Journal of Natural History
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tnah20

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Published online: 03 Dec 2010.

To cite this article: Hideyuki Mitsui, Kees Van Achterberg, Göran Nordlander & Masahito T. Kimura (2007) Geographical distributions and host associations of larval parasitoids of frugivorous Drosophilidae in Japan, Journal of Natural History, 41:25-28, 1731-1738, DOI: 10.1080/00222930701504797

To link to this article: http://dx.doi.org/10.1080/00222930701504797

Journal of Natural History, 2007; 41(25–28): 1731–1738

Geographical distributions and host associations of larval parasitoids of frugivorous Drosophilidae in Japan

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(*Accepted 8 June 2007)*

Abstract
In Japan, dominant parasitoids attacking frugivorous Drosophilidae species were *Asobara* (Braconidae, Alysiinae), *Leptopilina*, and *Ganaspis* species (Figitidae, Eucoilinae). *Asobara japonica* was found throughout Japan, and its populations in the main islands of Japan were parthenogenetic whereas those in the subtropical islands were sexually reproducing. Other parasitoids showed rather restricted distributions; *A. tabida*, *A. rossica*, *A. rufescens*, and *Leptopilina heterotoma* occurred mainly in northern to central parts of the main islands, *Ganaspis xanthopoda* from central to southern parts of the main islands, *A. leveri* in a southern part of the main islands, and *A. pleuralis*, *L. victoriae*, and *Ganaspis* sp. mainly in the subtropical islands. Their major hosts were species of the *D. melanogaster* species group in the main islands, and species of the *D. melanogaster*, *immigrans*, and *polychaeta* species groups in the subtropical islands. Host use considerably varied among parasitoid species, especially in the subtropical islands.

Keywords: *Braconidae, Drosophilidae, Figitidae, geographic distribution, host association, parasitism*

Introduction

The range of geographic distribution and resource use are basic information in the study of ecology, environmental adaptations, and evolution of species. In Drosophilidae, intensive studies have so far been performed on their geographic distributions and resource use (reviewed in Ashburner et al. 1981, 1982, 1983). In contrast, only fragmentary information is available on their parasitoids except for some European species, e.g. *Asobara tabida*, *Leptopilina heterotoma*, and *L. boulardi* (Carton et al. 1986), and for some African *Leptopilina* species (Allemand et al. 2002). In this paper, we report geographic distributions and host associations of parasitoids attacking frugivorous Drosophilidae in Japan. From Japan, seven parasitoid species, *Asobara japonica*, *A. tabida*, *A. rossica*, *Aphaereta* sp., *Phaenocarpa* sp., *Ganaspis xanthopoda*, and *Ganaspis* sp. have so far been recorded, and all of them are

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ISSN 0022-2933 print/ISSN 1464-5262 online
DOI: 10.1080/00222930701504797

reported to parasitize Drosophilidae larvae breeding in mushrooms (Yorozuya 2006; Ideo et al. 2008). However, major hosts of *A. japonica*, *A. tabida*, and *G. xanthopoda* are known to be Drosophilidae larvae breeding on fermenting fruits (Vet and Bakker 1985; Janssen et al. 1988; Ideo et al. 2008). Thus, parasitoids attacking Drosophilidae larvae often differ in habitats; some search larvae on mushrooms, some on fruits, and some on decayed leaves, although their habitat selection is not always rigid (Janssen et al. 1988; Ideo et al. 2008).

Methods

Collections were carried out in Sapporo (43.1°N, 141.3°E), Sendai (38.2°N, 140.9°E), Tokyo (35.6°N, 139.4°E), Kagoshima (31.5°N, 130.5°E), Amami-oshima (28.4°N, 129.5°E), Okinawa (26.2°N, 127.7°E), and Iriomote-jima (24.3°N, 123.8°E) (Figure 1). Sapporo and Sendai are located in a cool-temperate region, Tokyo and Kagoshima are in a warm-temperate region, and Amami-oshima, Okinawa and Iriomote-jima are in a subtropical region.

In Sapporo, collections were carried out in domestic areas (about 50 m above sea level) and forests at low (100 m) and high (600 m) altitudes 10 times from June to September in 2004–2006. In Tokyo, collections were carried out in domestic areas and lightly wooded areas at low altitudes (100–200 m) 29 times from early spring to late autumn in 2002–2005. At the remaining localities, collections were carried out in domestic, lightly wooded areas and/or forests at low altitudes (50–200 m) two or three times; i.e. in June (2004) and September (2003 and 2004) in Sendai, in May (2004) and July (2006) in Kagoshima, in

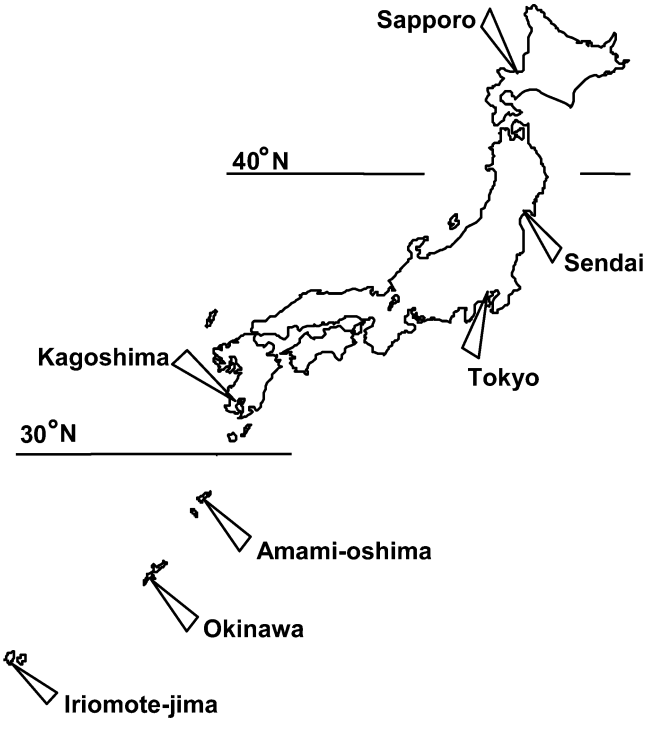

Figure 1. Collection localities.

July (2006) and November (2005) in Amami-oshima, in June and November (2005) in Okinawa, and in March (2006), July (2003), and December (2003) in Iriomote-jima.

Clumps of banana were placed in the collection sites, left for about a week, brought back to the laboratory, and placed in plastic containers with pieces of cloth or paper. Usually 30 g clumps of banana were used, and in most instances more than 10 such clumps were used in each collection. When smaller clumps (1, 2, 3 or 10 g) were used, the number of clumps was raised. When drosophilid larvae pupated on cloth or paper, they were collected, identified to species, placed on Petri dishes with wet filter paper, and examined for the emergence of flies or wasps. However, sibling species could not be discriminated by pupal morphology; i.e. *D. melanogaster* and *D. simulans*, a pair of *D. lutescens* and *D. takahashii*, and four species of the *auraria* species complex (*D. auraria*, *D. biauraria*, *D. triauraria*, and *D. subauraria*). In Tokyo, Kagoshima, and Iriomote-jima, some natural fruits were found. These fruits were collected to the laboratory, and drosophilid larvae in them were examined for parasitism as described above.

Results

Geographical distribution

Asobara japonica was the most abundant parasitoid found in all localities (Table I). In this species the sex ratio was biased towards females at the following localities: Sapporo (96.5%, $N=58$), Sendai (99.2%, $N=387$), Tokyo (95.4%, $N=503$), and Kagoshima (92.7%, $N=233$), but less biased in Amami-oshima (62.5%, $N=16$), Okinawa (38.7%, $N=31$), and Iriomote-jima (76.0%, $N=200$) (not all wasps emerged were sexed). The occurrence of other *Asobara* species was restricted to some districts (Table I); *A. tabida*, *A. rossica*, and *A.*

Table I. Number of parasitoids emerged from drosophilid pupae collected in Sapporo (SP), Sendai (SD), Tokyo (TK), Kagoshima (KG), Amami-oshima (AM), Okinawa (OK), and Iriomote-jima (IR).

	SP	SD	TK	KG	AM	OK	IR
Braconidae							
Asobara japonica Belokobylskij	312	1450	3081	343	92	60	281
A. rufescens Foerster	8	*					
A. rossica Belokobylskij	38	41	10				
A. tabida Nees von Esenbeck	4						
A. leveri Nixon				80			
A. pleuralis Ashmead							38
Figitidae							
Ganaspis xanthopoda (Ashmead)		657	513	25			
G. sp. 1							171
G. sp. 2			10				
Leptopilina heterotoma (Thompson)	117	4			*		
L. victoriae Nordlander				1	31	3	299
L. sp.			4				
Leptolamina sp.		7	*				
Diapriidae							
Trichopria sp.		41	68	15	8	14	20
Pteromalidae							
Pachycrepoideus vindemmiae Rondani	15		8				

*Adult wasps were collected in the fields or emerged from unidentified insects (probably drosophilids).

rufescens occurred in northern Japan, *A. leveri* in Kagoshima, and *A. pleuralis* in Iriomote-jima.

In the family Figitidae, *Leptopilina heterotoma* occurred in northern to central parts of the main islands (Sapporo, Sendai, and Tokyo), and an adult female of this species was collected in Amami-oshima. *Ganaspis xanthopoda* occurred in central to southern parts of the main islands (Sendai, Tokyo, and Kagoshima), and *Leptopilina victoriae* in Kagoshima and the subtropical islands (Amami-oshima, Okinawa, and Iriomote-jima). Two undetermined *Ganaspis* species were found; 171 individuals of sp. 1 from Iriomote-jima and 10 individuals of sp. 2 from Tokyo. In addition, an undetermined *Leptopilina* species was collected in Tokyo; an individual emerged from drosophilids and three individuals emerged from unidentified insects (probably drosophilids). Furthermore, seven individuals of undetermined *Leptolamina* species emerged from drosophilids collected in Sendai, and 57 individuals of this species emerged from unidentified insects (probably drosophilids) in Tokyo.

Trichopria specimens (Diapriidae) were widely found in Japan, and *Pachycrepoideus vindemmiae* (Pteromalidae) was found in Sapporo and Tokyo. It is uncertain whether the specimens of *Trichopria* from different localities are conspecific or not.

Host association

Tables II and III show host associations of parasitoid species in the main islands (Sapporo, Sendai, Tokyo, and Kagoshima) and the subtropical islands of Japan (Amami-oshima, Okinawa, and Iriomote-jima), respectively. In the main islands, drosophilids reared in large

Table II. Numbers of drosophilid pupae collected and numbers of parasitoid individuals emerged from these pupae in the survey in the main islands of Japan (Sapporo, Sendai, Tokyo, and Kagoshima). The rate of parasitism is also presented.

	Dsm	*Dlt*	*au*	*Drf*	*Dsz*	*Dbf*	*Dim*	*Dbz*	*Dst*	*Dts*	*Dbs*	*Ssb*	*Scr*
No. of drosophilid pupae collected	8225	29411	4147	309	1152	96	8589	251	99	128	20	172	215
Parasitism (%)	10.6	18.3	10.0	12.6	4.2	2.1	0.2	7.2	10.1	0.8	30.0	24.4	7.9
A. japonica	711	4081	281	36	2	2	2	18	10	1	2	37	3
A. rufescens	8												
A. rossica	15	15	61										
A. tabida	1		2		1						4		
A. leveri		79		1									
G. xanthopoda	5	1106	30	2	45							3	4
G. sp. 2													10
L. heterotoma	95	2	23				1						
L. victoriae		1											
L. sp.												4	
Leptolamina sp.		2					5						
Trichopria sp.	23	82	16				2					1	
P. vindemmiae	12	4	1				6						

Dsm, *Drosophila simulans* Sturtevant (*D. melanogaster* Meigen included); *Dlt*, *D. lutescens* Okada (*D. takahashii* Sturtevant included); *au*, the *D. auraria* species complex (*D. auraria* Peng, *D. biauraria* Bock and Wheeler, *D. triauraria* Bock and Wheeler, *D. subauraria* Kimura); *Drf*, *D. rufa* Kikkawa and Peng; *Dsz*, *D. suzukii* (Matsumura); *Dbf*, *D. bifasciata* Pomini; *Dim*, *D. immigrans* Sturtevant; *Dbz*, *D. bizonata* Kikkawa and Peng; *Dst*, *D. sternopleuralis* Okada and Kurokawa; *Dbs*, *D. busckii* Coquilett; *Dts*, *D. tsigana* Burla and Gloor; *Ssb*, *Scaptodrosophila subtilis* (Kikkawa and Peng); *Scr*, *S. coracina* (Kikkawa and Peng).

Table III. Numbers of drosophilid pupae collected and numbers of parasitoid individuals emerged from these pupae in the survey in the subtropical islands of Japan (Amami-oshima, Okinawa, Iriomote-jima). The rate of parasitism is also given.

	Dml	*Dtk*	*Dfc*	*Dlc*	*Dbp*	*Dal*	*Ddr*	Others
No. of drosophilid pupae collected	1275	3473	234	229	1399	2512	606	88
Parasitism (%)	0.5	12.8	3.8	2.6	10.9	9.1	27.7	
A. japonica	7	426						
A. pleuralis			2	3	1	32		
G. sp. 1						3	168	
L. victoriae			7	3	151	172		
Trichopria sp.		20				22		

Dml, *D. melanogaster*; *Dtk*, *D. takahashii* (*D. lutescens* included); *Dfc*, *D. ficusphila* Kikkawa and Peng; *Dlc*, *D. lacteicornis* Okada (*D. asahinai* Okada included); *Dbp*, *D. bipectinata* Duda; *Dal*, *D. albomicans* Duda; *Ddr*, *D. daruma* Okada.

numbers from banana were members of the *D. melanogaster* species group (*D. melanogaster*, *D. simulans*, *D. lutescens*, *D. takahashii*, *D. suzukii*, *D. rufa*, *D. auraria*, *D. biauraria*, *D. triauraria*) and *D. immigrans*. Among them, species of the *D. melanogaster* species group were used as major hosts by various parasitoids, but *D. immigrans* was rarely parasitized (Table II). Several species of the subgenera *Drosophila* (*D. bizonata*, *D. sternopleuralis*, and *D. tsigana*) and *Dorsilopha* (*D. busckii*) and the genus *Scaptodrosophila* (*S. subtilis* and *S. coracina*) were sometimes present in banana in the main islands, and they were often parasitized. In the subtropical islands, drosophilids reared in large numbers from banana were members of the *D. melanogaster* (*D. takahashii*, *D. lacteicornis*, *D. ficusphila*, and *D. bipectinata*), *immigrans* (*D. albomicans*), and *polychaeta* (*D. daruma*) species groups, and the rate of parasitism was often high (Table III). Host use varied considerably among parasitoid species, especially in the subtropical islands; *A. japonica* parasitized *D. melanogaster* and *D. takahashii*; *A. pleuralis* and *L. victoriae* attacked *D. ficusphila*, *D. lacteicornis*, *D. bipectinata* and *D. albomicans*, and *Ganaspis* sp. 1 parasitized *D. albomicans* and *D. daruma*.

Discussion

Asobara japonica was the most abundant species in the samples and was widely distributed in Japan. In this species, the sex ratio was much biased towards females in the specimens from the main islands of Japan but not in those from the subtropical islands. By our laboratory rearing, it was confirmed that individuals from Sapporo, Tokyo, and Kagoshima reproduce parthenogenetically, whereas those from Amami-oshima and Iriomote-jima reproduce sexually. The other *Asobara* species were limited to restricted districts; *A. tabida*, *A. rufescens*, and *A. rossica* were found in northern and central parts of the main islands, *A. leveri* in Kagoshima, and *A. pleuralis* in Iriomote-jima. The occurrence of *A. tabida* adults was also confirmed in Shiga-kogen (about 1500 m above sea level) located in central Japan (unpublished observation). *Asobara tabida* and *A. rufescens* have been previously recorded from Europe, *A. rossica* from Far East Russia, *A. leveri* from Fiji, and *A. pleuralis* from the Philippines (Carton et al. 1986; Belokobylskij 1998). Thus, the first three species are adapted to cool-temperate climates, and the last two are adapted to warm-temperate or subtropical climates.

In the Figitidae, *Leptopilina heterotoma* and *Ganaspis xanthopoda* were mainly collected in the main islands of Japan (the former in northern to central parts and the latter in central to southern parts), and an individual of the former was collected in a subtropical island, Amami-oshima. These two species are also recorded from wide areas; the former from Southeast Asia, Europe, Africa, and North America, and the latter from these regions except for Europe (Nordlander 1980; Carton et al. 1986; Schilthuizen et al. 1998; Allemand et al. 2002; Fleury et al. 2004). In contrast to the above two species, *L. victoriae* and *Ganaspis* sp. 1 occurred mainly in the subtropical islands in Japan. *L. victoriae* is also recorded from the Seychelles, Thailand, and Africa (Nordlander 1980; Schilthuizen et al. 1998; Allemand et al. 2002), suggesting that it is adapted to subtropical and tropical climates.

Among the present parasitoid species, *A. rufescens* mainly parasitizes drosophilid larvae growing on decayed plant materials in Europe (Vet et al. 1984). In our unpublished study, this species was also observed to parasitize larvae of *Scaptomyza pallida* (Zetterstedt) breeding on decayed leaves. The remaining parasitoid species are assumed to use frugivorous drosophilids as major hosts, although *A. japonica* sometimes attacks drosophilid larvae feeding on mushrooms (Ideo et al. 2008).

Species of the *D. melanogaster* species group and *D. immigrans* have been reported from the main islands of Japan as dominant drosophilids breeding on fruits (Kimura et al. 1977; Nishiharu 1980; Mitsui and Kimura 2000a, 2000b; Mitsui et al. 2006). Among them, species of the *D. melanogaster* species group were frequently parasitized. In contrast, *D. immigrans* larvae were rarely parasitized. It has also been confirmed in laboratory experiments that *D. immigrans* larvae are not or seldom parasitized, at least by *L. heterotoma*, *A. tabida*, or *A. japonica* (van Lenteren and Bakker 1978; van Alphen and Janssen 1982; Ideo et al. 2008). Van Alphen and Janssen (1982) suggested that the thick cuticle of *D. immigrans* larvae prevents insertion of the ovipositor of *A. tabida*. In Europe, *D. subobscura* Collin of the *D. obscura* species group is reported as a major native host of *A. tabida* and *L. heterotoma* (Carton et al. 1986; Janssen et al. 1988; Kraaijeveld and van der Wel 1994; Kraaijeveld et al. 1995). In this study, *D. bifasciata* of the *D. obscura* species group was parasitized by *A. japonica*. In addition, this species was observed to be parasitized in our preliminary study in Shiga-kogen (central Japan). Although these parasitoids could not be raised to adults, they presumably were *A. tabida* since this was the only one of the species that was found at the collection sites. On the other hand, *A. leveri* has been reported to parasitize Tephritidae species (Belokobylskij 1998). In the subtropical islands of Japan, *D. albomicans*, *D. daruma*, and several species of the *melanogaster* species group were observed to breed on banana (also see Hirai et al. 2000), and they were often parasitized.

Host use differed considerably among parasitoid species, especially in the subtropical islands. Such a pattern arises if the parasitoid species occur in different environments, if they attack different hosts in the same environment, or if the host species differ in resistance to different parasitoids.

Among parasitoids found in this study, *Trichopria* sp. and *P. vindemmiae* are known as pupal parasitoids (Carton et al. 1986; personal observation). In the present study, however, these species emerged from drosophilid individuals that remained as larvae when collected in fields. In our laboratory rearing, at least one *Trichopria* species was confirmed to parasitize full-grown scrolling larvae of *D. simulans*, although at a low rate. Thus, these parasitoids are able to parasitize late instar larvae, although they predominantly attack the pupal stage. They are widely distributed in Japan and seemed to use a variety of Drosophilidae species as hosts.

Acknowledgements

We are grateful to Dr K. Kamijo for identification of *Pachycrepoideus* species, and A. Oikawa and M. Kondo for their help with the field studies. This work was supported by a Grant-in-Aid from the Ministry of Education, Science, Sports and Culture of Japan (No. 17570010).

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