ORIGINAL ARTICLE

# Effects of parasitoids on a mycophagous drosophilid community in northern Japan and an evaluation of the disproportionate parasitism hypothesis

Hiroshi YOROZUYA

*Institute of Low Temperature Science, Hokkaido University, Sapporo, Japan*

## Abstract

In a host–parasitoid system comprising mycophagous drosophilids and their parasitoids, the drosophilid and parasitoid species assemblages, host use, and the prevalence of parasitism were assessed, and the "disproportionate parasitism hypothesis" was examined with consideration given to yearly variations. The mycophagous drosophilids, their fungal food resources and parasitoids were studied by carrying out an intensive census throughout the activity seasons of 4 years (2000–2003) in Hokkaido, northern Japan. Five hymenopterous parasitoid species, four braconids and one eucoilid, were found. Parasitoids of mycophagous drosophilids are reported for the first time from Asia. Most parasitism (99.2%) was by braconids, in contrast to the dominance of eucoilids in Europe. Parasitism was restricted to the summer, and the rate was high from early July to early August every year. There was considerable yearly variation in the composition of abundant fungus, drosophilid and parasitoid species, especially between 2000 and 2001. The alternation of dominant host species was coupled with the alternation of dominant parasitoid species that differed in host use. Despite the yearly variation in the system, the most dominant host species suffered disproportionately heavy parasitism by the correspondingly dominant parasitoid species every year. The parasitism rate was positively correlated with the relative host abundance. This thus indicates that the disproportionate parasitism mechanism may operate, via which species coexistence is promoted by a higher rate of parasitism of the dominant species.

**Key words:** Braconidae, coexistence, Diptera, Drosophilidae, fungi, Hymenoptera, long-term census.

## INTRODUCTION

Predators, parasitoids, parasites and pathogens may affect prey (host) community structure by reducing population densities below the level at which competition becomes important, or by selectively reducing the population sizes of certain competitors. If dominant competitors are affected, the top-down effects mediate the coexistence of competing prey species (Paine 1966; Freeland 1983; Sih *et al.* 1985; Dobson & Crawley 1994; Holt & Lawton 1994; Marcogliese & Cone

1997). Such an effect exists in drosophilid communities when staphilinid beetles reduce larval recruitment, relax larval competition and release the inferior competitors from competitive pressure (Worthen 1989). Parasitoids also affect competitive interactions between frugivorous drosophilid species in North Africa (Boulétreau *et al.* 1991). There is, furthermore, a positive correlation in mycophagous drosophilids between the rate of parasitism by nematodes and relative host abundance (Gillis & Hardy 1997; Hardy & Gillis 1998). These authors suggested that coexistence was promoted by disproportionately high parasitism that represses the population density of the dominant host species. They termed this the "disproportionate parasitism hypothesis".

The effect of parasitoids has been less explored in natural drosophilid communities (Fleury *et al.* 2004). Janssen *et al.* (1988) and Driessen *et al.* (1990) found

*Correspondence:* Hiroshi Yorozuya, Institute of Low Temperature Science, Hokkaido University, Sapporo, 060-0819 Japan. Email: hiroyoro@lowtem.hokudai.ac.jp

an unexpected and large impact of parasitoids on mycophagous drosophilid communities during their studies in the Netherlands. However, Davis *et al*. (1996) reported that parasitoids of drosophilids appear generally rare in England. Thus, parasitoid effects on natural drosophilid communities differ between sites and regions. There is no information from Asia about parasitoids of mycophagous drosophilids and their effects on community structure. At least 42 hymenopterous species are known to attack drosophilid flies (Carton *et al*. 1986), but this does not include any species from Japan, nor from Asia generally.

To document the tritrophic system comprising fungi, drosophilid flies and their parasitoids for the first time in Asia, I conducted an intensive census in a northern Japanese cool temperate forest. This census covered the entire season of fly activity for 4 years from 2000 to 2003. I then used these data to assess the potential role of disproportionate parasitism in structuring the drosophilid community, taking yearly variation into consideration. I therefore tested the null hypothesis that the parasitism rate is equal across all host species, irrespective of their relative abundance.

## MATERIALS AND METHODS

### Study site

The study was conducted from 2000 to 2003 on a permanent 4 ha plot in Tomakomai Experimental Forest (42°40′N, 141°36′E), Hokkaido, northern Japan. Nighttime temperatures at the study site are not reliably above zero between October and May. Snow first falls at the end of October or the beginning of November, and lies until early April. The site is a mature deciduous broad-leaved forest dominated by trees of *Quercus cispura* Bluma, *Tilia japonica* Simonkai and *Acer palmatum* var. *matsumura* Makino. The forest floor is sparsely covered with dwarf bamboo, ferns and saplings, and is also scattered with decayed trees and debris. The fruiting bodies of wood-decaying and mycorrhizal fungi emerge on the decayed trees and forest floor from the end of May to November.

### Monitoring and sampling procedures

Along a fixed research route of approximately 2 km, I censused fungi, drosophilid flies and parasitic wasps every day, except for days of heavy rain. I censused all fungal fruiting bodies found within 5 m of both sides of the route, so that the total area surveyed was approximately 2 ha. The censuses began in June, on the day when the first fungus fruiting bodies appeared, and con-

tinued to the end of October, when fungi disappeared. I defined a fungal patch as a clump of fruiting bodies of the same species, or a single fruiting body emerging separately. I marked all patches and recorded the species, the number of fruiting bodies, and the maximum diameter of each fruiting body in each fungus patch. Fungus species were identified by T. Igarashi or by me, with reference to Imazeki and Hongo (1987, 1989).

To estimate the amount of fungus biomass when patches consisted of a large number of fruiting bodies, I measured the wet weights and the maximum diameters of 10–30 fresh fruiting bodies for each species. A regression equation of the weight of a fruiting body on its maximum diameter for each fungal species was used to estimate total biomass from the number and size of fruiting bodies. During each census, I collected all drosophilid adults and parasitic wasps on every fungal patch. After the fungi decayed but before the emergence of drosophilids, I collected all, or some (if the patch was large), of the fruiting bodies from each patch and reared out the drosophilids and the parasitoids. The fungi were weighed and put on moist, sterilized soil in a 1 L plastic jar with a 25 mm cotton-plugged ventilation hole in the lid. After all drosophilid larvae pupated, the drosophilid puparia were carefully washed out in water and collected. The puparia were maintained individually in small plastic tubes until drosophilid adults or parasitoids emerged. When puparia contained parasitoid larvae in diapause, they were maintained at room temperature until the following spring. Puparial capsules from which drosophilids or parasitoids emerged were kept together with the eclosed adult insects. Drosophilid species were identified based on the key of Beppu *et al*. (1977). The parasitoid species were identified by C. van Achterberg (Braconidae) and Y. Abe (Eucoilidae). The species identity of the hosts of individual parasitoids was determined by identifying the puparia from which they had emerged. This was done based on descriptions of the puparial morphology by Okada (1968) and/or by comparing the puparia that had produced parasitoids with those that had produced identified drosophilid flies.

### Estimation of drosophilid and parasitoid population sizes

The estimated weights of the fungus patches were summed for each fungus species and for each 10-day period of a month. A 10-day period was chosen because most fungus patches disappeared within 10 days. The utilization of fungi by drosophilid larvae was evaluated by calculating the number of puparia of each species,

including those parasitized, obtained from 1 g of fungus for each patch. These data were then multiplied by the estimated total weight of the patch. The parasitism rates of wasp species on each drosophilid species were expressed as the ratio of the number of emerged parasitoids to the total number of host larvae.

## Statistical analysis

To allow direct comparison, I used the statistical methods of Gillis and Hardy (1997). The null hypothesis of no difference in parasitism rate between host species was first tested by analysis of variance (ANOVA) with post-hoc Bonferroni's multiple comparison (StatView 5.0, SAS Institute, Cary, NC, USA). Parasitism of an individual drosophilid fly was represented by a binary response variable (1 = parasitized, 0 = unparasitized). The difference in host utilization between parasitoid species was examined by using a $\chi^2$ test. The null hypothesis of no relationship between relative abundance and parasitism rate in drosophilid species was examined by Kendall rank correlation, and Fisher's combined probability method was applied to the overall test for the 4 census years.

## RESULTS

### Fungi

Over the 4-year census, a total of 43 fungus species were found on the census route. Of these, 32 species were found to be breeding resources of drosophilids (Table 1). The biomass of fungi changed seasonally and between years, the yearly total was the largest in 2002 (Fig. 1). In general, the total fungal biomass was greater in autumn than in summer, but the seasonal pattern varied considerably between years. In 2000, total biomass was lowest from late June to late July, a period of high parasitoid activity (see later for more detail), but greatest in October. In 2001 and 2002, the biomass peaked in September. In 2003, however, the seasonal change pattern was distinct, with two peaks in early July and in late August, and the lowest biomass in autumn. In addition, there was marked variation in the emergence pattern of fungal species (Table 1). Several species did not emerge every year, and some emerged in only one of the 4 years censused. Even abundant species that were important breeding resources for drosophilids showed considerable yearly variation in biomass. For example, *Oudemansiella mucida* Hounel was extraordinarily abundant in 2002. Furthermore, in 2000, *Pleurotus pulmonarius* Quel. was scarce and *Amanita citrina* var. *citrina* Pers. was abundant, but in 2003, the pattern was reversed.

### Drosophilids

Twelve drosophilid species emerged from fungi collected over the 4 years of the census (Table 1). Adult flies visited fungi from the end of May to the beginning of November, but stopped breeding in late September. The overall population of mycophagous drosophilid larvae exhibited different seasonal trends among the 4 survey years (Fig. 2). In 2000 and 2002, the population increased or was nearly constant as the season progressed, with a depression in summer (from late June to July), whereas it decreased in 2001. In 2003, the population increased in early July and late August. Two *Hirtodrosophila* species, *H. trilineata* (Chung, 1960) and *H. sexvittata* (Okada, 1956), dominated, but their population sizes varied over the 4 years (Table 1).
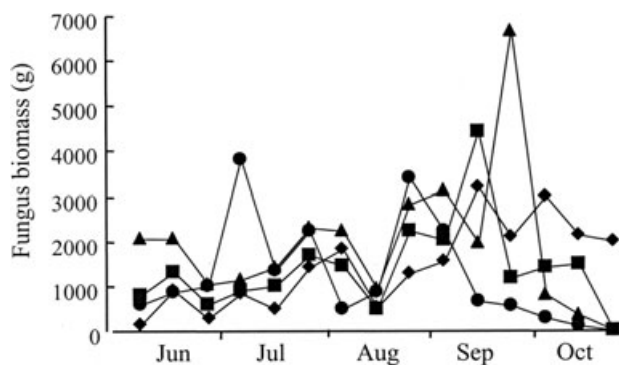


Figure 1 Seasonal changes in the estimated fungus biomass that emerged along the census route during the years 2000–2003: ◆, 2000; ■, 2001; ▲, 2002; ●, 2003.
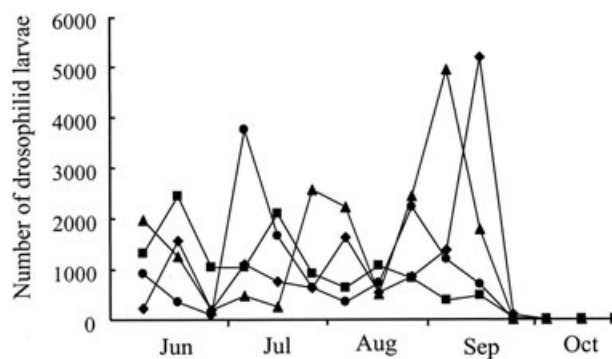


Figure 2 Seasonal changes in the estimated number of drosophilid larvae in fungi along the census route during the years 2000–2003: ◆, 2000; ■, 2001; ▲, 2002; ●, 2003.

**Table 1** Fungus biomass, numbers of drosophilid larvae (including parasitized ones) and eclosed parasitoids in each of the four census years, separately estimated for each species over the census route (2 km)

| | Estimated fungus biomass (g) | | | |
| --- | --- | --- | --- | --- |
| | 2000 | 2001 | 2002 | 2003 |
| Fungus species | | | | |
| *Pleurotus pulmonarius* Quel. | 762 | 2 427 | 5 940 | 6 598 |
| *Oudemansiella mucida* Hounel | 3 314 | 1 707 | 9 395 | 1 098 |
| *Oudimansiella brunneomarginata* Vassilieva | 1 068 | 1 482 | 4 303 | 232 |
| *Amanita citrina* var. *citrina* Pers. | 3 063 | 437 | 1 339 | 530 |
| *Oudemansiella platyphylla* Moser | 1 123 | 1 776 | 557 | 320 |
| *Amanita pantherina* Krombh. | 524 | 262 | – | 1 563 |
| *Armillariella mellea* Kummer | 942 | 110 | – | 1 191 |
| *Pluteus atricapillus* Fayod | 278 | 762 | 637 | 158 |
| *Plotodaedalea hispia* Imazeki | 320 | 722 | 534 | 176 |
| *Polyporus tuberaster* Pers. | – | 581 | 282 | 722 |
| *Clitocybe lignatilis* Karst. | 666 | 74 | 326 | 200 |
| *Mycoleptodonoides aitchisonii* Maas G. | 1 200 | – | – | – |
| *Boretus* sp.2 | – | – | 606 | 497 |
| *Russula cyanoxantha* (Schaeff.) Fr. | – | – | 666 | 173 |
| *Stereum gausapatum* Fr. | – | 700 | – | – |
| *Psathyrella* sp. | – | 341 | 24 | 221 |
| *Boretus pulverulentus* Opat. | 400 | – | – | – |
| *Boretus* sp. | – | 400 | – | – |
| *Polyporus alveolaris* Boud. Et Sing | 100 | 73 | 141 | 45 |
| *Hericium ramosum* Letellier | 149 | 201 | – | – |
| *Collybia* sp. | – | – | 100 | 223 |
| *Panellus serotinus* (Pers.: Fr.) Kuhn | – | – | 320 | – |
| *Trichaptum elongatum* Imazeki | 306 | – | – | – |
| *Mycena galericulata* S. F. Gray | 26 | 8 | 165 | 84 |
| *Gymnopilus liquiritiae* Karst. | 106 | 159 | – | – |
| *Crepidotus mollis* Kummer | 53 | 36 | 115 | 8 |
| *Xanthoconium affinae* Sing. | 200 | – | – | – |
| *Amanita vaginata* var. *fulva* Gill. | 84 | 21 | 91 | – |
| *Panus suaviaaimus* Sing. | 33 | 135 | – | – |
| *Dendropolyporus umbellatus* Julich | – | 164 | – | – |
| *Pluteus tricuspidatus* Vel. | – | – | 114 | 41 |
| *Mycena inclinata* (Fr.) Quel. | – | 140 | – | – |
| *Coprinus micaceus* Fr. | 90 | 36 | – | – |
| *Agrocybe praecox* (Pers.: Fr.) Fayod | – | – | 116 | – |
| *Amanita hemibapha* subsp. hemibapha Sacc. | – | 107 | – | – |
| *Tylopilus castaneiceps* Hongo | 30 | 60 | – | – |
| *Resupinatus applicatus* S. F. Gray | 88 | – | – | – |
| *Marasmius siccus* Fr. | 20 | 20 | – | – |
| *Lactarius torminosus* (Schaeff.: Fr.) S. F. Gray | – | – | 36 | – |
| *Lentinus edods* Sing. | – | 31 | – | – |
| *Flammulina velutipes* Sing. | – | 30 | – | – |
| *Phallus costatus* Lloyd | 10 | – | 10 | 4 |
| *Mycena polygramma* Glay. | 2 | 1 | – | – |
| Total | 14 957 | 13 003 | 25 817 | 14 084 |
| Drosophilid species | | | | |
| *Hirtodrosophila trilineata* (Chung) | 5 624.1 | 5 763.1 | 12 458.6 | 7904.4 |
| *Hirtodrosophila sexvittata* (Okada) | 4 721.6 | 3 281.7 | 3 851.6 | 3501.6 |
| *Mycodrosophila atrithorax* Okada | 1 141.0 | 1 250.0 | 84.0 | 299.0 |

**Table 1** *Continued*

| | Estimated fungus biomass (g) | | | |
| | 2000 | 2001 | 2002 | 2003 |
|---|---|---|---|---|
| *Drosophila busckii* Coquilett | 703.7 | 433.9 | 503.8 | 33.3 |
| *Hirtodrosophila histrioides* (Okada & Kurokawa) | 221.7 | 668.6 | 463.5 | 117.7 |
| *Drosophila unispina* Okada | 975.4 | 148.7 | 157.2 | 131.9 |
| *Hirtodrosophila alboralis* (Momma & Takada) | 261.8 | 412.5 | 360.8 | 45.0 |
| *Drosophila orientacea* Grimaidi *et al.* | 222.2 | 114.0 | 315.7 | 316.3 |
| *Drosophila histrio* Meigan | 10.0 | – | 265.5 | 132.7 |
| *Mycodrosophila poecilogastra* (Loew) | 190.5 | 126.5 | 69.5 | – |
| *Hirtodrosophila quadrivittata* (Okada) | 28.5 | – | 43.0 | – |
| *Drosophila immigrans* Sturtevant | 4.0 | – | – | – |
| Total | 14 104.5 | 12 199 | 18 573.2 | 12 481.9 |
| Parasitoid species | | | | |
| Braconidae | | | | |
| *Phaenocarpa* sp. | 131.7 | 913.8 | 1 519.7 | 755.3 |
| *Aphaereta* sp. | 1 238.7 | 183.8 | 204.3 | 84.0 |
| *Asobara rossica* Bel. | 1.0 | – | – | – |
| *Asobara tabida* (Nees) | 1.0 | – | – | – |
| Eucoilidae | | | | |
| *Ganaspis* sp. | 6.0 | 8.0 | 25.8 | – |
| Total | 1372.4 | 1 097.6 | 1724 | 839.3 |

*Hirtodrosophila trilineata* was the most abundant throughout the survey, especially so in 2002. *Hirtodrosophila sexvittata* was always the second most abundant with respect to the yearly total, but outnumbered *H. trilineata* from June to early September, the breeding season, in 2000. Of the other species, *Mycodrosophila atrithorax* Okada, 1968 was relatively abundant, ranking third in 2000 and 2001.

## Parasitoids

Five hymenopterous species, four braconids and one eucoilid, were found to attack drosophilid larvae (Table 1). The census and rearing data revealed that parasitoid adults were active from late June to late September, with a peak in mid-July to early August (Fig. 3). At least some of their offspring larvae entered diapause in early July, the earliest on 6 July 2001. The total number of parasitoids emerging was greatest in 2002, followed by 2000 and 2001, and least in 2003 (Table 1). In 2000, the dominant species was *Aphaerata* sp. but it was *Phaenocarpa* sp. in the other 3 years. These two dominant parasitoid species shared some host species, in particular the two dominant drosophilid species, but differed significantly from each other with respect to the proportion of each host used ($\chi^2$ test, $P < 0.0001$; Table 2). *Aphaerata* sp. most frequently attacked
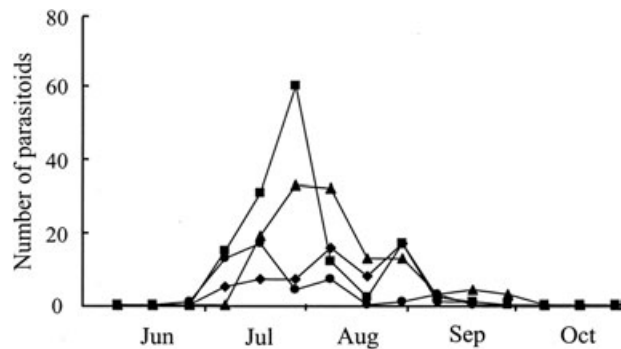


**Figure 3** Seasonal changes in the number of adult parasitoids collected on fungi along the census route during the years 2000–2003: ◆, 2000; ■, 2001; ▲, 2002; ●, 2003.

*H. sexvittata* but did not attack *Drosophila unispina* Okada, 1956. *Phaenocarpa* sp. selected *H. trilineata* as its main host species, but did not use *Hirtodrosophila histrioides* (Okada and Kurokawa, 1957), *Hirtodrosophila alboralis* (Momma and Takada, 1954) or *M. atrithorax*.
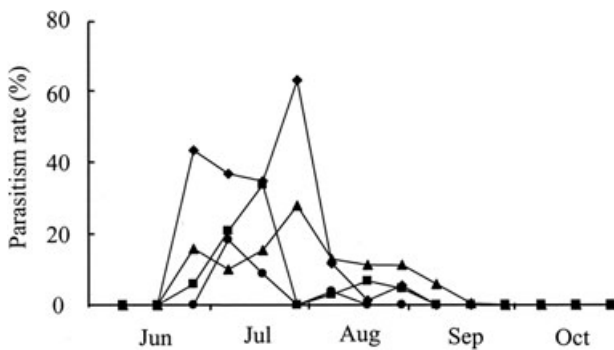
## Parasitism

The total yearly parasitism rate was relatively constant: 9.8% in 2000, 9.1% in 2001, 9.4% in 2002, and 6.7%

**Table 2** Estimated number of parasitoids reared from each drosophilid species throughout the four census years

|                   | Hs     | Ht     | Hh   | Ha  | Du   | Do   | Ma   |
|-------------------|--------|--------|------|-----|------|------|------|
| *Phaenocarpa* sp. | 126.6  | 3168.8 | –    | –   | 11.5 | 13.7 | –    |
| *Aphaereta* sp.   | 1054.2 | 431.7  | 77.8 | 3.0 | –    | 6.0  | 30.0 |
| *Asobara rossica* | –      | –      | –    | –   | 1.0  | –    | –    |
| *Asobara tabida*  | –      | –      | –    | –   | 1.0  | –    | –    |
| *Ganaspis* sp.    | –      | 25.8   | –    | 8.0 | –    | 6.0  | –    |

Hs, *Hirtodrosophila sexvittata*; Ht, *Hirtodrosophila trilineata*; Hh, *Hirtodrosophila histrioides*; Ha, *Hirtodrosophila alboralis*; Du, *Drosophila unispina*; Do, *Drosophila orientacea*; Ma, *Mycodrosophila atrithorax*.



**Figure 4** Seasonal changes in the parasitism rate of drosophilid flies during the years 2000–2003: ◆, 2000; ■, 2001; ▲, 2002; ●, 2003.

in 2003. There were, however, large seasonal fluctuations (Fig. 4). Parasitism was usually high in late June to late July, with a peak in late July in 2000 (62.9%), mid-July in 2001 (33.7%), late July in 2002 (28.1%), and early July in 2003 (18.2%). In addition to the temporal variation, the parasitism rate varied among drosophilid species (Table 3). The parasitism rates were significantly different among drosophilid species every year and also for the 4-year combined dataset (ANOVA, $P < 0.0001$; Table 4). Post-hoc Bonferroni multiple comparison revealed that the most dominant drosophilid species during the parasitoid active period, *H. sexvittata* in 2000 and *H. trilineata* in other years, was significantly more heavily parasitized than the other species every year (Table 3); *H. histrioides* was exceptionally heavily parasitized in 2000 (Table 3). When all the data for the 4 years were combined, the parasitism rate was found to be significantly higher in the first and second most dominant species, *H. trilineata* and *H. sexvittata*, than in most other species. There were significant positive correlations between parasitism rate and relative abundance in 2000 and in the overall test of significance for the 4 census years (Fisher's combined probability $\chi_8^2 = 18.6$, $P = 0.017$; Table 5).

## DISCUSSION

There are several differences between the fungal-based tritrophic system in Hokkaido and those elsewhere. The present study showed that most parasitism (99.2%) was caused by braconids in Hokkaido, but eucoilids are known to be major parasitoids of drosophilids (77.9%) in Europe (Driessen *et al.* 1990). However, *Asobara tabida* (Nees von Esenbeck, 1834), a braconid species, is known to be dominant in the parasitoid complex of frugivorous and mycophagous drosophilids, such as *Drosophila obscura* Fallén, 1823, *Drosophila kuntzei* Duda, 1924, and *Drosophila busckii* Coquillett, 1901, in central and western Europe (van Alphen & Drijver 1982). Parasitoid phenology also differs between Hokkaido and Europe. In the Netherlands, parasitoids have a long activity period from late June to early October (Driessen *et al.* 1990). In Hokkaido, however, parasitoids were active over a shorter period, from late June or early July to early or mid-August. Despite such differences in the adult occurrence period, Driessen *et al.* (1990) suggested that parasitoids of mycophagous drosophilids tend to be univoltine in the Netherlands. In this respect, therefore, the two communities are similar, because most Hokkaido parasitoids enter diapause from July onward.

Each trophic level showed a considerable yearly variation in the abundance of component species. The emergence of fungi is generally unpredictable (Shorrocks & Charlesworth 1980; Lacy 1984; Ohenoja & Koistinen 1984; Bills *et al.* 1986). In fact fungal biomass and species composition changed greatly between years in the present study. Such changes in breeding resources are likely to affect the mycophagous drosophilid community, as fly species appear to have species-specific

**Table 3** Relative abundance and parasitism rate of each drosophilid species in each year and the whole four-year census period

| Drosophilid species | 2000 | | 2001 | | 2002 | | 2003 | | 2000–2003 | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Relative abundance | Parasitism rate | Relative abundance | Parasitism rate | Relative abundance | Parasitism rate | Relative abundance | Parasitism rate | Relative abundance | Parasitism rate |
| H. trilineata | 0.399 | 0.042[c] | 0.472 | 0.167[a] | 0.671 | 0.131[a] | 0.633 | 0.102[a] | 0.554 | 0.114[a] |
| H. sexvittata | 0.335 | 0.191[b] | 0.269 | 0.043[b] | 0.207 | 0.029[b] | 0.281 | 0.009[b] | 0.268 | 0.077[b] |
| M. atrithorax | 0.081 | 0.026[cd] | 0.102 | 0[c] | – | – | 0.024 | 0[b] | 0.048 | 0.011[c] |
| D. busckii | 0.049 | 0[d] | 0.036 | 0[bc] | 0.027 | 0[b] | – | – | 0.029 | 0[c] |
| H. histrioides | 0.016 | 0.336[a] | 0.055 | 0.005[c] | 0.025 | 0[b] | 0.009 | 0[b] | 0.025 | 0.053[c] |
| D. unispina | 0.069 | 0.010[cd] | 0.012 | 0[bc] | 0.008 | 0.022[b] | 0.011 | 0[b] | 0.025 | 0.010[c] |
| H. alboralis | 0.019 | 0.011[cd] | 0.034 | 0.019[bc] | 0.019 | 0[b] | – | – | 0.019 | 0.010[c] |
| D. orientacea | 0.016 | 0.063[c] | 0.009 | 0[bc] | 0.017 | 0.031[b] | 0.025 | 0[b] | 0.017 | 0.026[bc] |
| D. histrio | – | – | – | – | 0.014 | 0[b] | 0.011 | 0[b] | 0.007 | 0[bc] |
| M. poecilogastra | 0.014 | 0[cd] | 0.010 | 0[bc] | – | – | – | – | – | – |
| Others† | 0.003 | 0[cd] | – | – | 0.011 | 0[b] | 0.006 | 0[b] | 0.008 | 0[bc] |
| Total | | 0.098 | | 0.091 | | 0.094 | | 0.067 | | 0.087 |

†The "others" category sums up rare species with a total number of individuals less than 100. The same letters within a column indicate non-significant differences according to Bonferroni's multiple comparison at $\alpha = 0.05$.

**Table 4** ANOVA table to test interspecific differences in parasitism rates in each year and over the whole four-year census period

| Year | d.f. | Sum of squares | Mean square | F | P |
|---|---|---|---|---|---|
| 2000 | 9 | 69.61 | 7.74 | 108.29 | <0.0001 |
| 2001 | 8 | 49.54 | 6.19 | 85.38 | <0.0001 |
| 2002 | 8 | 20.27 | 2.53 | 33.02 | <0.0001 |
| 2003 | 7 | 22.53 | 3.22 | 56.11 | <0.0001 |
| 2000–2003 | 9 | 16.39 | 1.82 | 25.18 | <0.0001 |

**Table 5** Kendall rank correlation between relative abundance and parasitism rate of host drosophilid species in each year

| Year | Coefficient | n | P |
|---|---|---|---|
| 2000 | 0.489 | 10 | 0.049 |
| 2001 | 0.500 | 9 | 0.060 |
| 2002 | 0.278 | 9 | 0.297 |
| 2003 | 0.464 | 8 | 0.107 |

patterns of fungal use (Kimura 1976; Kimura & Toda 1989; Toda & Kimura 1997).

Because the rate of parasitism was highest in the most dominant species, the disproportionate parasitism hypothesis (Gillis & Hardy 1997) seems likely to apply in the Hokkaido community. This is especially true considering that the most abundant host species are most heavily parasitized, despite alternation of the most dominant species between 2000 and 2001, and considerable yearly variation in the composition of the drosophilid community. Disproportionate parasitism could not promote species coexistence if the highest rate of parasitism was bound to a particular host species, irrespective of the host's abundance. However, the tests were based on annual totals, ignoring spatio-temporal variation in the relative abundance of host species and parasitism rate. It is impossible to state whether parasitoids disproportionately heavily attack dominant host species in each season, on each fungus species and at each fungus patch. Such fine-scale tests are necessary to understand the host-selection mechanisms for the disproportionate parasitism. In the present study, however, I was interested in the consequences rather than the mechanisms of the disproportionate parasitism. A scale of 1 or several years seems to be reasonable for evaluating the impacts of parasitoids on species coexistence in the host community.

Mycophagous insects are often found in densities high enough that resource competition is likely to occur (Grimaldi & Jaenike 1984; Hanski 1989; Worthen 1989). The depressant effect of parasitoids on the dominant host populations may contribute to species coexistence by relaxing interspecific competition for the rare species. However, this was not due to a behavioral-level response, that is, a switching of host species selection by the same parasitoid species. Instead it was clearly a community-level response, where parasitoids alternated in response to changes in the population density of the

host species. In Hokkaido, disproportionate parasitism was achieved by the alternation of corresponding parasitoid species coupled with the alternation of dominant drosophilid species.

Parasitism may promote prey coexistence through, for example, spatial- and temporal-refuge effects for hosts, parasitoid behaviors (host switching and aggregative response) and higher-order predation (predation on parasitoids) (Holt 1984; Holt & Lawton 1993). I have suggested a mechanism whereby dominant parasitoid species alternation in response to changes in dominant host species promotes species coexistence in host communities. This implies that the species richness in a parasitoid community functions to maintain the diversity of their host species. Parasitoid species richness is, in fact, linked to the suppression of overall host population density, although details of the mechanisms by which this occurs are still unknown (Hawkins 1993; Cornell & Hawkins 1993; Kato 1994). The positive effect of parasitoid species richness on the diversity of host species, however, has not been explored adequately.

In the present study I found that disproportionate parasitism operated in the studied mycophagous drosophilid community. Its effect on species coexistence in the host community, if present, should be carefully evaluated, because the effect of disproportionate parasitism on host competition has a delay of one generation; that is, parasitoids do not kill their host larvae immediately. In the present case, where the parasitoids have univoltine life-cycles, this delayed effect acts on the host populations 1 year later, in two ways. When a parasitoid species attacks two host species, parasitoids having emerged from one host species attack not only the same host species but also the other species. The effect on the originally parasitized host species sets up a self feedback loop, through which the disproportionate parasitism will facilitate species coexistence in the host community. However, the process by which the other species is also parasitized has been termed "apparent competition" by Holt (1977), and has negative effects on species coexistence in the host community. The relative importance

of these antagonistic effects will be evaluated elsewhere by using quantitative parasitoid-overlap analyses (see Müller *et al.* 1999; Rott & Godfray 2000; Lewis *et al.* 2002), using the same census data as used the present study. In addition, the period with high parasitism rates was restricted to 4 or 5 weeks in summer, whereas the mycophagous drosophilid species are multivoltine in Hokkaido (Kimura *et al.* 1978; Kimura 1980; Watabe *et al.* 1985; Toda *et al.* 1986; Kimura & Toda 1989), breeding from early June to late September at the study site. Therefore, they are free from parasitism, and disproportionate parasitism cannot function, in spring and autumn. If no other mechanisms for promoting species coexistence operate in those seasons, species diversity will decrease in the host community. Over the years, various hypotheses have been proposed to understand the mechanisms for species coexistence and community diversity. There are a number of studies emphasizing the importance of intraspecific aggregation (e.g. Toda *et al.* 1999; Wertheim *et al.* 2000; Takahashi *et al.* 2005), resource partitioning (e.g. Toda *et al.* 1999; Takahashi *et al.* 2005) and temporal differentiation in resource use (Shorrocks & Bingley 1994) as species-coexistence mechanisms in some communities depending on fragmented resources such as fungi. Thus, species diversity in a mycophagous drosophilid community is maintained by multiple factors, which vary spatio-temporally at different scales. The present study suggested an additional role of disproportionate parasitism for species coexistence in the mycophagous drosophilid community.

## ACKNOWLEDGMENTS

## REFERENCES

van Alphen JJM, Drijver RAB (1982) Host selection by *Asobara tabida* Nees (Braconidae; Alysiinae), a larval parasitoid of fruit inhabiting *Drosophila* species. I. Host stage selection with *Drosophila melanogaster* as host species. *Netherlands Journal of Zoology* 32, 194–214.

Beppu K, Kaneko A, Toda MJ, Kimura MT (1977) [Methods in the studies of wild drosophilid flies in Hokkaido. 2. Key to species of Drosophilodae in Hokkaido with a supplementary note on phylogeny]. *Seibutsu Kyouzai* 12, 6–30. (In Japanese.)

Bills GF, Holtzman GI, Miller OK Jr (1986) Comparison of ectomycorrhizal–basidimycete communities in red spruce versus northern hardwood forest of West Virginia. *Canadian Journal of Botany* 64, 760–768.

Boulétreau M, Fouillet P, Allemand R (1991) Parasitoids affect competitive interactions between the sibling species, *Drosophila melanogaster* and *D. simulans*. *Redia* 74, 171–177.

Carton Y, Boulétreau M, van Alphen JJM *et al.* (1986) The *Drosophila* parasitic wasps. In: Ashburner M, Carson HL, Thompson JN (eds) *The Genetics and Biology of Drosophila*, Vol. 3E, pp. 347–394. Academic Press, London.

Cornell HV, Hawkins BA (1993) Accumulation of native parasitoid species on introduced herbivores: a comparison of hosts as natives and hosts as invaders. *American Naturalist* 141, 847–865.

Davis AJ, Varley M, Baker RHA, Hardy ICW (1996) Parasitoids of *Drosophila* in the British Isles. *Entomologist* 115, 1–13.

Dobson A, Crawley M (1994) Pathogens and the structure of plant communities. *Trends in Ecology and Evolution* 9, 393–398.

Driessen G, Hemerik L, van Alphen JJM (1990) *Drosophila* species, breeding in the stinkhorn (*Phallus impudicus* pers.) and their larval parasitoids. *Netherlands Journal of Zoology* 40, 409–427.

Fleury F, Ris N, Allemand R, Fouillet P, Carton Y, Boulétreau M (2004) Ecological and genetic interactions in *Drosophila*-parasitoids communities: a case study with *D. melanogaster*, *D. simulans* and their common *Leptopilina* parasitoids in south-eastern France. *Genetica* 120, 181–194.

Freeland W (1983) Parasites and the coexistence of animal host species. *American Naturalist* 121, 223–236.

Gillis JEM, Hardy ICW (1997) Nematode parasitism in a northern European drosophilid community. *Entomologia Experimentalis et Applicata* 84, 275–291.

Grimaldi D, Jaenike J (1984) Competition in natural populations of mycophagous *Drosophila*. *Ecology* 65, 1113–1120.

Hanski I (1989) Fungivory: fungi, insects and ecology. In: Wilding N, Collins NM, Hammond PM, Webber JF (eds) *Insect–Fungus Interactions*, pp. 25–68. Academic Press, London.

Hardy ICW, Gillis JEM (1998) Nematode parasitism in a Danish drosophilid community: further evaluation of the disproportionate parasitism hypothesis. *Entomologia Experimentalis et Applicata* 88, 67–71.

Hawkins BA (1993) Parasitoid species richness, host mortality, and biological control. *American Naturalist* **141,** 634–641.

Holt RD (1977) Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* **12,** 197–229.

Holt RD (1984) Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist* **124,** 377–406.

Holt RD, Lawton JH (1993) Apparent competition and enemy-free space in insect host-parasitoid communities. *American Naturalist* **142,** 623–645.

Holt RD, Lawton JH (1994) The ecological consequences of shared natural enemies. *Annual Reviews of Ecology and Systematics* **25,** 495–520.

Imazeki R, Hongo T (1987) *Colored Illustrations of Mushrooms of Japan*, Vol. I. Hoikusya, Osaka.

Imazeki R, Hongo T (1989) *Colored Illustrations of Mushrooms of Japan*, Vol. II. Hoikusya, Osaka.

Janssen A, Driessen G, de Haan M, Roodbol N (1988) The impact of parasitoids on natural populations of temperate woodland *Drosophila*. *Netherlands Journal of Zoology* **38,** 61–73.

Kato M (1994) Structure, organization, and response of a species-rich parasitoid community to host leafminer population dynamics. *Oecologia* **97,** 17–25.

Kimura MT (1976) *Drosophila* survey in Hokkaido, XXXII. A field survey of fungus preference of drosophilid flies in Sapporo. *Journal of Faculty of Science, Hokkaido University, VI Zoology* **20,** 288–298.

Kimura MT (1980) Bionomics of Drosophilidae (Diptera) in Hokkaido. IV. *Drosophila sexvittata, D. trivittata*, and *D. alboralis*. *Zoological Magazine* **89,** 206–209.

Kimura MT, Toda MJ (1989) Food preferences and nematode parasitism in mycophagous *Drosophila*. *Ecological Research* **4,** 209–218.

Kimura MT, Beppu K, Ichijô N, Toda MJ (1978) Bionomics of Drosophilidae (Diptera) in Hokkaido. II. *Drosophila testacea*. *Kontyû* **46,** 585–595.

Lacy RC (1984) Predictability, toxicity, and trophic niche breadth in fungus-feeding Drosophilidae (Diptera). *Ecological Entomology* **9,** 43–54.

Lewis OT, Memmott J, LaSalle J, Lyal CHC, Whitefoord C, Godfray HCJ (2002) Structure of a diverse tropical forest insect-parasitoid community. *Journal of Animal Ecology* **71,** 855–873.

Marcogliese DJ, Cone DK (1997) Food webs: a plea for parasites. *Trends in Ecology and Evolution* **12,** 320–325.

Müller CB, Adriaanse ICT, Belshaw R, Godfray HCJ (1999) The structure of an aphid-parasitoid community. *Journal of Animal Ecology* **68,** 346–370.

Ohenoja E, Koistinen R (1984) Fruiting body production of larger fungi in Finland. 2. Edible fungi in northern Finland 1976–78. *Annales Botanici Fennici* **21,** 357–366.

Okada T (1968) *Systematic Study of the Early Stages of Drosophilidae*. Bunka Zugeisya, Tokyo.

Paine RT (1966) Food web complexity and species diversity. *American Naturalist* **100,** 65–75.

Rott AS, Godfray HCJ (2000) The structure or a leafminer-parasitoid community. *Journal of Animal Ecology* **69,** 274–289.

Shorrocks B, Bingley M (1994) Priority effects and species coexistence: experiments with fungal-breeding *Drosophila*. *Journal of Animal Ecology* **63,** 799–806.

Shorrocks B, Charlesworth P (1980) The distribution and abundance of the British fungal-breeding *Drosophila*. *Journal of Animal Ecology* **63,** 799–806.

Sih A, Crowley P, McPeek M, Petranka J, Strohmeier K (1985) Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* **16,** 269–311.

Takahashi KH, Tuno N, Kagaya T (2005) The relative importance of spatial aggregation and resource partitioning on the coexistence of mycophagous insects. *Oikos* **109,** 125–134.

Toda MJ, Kimura MT (1997) Life-history traits related to host selection in mycophagous *Drosophila*. *Journal of Animal Ecology* **66,** 154–166.

Toda MJ, Kimura MT, Takeda E, Beppu K, Iwao Y (1986) Bionomics of Drosophilidae (Diptera) in Hokkaido. VIII. *Drosophila confusa and D. bifasciata*, with special reference to local variation in annual life cycle. *Kontyû* **54,** 33–40.

Toda MJ, Kimura MT, Tuno N (1999) Coexistence mechanisms of mycophagous drosophilids on multispecies fungal hosts: aggregation and resource partitioning. *Journal of Animal Ecology* **68,** 794–803.

Watabe H, Kimura MT, Toda MJ, Iwao Y (1985) Bionomics of Drosophilidae (Diptera) in Hokkaido. VII. *Drosophila nigromaculata and D. brachynephros*. *Kontyû* **53,** 34–41.

Wertheim B, Sevenster JG, Eijs IEM, van Alphen JJM (2000) Species diversity in a mycophagous insect community: the case of spatial aggregation *vs* resource partitioning. *Journal of Animal Ecology* **69,** 335–351.

Worthen WB (1989) Predator-mediated coexistence in laboratory communities of mycophagous *Drosophila* (Diptera: Drosophilidae). *Ecological Entomology* **14,** 117–126.