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Reproductive strategy of a woodwasp with no fungal symbionts, *Xeris spectrum* (Hymenoptera: Siricidae)

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Abstract Experiments were conducted to elucidate the reproductive strategy of the siricid woodwasp, *Xeris spectrum*, which carries no substantial symbiotic fungi in its body, in a comparison with the life cycles of two fungus-carrying siricid woodwasp species, *Sirex nitobei* and *Urocerus japonicus*, by considering ecological traits such as seasonal patterns of occurrence, spatial distribution of emergence on a tree, and oviposition activities. Part of the *X. spectrum* populations emerged in spring, during May and June, while others emerged in summer, during August and September, simultaneously with other siricid fungus-carrying woodwasps. The vertical distribution pattern of *X. spectrum* emergence holes on the trunk closely coincided with the emergence hole pattern of *S. nitobei*. *X. spectrum* laid few eggs on fresh logs, old logs, or on logs inoculated with potato dextrose agar, whereas on logs inoculated with *Amylostereum chailletii* or *A. areolatum*, *X. spectrum* females oviposited no less than 30%, on average, of their potential eggs. Moreover, the oviposition sites on these logs were concentrated near the *Amylostereum* inoculation positions. These results indicate that *X. spectrum* has evolved a life history that utilizes fungal symbionts of other woodwasp species without itself possessing any symbiotic fungus. Moreover, *X. spectrum* has evolved a dual reproductive system in that (1) some adults emerge in summer during the same emergence period as the fungus-carrying woodwasps and thereby oviposit on host trees already inoculated with fungi, and (2) other adults emerge the next spring and oviposit on trees that were inoculated with fungi a year earlier.

Key words *Xeris spectrum* · *Amylostereum* fungi · Fungal symbiont · Oviposition behavior · Seasonal emergence

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Introduction

For insects, wood is a food resource of particularly low nutritional quality compared to other plant parts such as leaves, flower, seeds, or phloem sap (Haack and Slansky 1987). Carbohydrates, which form the major energy source for herbivorous insects, are abundant in green plant tissues but mostly occur as complex polysaccharides in woody tissues. Most insects are incapable of decomposing polysaccharides such as cellulose because they lack the necessary cellulolytic enzymes. Therefore, most wood-feeding insects utilize woody tissues as a food resource with the aid of microbial symbionts that can digest cellulose (Haack and Slansky 1987). Populations of hindgut protozoa are responsible for cellulose digestion in the lower termites (e.g., Breznak 1982) and in the wood roach (Bignell 1977; Cruden and Markovetz 1979), as well as in the rhinoceros beetle (Bayon and Mathelin 1980). Moreover, Martin and Martin (1978, 1979) and Martin (1979, 1984) suggest another mechanism by which insects achieve the digestion of refractory compounds, namely through ingestion of fungal enzymes that actively degrade plant cell wall polysaccharides. These insects, along with their acquired enzymes, become a digestive symbiotic system.

Woodwasps (Siricidae) are a group of hymenopterans with a specific feeding habit in that their larvae exclusively feed on the sapwood and heartwood of various coniferous and broad-leaved trees. Most species of woodwasp carry arthrospores of one of the specific basidiomycete fungi in the genus *Amylostereum*. These fungi serve as symbionts and are carried in a pair of small intersegmental sacs called "mycangia" (Francke-Grosmann 1939). Soon after a short dispersal flight following emergence, adult females make several oviposition holes through the bark deep into the sapwood of new host trees and then deposit fungal arthrospores together with their eggs in the holes (Coutts and Dolezal 1969; Madden 1988; Morgan 1968). The fungi are presumed to alter the host tree tissues into readily assimilable forms

(Madden 1988; Morgan 1968; Stillwell 1966) or to produce enzymes that decompose the cellulose or lignin in the wood (Kukor and Martin 1983; Martin 1984). Thus, woodwasps are one of the typical groups of insects in which digestion is aided by symbiosis.

However, it is known that female adults of *Xeris spectrum* L. carry no symbiotic fungi in their bodies (Morgan 1968). Therefore, clarifying the reproductive strategy of this species will allow us to reveal what role fungal symbionts may play in the development of siricid woodwasps. The present study aims to elucidate the reproductive strategy of *X. spectrum* through a comparison with those of two other fungus-carrying woodwasp species: *Sirex nitobei* Matsumura and *Urocerus japonicus* Smith. We will compare such ecological traits as seasonal occurrence, spatial distribution of emergence holes, and oviposition behavior.

Materials and methods

Biology of the woodwasps

X. spectrum is widely distributed in many parts of the world including Asia, Europe, North America, and Japan (Madden 1988; Morgan 1968; Takeuchi 1962). It usually emerges from dead or recently felled conifers (Kanamitsu 1978; Morgan 1968; Takeuchi 1962). In Japan, about half of the *X. spectrum* population is univoltine, while the other half completes its life cycle in 2 years (Kanamitsu 1978).

S. nitobei is distributed all over Japan except on Hokkaido Island. The life cycle of this species is usually completed in 1 year. It emerges during August and October from dead pine trees and usually oviposits on weakened or stressed *Pinus* and *Abies* (Fukuda and Hijii 1996a; Fukuda et al. 1993; Kanamitsu 1978; I. Togashi, personal communication). *S. nitobei* is symbiotically associated with the basidiomycete fungus, *Amylostereum areolatum* Boidin (Terashita 1970).

U. japonicus is distributed all over Japan (Takeuchi 1962). The life cycle of this species is usually completed in 1 year. It emerges from dead or recently felled trees of Japanese cypress (*Chamaecyparis obtusa* Sieb et Zucc.) and Japanese cedar (*Cryptomeria japonica* D. Don) from July to September (Sano 1992). *U. japonicus* carries the fungal symbiont *A. chailletii* Boidin within its mycangia (Kanamitsu 1978; Sano et al. 1995).

Collection of infested sample trees and emerging adults

Sample trees were taken from the following two mixed stands: (1) the Nagoya University Forest (35°11′ N, 137°10′ E), Inabu Town, situated about 70 km east of Nagoya City and denoted as IN and (2) Owase City (35°5′ N, 136°13′ E), situated about 160 km southwest of Nagoya City, and denoted as OW. On the IN plot, four 1-m-long logs were collected in July 1991 from an *Abies firma* Sieb. et Zucc. tree [19 cm in diameter at breast height (DBH) and 17 m high] that was infested by woodwasps between 10 and 14 m above the ground. Prior to log collection, the tree had been girdled in June 1990. On the OW plot, 12 1-m-long logs were collected in June 1993 from an infested tree of *C. japonica* (16 cm DBH and 17 m high) at a height of 2–14 m. This sample tree had been felled during a thinning operation in August 1992. All logs were transferred to an outdoor cage on the Nagoya University Campus.

From July to October 1991 and from April to October in 1992–1995, emerging woodwasps were collected every day. Species and sex were recorded for each individual. The fresh body weight of each emerged adult was obtained on a microbalance immediately after collection. Two *X. spectrum* populations (abbreviated as IN-91 and IN-92) emerged from the *A. firma* sample tree along with a *S. nitobei* population; two *X. spectrum* populations (OW-93 and OW-94) and a *U. japonicus* population emerged from the *C. japonica* sample tree.

The position of *X. spectrum* and *S. nitobei* emergence holes on the trunk of *A. firma* was also recorded. For 18 females of the *X. spectrum* IN-92 population, the number of mature eggs in their ovaries was counted immediately after the females died. In this study, the body weight of females included the weight of their eggs because most eggs have already matured at the time of emergence.

Oviposition activity of *X. spectrum*

Some of the *X. spectrum* females were used in oviposition experiments (Table 1). Females were allowed to mate with males that emerged on almost the same day and from the same population. After weighing, they were placed in a clear cylindrical box made of polyvinylchloride (30 cm in diameter and 110 cm long) under laboratory conditions (about 25°C), and were allowed to oviposit on five types of 1-m-long logs (7–14 cm in diameter) of *C. japonica*: fresh logs (FL), logs inoculated with *A. chailletii* (ACL), logs inoculated with *A. areolatum* (AAL), logs inoculated with only potato dextrose agar (PDA) culture medium (PDL), and old logs felled about 1 year earlier (OL). These five types of logs were prepared as follows. Twelve uninfested living *C. japonica* trees were felled in the IN plot and 1-m-long logs taken from these trees were stored in an outdoor cage on Nagoya University Campus until the oviposition experiment was initiated. A silicon paste was applied to the ends of each log to prevent desiccation. FL were stored less than 7 days before the oviposition experiment started. The three types of inoculated logs were prepared by inoculating logs within 7 days of felling with (1) PDA plus *A. chailletii* isolated from the intersegmental sacs of adult female *U. japonicus*, (2) PDA plus *A. areolatum* isolated from intersegmental sacs of adult female *S. nitobei*, or (3) PDA only. The procedure for the preparation of the "inoculated logs" was as follows. Patches of hyphae of each fungus species growing on PDA plates for 15 days at 25°C or only PDA were aseptically placed in holes (10 mm in diameter and 5 mm deep) that had been excavated in the fresh logs using a sterilized cork borer. There were 16 inoculation points on each log. The OL were taken from trees that had been felled about 1 year earlier in the IN plot and had been stored in the outdoor cage (the ends of the logs were treated with silicon paste). The numbers of wasps used in this oviposition experiment are summarized in Table 1.

Soon after the female adults finished oviposition and died, the numbers of mature eggs remaining in their ovaries were counted under a stereomicroscope. After this oviposition experiment, the bark was peeled off three of the logs inoculated with *A. chailletii*

Table 1 Number of *Xeris spectrum* females induced to oviposit on five types of logs (*FL* fresh logs stored within 7 days of felling, *ACL* logs inoculated with *Amylostereum chailletii*, *AAL* logs inoculated with *A. areolatum*, *PDL* logs inoculated with the fungal culture medium potato dextrose agar, *OL* old logs stored about 1 year, *IN-92* population of *X. spectrum* that emerged from the sample tree of *Abies firma* in 1992, *OW-93* population of *X. spectrum* that emerged from the sample tree of *Cryptomeria japonica* in 1993, *OW-94* population of *X. spectrum* that emerged from the sample tree of *C. japonica* in 1994)

Log type	Number of logs used	Number of insects used	Population code
FL	21	21	IN-92
ACL	5	18	OW-93
AAL	4	11	OW-94
PDL	3	10	OW-94
OL	8	8	OW-93

and two of the logs inoculated with *A. areolatum* to determine the exact position of all oviposition sites.

Results

Seasonal occurrence of woodwasps

From all the logs of *A. firma* collected in July 1991, adult emergence of *X. spectrum* (IN-91 population) continued for about 1 month from late August to late September, coinciding with the adult emergence period of *S. nitobei* (Fig. 1). In spring 1992, adult emergence of *X. spectrum* (IN-92 population) continued for one-and-a-half months from late April to mid-June (Fig. 1). In 1993, however, no adult woodwasps emerged.

From all logs of *C. japonica* collected in June 1993, adult emergence of *X. spectrum* (OW-93 population) continued for about one-and-a-half months from early August to mid-September, and coincided closely with adult emergence of *U. japonicus*, which continued for about 2 months (Fig. 1). In spring 1994, adult emergence of *X. spectrum* (OW-94 population) continued for 2 months from early May to late June (Fig. 1). In 1995, there was no woodwasp emergence.

These seasonal emergence patterns of *X. spectrum*, *S. nitobei*, and *U. japonicus* showed that *X. spectrum* has two distinct types of populations. One population emerged in late summer, simultaneously with the two fungus-carrying woodwasp species, and a second *X. spectrum* population emerged the following spring, when no fungus-carrying woodwasps were emerging. Moreover, it also suggests that the fungus-carrying woodwasps, *S. nitobei* and *U. japonicus*, can utilize a host tree only for 1 year, whereas *X. spectrum* can utilize a host tree for 2 years (Fig. 1).

Spatial patterns of emergence holes in *X. spectrum* and *S. nitobei*

The *X. spectrum* and *S. nitobei* emergence holes on the *A. firma* tree were distributed over the trunk from 10.8 to 13.4 m above the ground (Fig. 2); the *X. spectrum* emergence holes were concentrated between 11.6 and 12.4 m in height. The vertical distribution pattern of *X. spectrum* emergence holes on the trunk closely coincided with that of the *S. nitobei* emergence holes (Fig. 2).

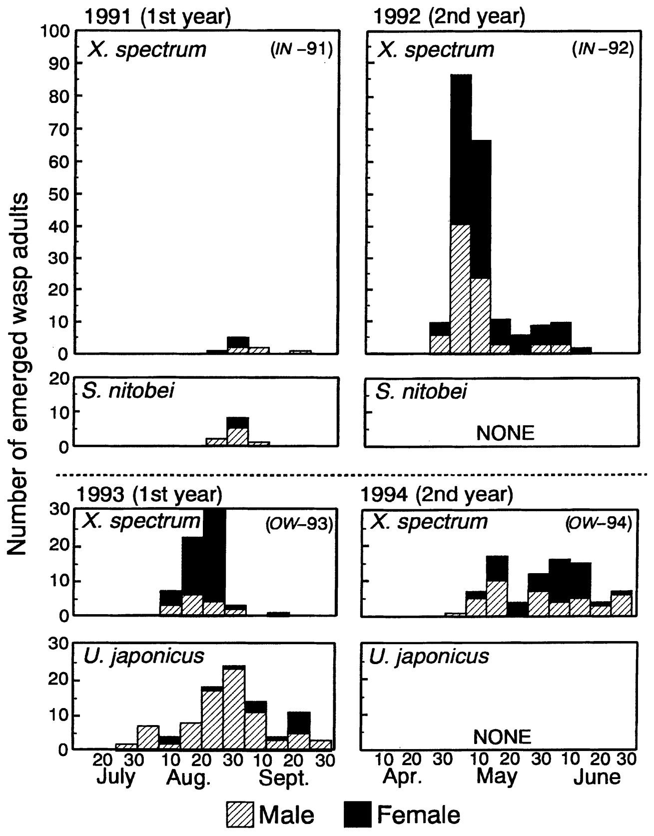


Fig. 1 Seasonal adult emergence of *Xeris spectrum*, *Sirex nitobei*, and *Urocerus japonicus* from the sample trees of *Abies firma* and *Cryptomeria japonica*

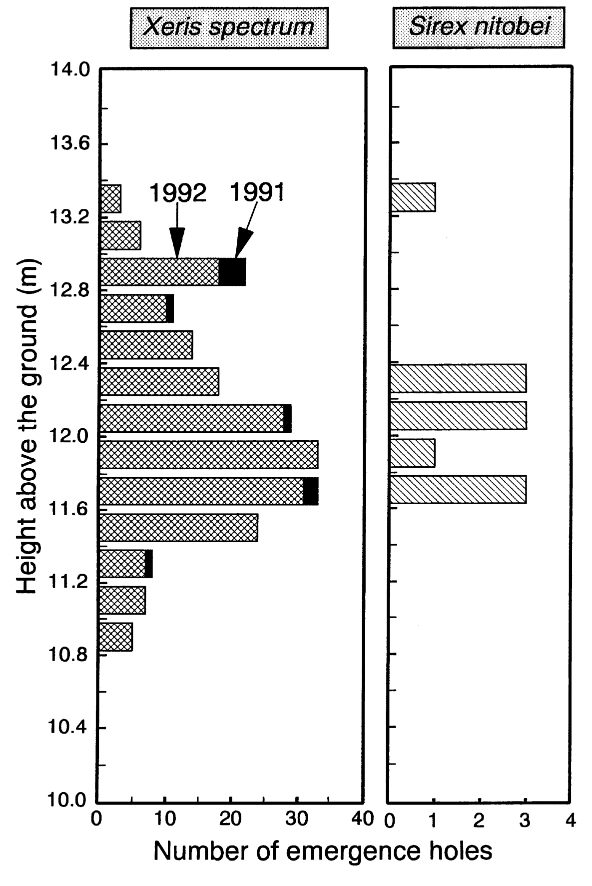


Fig. 2 Vertical emergence hole distribution of *X. spectrum* and *S. nitobei*, on an *A. firma*

Estimation of realized fecundity and oviposition activity of *X. spectrum*

The total number of eggs produced (N_P, potential fecundity) varied from about 30 to 400 eggs per female *X. spectrum*, and was positively correlated with fresh body weight of the parent female (W) (Fig. 3):

$$N_P = 2.07\ W^{1.04}\ (n = 18,\ r^2 = 0.95,\ P < 0.01) \qquad (1)$$

Since it is difficult to determine the exact number of eggs actually laid in the wood, because adult females oviposit through the bark into the sapwood, potential fecundity (N_P) was determined from body weight (W) of a female before oviposition as given in Eq. 1. The number of eggs actually laid by the female (N_L) and the percentage oviposition (P_E) (defined as the proportion of eggs laid with regard to the potential fecundity of a female during her lifetime) were estimated as follows (Fukuda et al. 1993):

$$N_L = N_P - N_R \qquad (2)$$

$$P_E = (N_L/N_P) \times 100\% \qquad (3)$$

where N_R denotes the number of eggs remaining in the female body after oviposition.

Using Eqs. 1–3, the mean proportion of oviposition by *X. spectrum* on FL and OL was estimated to be no more than 3% and 4%, respectively. However, *X. spectrum* oviposition on ACL and AAL averaged 33% and 30%, respectively, but varied greatly from 0 to 100%. On PDL, oviposition averaged about 10% (Fig. 4). Most *X. spectrum* oviposition on ACL and AAL was concentrated near the fungal inoculation points (Fig. 5).

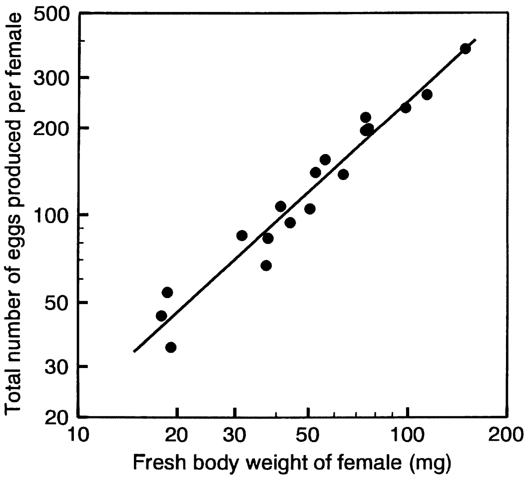
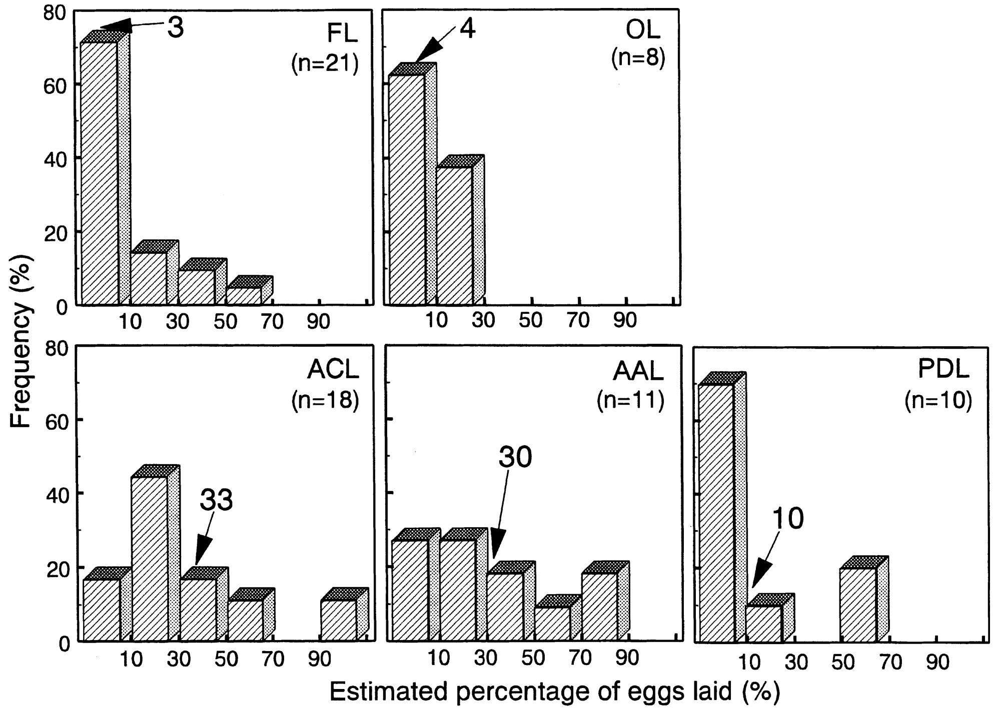


Fig. 3 Relationship between *X. spectrum* fresh body weight and total number of eggs produced per adult female. Note log-log scale

Discussion

The oviposition experiment revealed that *X. spectrum* rarely oviposited on FL, OL, or PDL, whereas on both ACL and AAL, females oviposited no less than 30% of their potential fecundity (Fig. 3). More interestingly, oviposition on these logs was evidently concentrated near the fungal inoculation points and was similar on both ACL and AAL (Fig. 5). These facts strongly support earlier records that *X. spectrum* females often deposit their eggs in trees that are already infested with other woodwasp species (Francke-Grosmann 1954; J.P. Spradbery, unpublished observation). Our results demonstrate that a major factor affecting *X. spectrum*

Fig. 4 Difference in the percentage of oviposition of *X. spectrum* on five log treatments. See Table 1 for detailed explanations of the treatments (*arrow* mean percentage value)



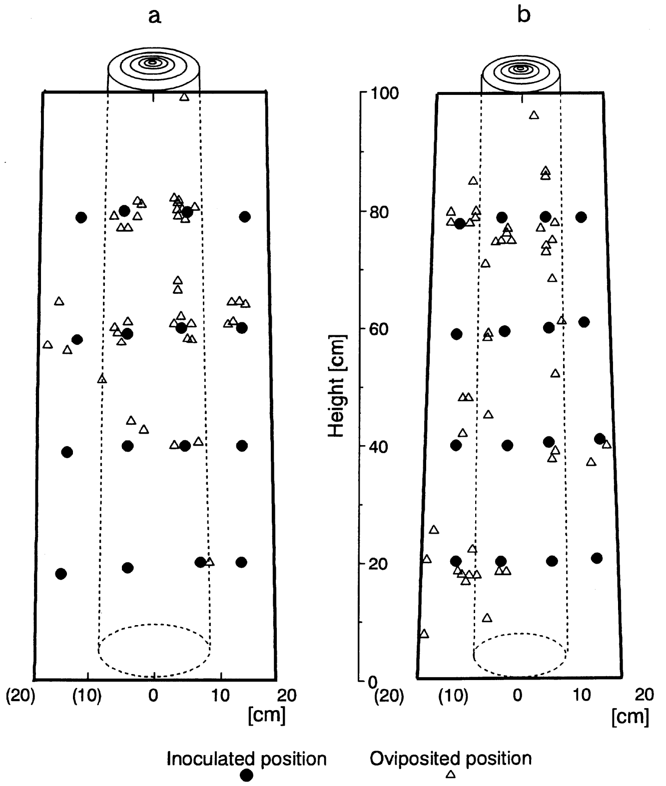


Fig. 5a,b Distributions of the oviposition holes of *X. spectrum* on the two sample logs inoculated with *Amylostereum* fungi: ACL (**a**), AAL (**b**). See Table 1 for explanation of ACL and AAL

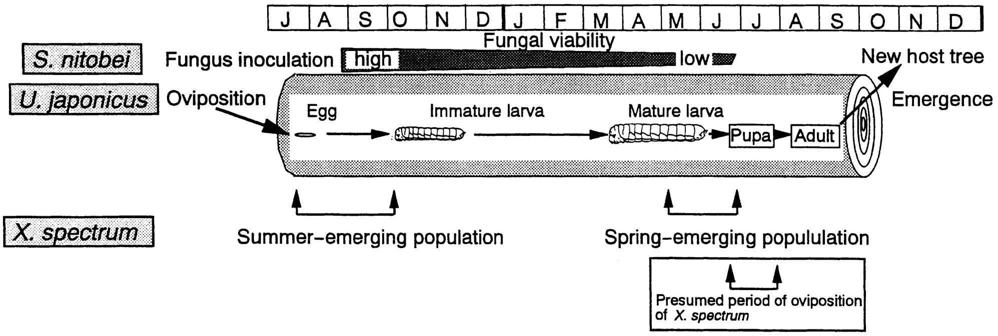
oviposition was the presence or not of symbiotic fungi of other woodwasps in the potential host trees. The concentration of *X. spectrum* emergence holes, which usually occur within 7 cm of their oviposition sites (Kanamitsu 1978), near to those of the other woodwasp species (Fig. 2), suggests that *X. spectrum* females are attracted to host trees by odors, such as those emitted by *Amylostereum* fungi introduced by other fungus-carrying woodwasp species.

Figure 6 is a hypothetical diagram showing when *X. spectrum* oviposition occurs in relation to the life cycles of *S. nitobei* and *U. japonicus*. *X. spectrum* has a dual reproductive strategy. One population emerges in summer, at about the same time the fungus-carrying woodwasps emerge. These *X. spectrum* females presumably oviposit on host trees soon after the other siricid species have oviposited and inoculated the wood with *Amylostereum* fungi. The second population emerges the following spring, and probably oviposits in host trees that have been inoculated with *Amylostereum* fungi in the preceding year.

Why does *X. spectrum* have such a reproductive strategy? If all *X. spectrum* adults emerged within a limited period of a single year, the chance of locating suitable larval food resources may be less predictable, because the amount of suitable available food resources critically depends on the densities of fungus-carrying woodwasps, which show great annual variation within local areas (Madden 1988; Sano 1992). The strategy of emerging over a 2-year period therefore 'spreads the risk' for *X. spectrum*. There is another important difference between the two generations. The offspring of the summer-emerging *X. spectrum* population are exposed to recently inoculated *Amylostereum* fungi, but may be subject to interspecific competition with other woodwasp species. On the other hand, offspring of the spring-emerging population can avoid interspecific competition with other woodwasps by utilizing host trees in which larvae of other fungus-carrying woodwasp species have finished feeding. In this latter period, however, the viability of *Amylostereum* fungi may be reduced, as suggested by the fact that *Amylostereum* fungi are more difficult to isolate from aged wood (H. Fukuda, unpublished data).

Why has *X. spectrum* evolved a life history that utilizes the fungal symbionts of other woodwasp species without possessing any symbiotic fungi itself? Each of the two fungus-carrying woodwasp species has formed a specific relationship with a particular *Amylostereum* fungus (Morgan 1968; Talbot 1977), while *X. spectrum*, with no fungal symbionts of its own, can utilize both of these *Amylostereum* fungi. This is supported by the fact that *X. spectrum* emerged from logs with either *U. japonicus* or *S. nitobei*, each of which has a different symbiotic fungus (Fig. 1). The ability to use two different fungal symbionts apparently extends the host range of *X. spectrum*. Moreover, perhaps this wider host range has also allowed *X. spectrum* to have a wider worldwide distribution than other siricid species with species-specific fungal symbionts (Morgan 1968; Takeuchi 1962).

Fig. 6 A diagram illustrating hypothetical periods of oviposition by *X. spectrum* in relation to developmental stages of *S. nitobei* and *U. japonicus* in a host tree. The life cycles of *S. nitobei* and *U. japonicus* are based on data from the present study and from Kato (1966)



Finally, parasitoids in the genera *Rhyssa*, *Megarhyssa*, and *Ibalia* often parasitize a high proportion of woodwasps (Fukuda and Hijii 1996b). These parasitoids of woodwasps are thought to be attracted to odors associated with the fungal symbionts or certain decay products (Madden 1968, 1988; Nuttall 1980a; Spradbery 1970). In addition, many woodwasps are parasitized by *Deladenus* nematodes (Bedding and Akhurst 1978; Fukuda and Hijii 1997), which have both entomophagous and mycetophagous life cycles (Bedding 1972, 1993; Nuttall 1980b). If *X. spectrum* carried specific fungal symbionts, they might attract specific parasitoids and nematode parasites. Therefore, to clarify the adaptive significance of the lack of a specific fungal symbiont in *X. spectrum*, all aspects of the symbiotic relationship need to be taken into consideration, as well as the metabolic costs of carrying specific fungal symbionts within the insect.

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References

Bayon C, Mathelin J (1980) Carbohydrate fermentation and by-product absorption studied with labelled cellulose in *Orytes nasicornis* larvae (Coleoptera: Scarabaeidae). J Insect Physiol 26: 833–840

Bedding RA (1972) Biology of *Deladenus siricidicola* (Neotylenchidae) an entomophagous-mycetophagous nematode parasitic in siricid woodwasps. Nematologica 18: 482–493

Bedding RA (1993) Biological control of *Sirex noctilio* using the nematode *Deladenus siricidicola*. In Bedding RA, Akhurst RJ, Kaya HK (eds) Nematodes and the biological control of insect pests. CSIRO, Victoria pp 11–20

Bedding RA, Akhurst RJ (1978) Geographical distribution and host preferences of *Deladenus* species (Nematoda: Neotylenchidae) parasitic in siricid woodwasps and associated hymenopterous parasitoids. Nematologica 24: 286–294

Bignell DE (1977) An experimental study of cellulose and hemicellulose degradation in the alimentary canal of American cockroach. Can J Zool 55: 579–589

Breznak JA (1982) Intestinal microbiota of termites and other xylophagous insects. Annu Rev Microbiol 36: 323–343

Coutts MP, Dolezal JE (1969) Emplacement of fungal spores by the woodwasp, *Sirex noctilio*, during oviposition. For Sci 15: 412–416

Cruden DL, Markovetz AJ (1979) Carboxymethylcellulose decomposition by intestinal bacteria of cockroaches. Appl Environ Microbiol 38: 369–372

Francke-Grosmann H (1939) Uber das Zusammenleben von Holzwespen (Siricinae) mit Pilzen. Z Angew Entomol 25: 647–680

Francke-Grosmann H (1954) Tierische Holzschadlinge, Holzwespen. Holz Roh Werkst 12: 35–38

Fukuda H, Hijii N (1996a) Host-tree conditions affecting the oviposition activities of the woodwasp, *Sirex nitobei* Matsumura (Hymenoptera: Siricidae). J For Res 1: 177–181

Fukuda H, Hijii N (1996b) Different parasitism patterns of two hymenopterous parasitoids (Ichneumonidae and Ibaliidae) depending on the development of *Sirex nitobei* (Hymenoptera: Siricidae). J Appl Entomol 120: 301–305

Fukuda H, Hijii N (1997) Delayed emergence and reduced bodyweight of *Xeris spectrum* (Hymenoptera: Siricidae) due to nematode infection. J For Res 2: 183–186

Fukuda H, Kajimura H, Hijii N (1993) Fecundity of the woodwasp, *Sirex nitobei* Matsumura, in relation to its body size. J Jpn For Soc 75: 405–408

Haack RA, Slansky JR (1987) Nutritional ecology of wood-feeding Coleoptera, Lepidoptera, and Hymenoptera. In: Slansky JR, Rodriguez JG (eds) Nutritional ecology of insects, mites, spiders, and related invertebrates. Wiley, New York, pp 449–486

Kanamitsu K (1978) Woodwasps and their hymenopterous parasitoids in Japanese conifers. Kontyu Tokyo 46: 498–508

Kato Y (1966) The developmental processes of pine bark beetles and patterns of tree decline. For Pests 15: 178–185

Kukor JJ, Martin MM (1983) Acquisition of digestive enzymes by siricid woodwasps from their fungal symbiont. Science 220: 1161–1163

Madden JL (1968) Behavioral responses of parasites to symbiotic fungus associated with *Sirex noctilio* F. Nature 218: 189–190

Madden JL (1988) *Sirex* in Australasia. In: Berryman AA (ed) Dynamics of forest insect populations – patterns, causes, implications. Plenum, New York, pp 407–429

Martin MM (1979) Biochemical implications of insect mycophagy. Biol Rev 54: 1–21

Martin MM (1984) The role of ingested enzymes in the digestive process of insects. In: Anderson AD, Rayner ADM, Walton DWH (eds) Invertebrate-microbial interactions. Cambridge University Press, Cambridge, pp 155–172

Martin MM, Martin JS (1978) Cellulose digestion in the midgut of the fungus-growing termite *Macrotermes natalensis*: the role of acquired digestive enzymes. Science 199: 1453–1455

Martin MM, Martin JS (1979) The distribution and origins of cellulolytic enzymes of the higher termite *Mactrotermes natalensis*. Physiol Zool 52: 1–11

Morgan FD (1968) Bionomics of Siricidae. Annu Rev Entomol 13: 239–256

Nuttall MJ (1980a) Insect parasites of *Sirex* (Hymenoptera: Ichneumonidae, Ibaliidae, and Orussidae). NZ For Serv, For Res Inst, Forest and Timber Insects in New Zealand 47

Nuttall MJ (1980b) Nematode parasites of *Sirex*, *Deladenus siricidicola* Bedding (Nematoda: Neotylenchidae). NZ For Serv, For Res Inst, Forest and Timber Insects in New Zealand 48

Sano A (1992) *Urocerus japonicus*. For Med 122: 1–8

Sano A, Mihara Y, Ito S (1995) The fungi isolated from the intersegmental sacs of two *Urocerus* species. Trans Annu Meet Chubu Branch Jpn For Soc 42: 125–126

Spradbery JP (1970) Host finding by *Rhyssa persuasoria* (L.), an ichneumonid parasite of siricid woodwasps. Anim Behav 18: 103–114

Stillwell MA (1966) Woodwasps (Siricidae) in conifers and associated fungus, *Stereum chailletii* in eastern Canada. For Sci 12: 121–128

Takeuchi K (1962) Insecta Japonica, Hymenoptera: Siricidae, ser 2 part 2. Hokuryukan, Tokyo

Talbot PHB (1977) The *Sirex-Amylostereum-Pinus* association. Annu Rev Phytopathol 15: 41–54

Terashita T (1970) A basidiomycete symbiotic to a siricid in Japan. J Jpn For Soc 52: 313–316