (Figs. 3, 4). Contagious spatial distribution of parasitism is often seen at the behavioral level in which the aggregative response of adult female parasitoids in patches of different host density is examined (Hassell, 1982). Adults of inquilines generally emerge from galls soon after the gall maker and oviposit in freshly initiated galls (Wiebes-Rijks and Shorthouse, 1992). *D. aiolomorpha* also emerges from galls 15–20 days later than *A. rhopaloides* (Shibata, 2001, 2005). Unlike *A. rhopaloides*, *D. aiolomorpha* is synovigenic; *D. aiolomorpha* females have no eggs in their ovaries when they emerge but develop eggs continuously as adults age (ca. 20 eggs after 10 days longevity). Consequently, new *D. aiolomorpha* females cannot lay eggs on freshly initiated galls aggregatively and successively, suggesting that *D. aiolomorpha* attacks regardless of gall density. In addition, the number of galls was different among height classes but %INQ was not (Fig. 2), suggesting that females of *D. aiolomorpha* parasitize galls independently of culm height. This result consists with the density-independent parasitism by *D. aiolomorpha* females.

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