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ORIGINAL ARTICLE

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Expansion of the geographical distribution of an exotic ladybird beetle, *Adalia bipunctata* (Coleoptera: Coccinellidae), and its interspecific relationships with native ladybird beetles in Japan

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Abstract The first record of the exotic ladybird beetle, *Adalia bipunctata* (Coleoptera; Coccinellidae), in Japan was in 1993 at Osaka Nanko Central Park. Since that time, studies on the life history and geographical distribution of *A. bipunctata* have been ongoing, and its establishment in the Osaka Nanko area has been confirmed. *A. bipunctata* is a predacious ladybird beetle and a member of a guild that overlaps in habitat and prey with that of native ladybird beetles such as *Harmonia axyridis* and *Menochilas sexmaculatus*. We investigated the distribution of *A. bipunctata* and its interspecific relationships with native predacious ladybird beetles. In some areas, *A. bipunctata* was dominant in interspecific relationships with native ladybird beetles. For the first 10 years after *A. bipunctata* was discovered, it occurred only in the Osaka Nanko area, but the present geographical distribution indicates that it has expanded its range. Though the population density of this species was highest at the area recorded first, and tended to decrease in inverse proportion to the distance from Osaka Nanko Central Park, a satellite occurrence was observed in a remote area. The numbers of aphid and tree species (leaf shelter for aestivation and over-wintering) utilized by *A. bipunctata* have recently increased. Such increases will cause the rate of distribution of *A. bipunctata* to accelerate. Interspecific competition between *H. axyridis* and *A. bipunctata*, which occurs earlier than *H. axyridis*, may be avoided by desynchronization of the occurrence seasons, and another common predacious ladybird beetle, *Coccinella septempunctata*, may escape interspecific competition by habitat segregation.

Keywords *Adalia bipunctata* · Exotic species · Native ladybird beetles · Distribution · Interspecific relationships

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Introduction

The problem of invasive species is a very important one that has attracted much attention (Elton 1958; Enserink 1999; Levine 2000; Ecological Society of Japan 2002). In the case of invasion of agricultural pests, the damage to crops is more serious than it is from native species. The decline of native populations from competition with alien species and the changes to native ecosystems by the inevitable formation of undesirable food webs are also important problems (Ecological Society of Japan 2002). Thus, it is essential that the processes of establishment of populations and expansion of the distributions of alien species, as well as their influences on native ecosystems be analyzed.

Recently, there has been a worldwide trend to utilize predacious ladybird beetles in bio-control programs throughout the world. For example, the introduction and establishment of *Coccinella septempunctata* in North America for control of aphids in the 1950s (Obrycki and Kring 1998; Angalet and Jacques 1975; Angalet et al. 1979; Schaefer et al. 1987) and *Harmonia axyridis* in Europe and North America in the 1990s (Coderre et al. 1995; LaMana and Miller 1996; Ferran et al. 1996; Hodek and Honěk 1996) are well known. However, these introduced ladybird beetles became the dominant species and caused decreases in the populations of smaller native ladybird beetles, such as *Adalia bipunctata* and *Coccinella transversoguttata* (Elliott et al. 1996; Brown and Miller 1998; Horn 1999; Brown 2003; Evans 2004; Bazzocchi et al. 2004).

In Japan, *Rodolia cardinalis* was introduced to control a serious pest of citrus, *Icerya purchasi*, in 1911, and this project was a success (Shiga 1996). There were no reports of an important influence of *R. cardinalis* on Japanese ecosystems. For the 8 years from 1985 to 1992, ten species of ladybird beetle were newly recorded in Japan, and most of these are considered alien species (Sasaji 1992). For example, *Psyllobora vigintimaculata*, which feeds on powdery mildew spawn that are parasitic

on *Solidago altissima*, is an alien species that was first recorded in 1984 (Kuboki and Izumi 1985), and its geographical distribution has expanded (Sasaji 1992). A predacious ladybird beetle, *Olla v-nigrum*, first recorded in 1987 in Okinawa (Ueno and Sasaji 1989; Omomo and Sasaji 1989), is also an alien species (Sasaji 1992) with an expanding distribution that is mostly confined to the Ryukyu Islands (Minato 1998). Moreover, recently (1997), the ladybird beetle *Epilachna varivestis*, a pest of kidney bean, invaded into the Nagano and Yamanashi Prefectures of Japan, and the geographical distribution of this species is also expanding (Fujiyama et al. 1998).

The predacious ladybird beetle *A. bipunctata* (Coleoptera: Coccinellidae) was first recorded in Japan in 1993 (Osaka Nanko, Osaka Prefecture; Sakuratani 1994), and studies on its life history and geographical distribution are ongoing. This ladybird beetle is a common species in Europe and North America (Hodek 1973; Hodek and Honěk 1996), and many studies on this species have been carried out (e.g., Dixon 1970; Hodek and Honěk 1996; Jervis and Kidd 1996; Hemptinne and Naisse 1988; Dixon 2000; Francis et al. 2001). *A. bipunctata* is a member of the same guild as the native ladybird beetles, *H. axyridis* and *Menochilas sexmaculatus*, occurring in the same habitat and feeding on the same species of aphids (Kajita et al. 2000). The adult body size of *H. axyridis* is 4.2–8.2 mm (Sasaji 1971), which is larger than that of *A. bipunctata* (3.0–5.0 mm). Feeding behavior of *H. axyridis* larvae on prepupae and pupae of *A. bipunctata* is often observed in the fields of Japan (Sakuratani et al. 2000). However, the competition between these two ladybird beetles may be indirect, because of seasonal differences in their occurrence; the occurrence of *H. axyridis* is late compared to that of *A. bipunctata*. Whereas the population of *A. bipunctata* in Europe is multivoltine (Hemptine and Naisse 1988; Hodek and Honěk 1996), that in Japan is univoltine (Sakuratani et al. 2000), utilizing aestivo-hibernation (Hagen 1962), and the life history patterns of Japanese populations differ from those of European populations. Japanese populations may adapt to the Japanese climate with very hot summers and a decrease in the numbers of aphids in summer (Toda and Sakuratani 2005). If the geographical distribution of *A. bipunctata* expands, it is possible that competition with native ladybird beetles will occur over wide areas.

Adalia bipunctata was first found in Japan in 1993, and its range of distribution was limited to the 25-ha area of Osaka Nanko Central Park for the first several years (Sakuratani et al. 2000). This fact indicates that the time required for invasion to take place is not very long. Few studies on alien species in Japan were initiated just after invasion. In this study, we report on the geographical distribution of *A. bipunctata* and its interspecific relationships with native ladybird beetles in Japan.

Materials and methods

The studies on geographical distribution and interspecific relationships were carried out from 1993 to 2004 in Osaka Nanko Central Park, where *A. bipunctata* was first recorded, and the surrounding parks and wooded areas. The number of observation points in each year is shown in Table 1. Three to eleven points were observed in each year. Though several observation points were added in 2004, the same points were observed every year. Censuses were carried out on several tree species: *Acer buergerianum*, *Hibiscus syriacus*, *Rhaphiolepis umbellata*, *Quercus glauca* and other species of plants that are utilized by *A. bipunctata* for development and as aestivating and over-wintering sites. Concentrated observations were carried out in Osaka Nanko Central Park, Osaka Nanko district and the Osaka Bay area including Kobe City of Hyogo Prefecture from March to August during every year of the study. These areas are reclaimed land, and there are wooded areas and parks with many planted species, including plants utilized by *A. bipunctata*. The numbers of *A. bipunctata* and native predacious ladybird beetles were counted at 19 sites in the above areas from 1993 to 2004. The count unit was one shoot; the length of the shoot was 0.5 m from the tip of each tree, and one shoot of *R. umbellata* had five to ten leaves. From April to June in each year, the number of active ladybird beetles on each tree with aphids and psyllas was counted at every stage. The behavior of these ladybird beetles was also observed occasionally. The adults of *A. bipunctata* aestivate and over-winter in leaf shelters formed on trees, such as *Q. glauca*, *Celtis sinensis*, *Zelkova serrata* and *Pasania edulis* (Sakuratani et al. 2000). In this study, the number of aestivating and over-wintering adults of *A. bipunctata* and other native ladybird beetles was counted in every leaf shelter of the above trees within 3 m above the ground.

For the observation of adult emergence from pupae of *A. bipunctata* collected from *A. buergerianum* and *R. umbellata*, pupae were reared in an incubator at 22.5°C 14:10 L:D. The percentage of emergence was checked, and mortality factors were assessed.

Table 1 The number of observation points in each year and the number of points where *Adalia bipunctata* was found

Year	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
No. of observation points	3	11	8	11	7	3	5	7	3	11	11	19
No. of points with *A. bipunctata*	1	2	0	1	1	1	1	2	1	3	5	7

Results

Distribution and population density

The geographic distribution of *A. bipunctata* from its first record (1993) up to the present (2004) is shown in Fig. 1. A few individuals were discovered in the wooded area of El-City (Nanko Thermal Power Station of the Kansai Electric Power Company), 3 km distant from Osaka Nanko Central Park in 1994. However, between 1995 and 1999, *A. bipunctata* occurred only in Osaka Nanko Central Park. In 2000, it was found in the neighborhood of a ferry terminal 2 km away from Osaka Nanko Central Park. In 2003, aestivating adults were found at a trade center and a wild bird sanctuary, 1 and 3 km away from Osaka Nanko Central Park, respectively. In the spring of 2004, larvae, pupae and active adults were found at the trade center, Hirabayashi and Suminoe Park at distances of 2, 3 and 4.5 km from Osaka Nanko Central Park, respectively. In addition, in 2004, larvae, pupae, active adults and aestivating adults were recorded at Port Island in Kobe City, Hyogo Prefecture, where this species had not been previously recorded, 20 km from Osaka Nanko Central Park. Though for several years after the initial invasion the geographical distribution of *A. bipunctata* did not expand, the distribution of *A. bipunctata* has expanded within the past 2–3 years (Fig. 1, Table 1).

During the developmental season, the density of individuals of this species was highest at Osaka Nanko Central Park, and the density decreased in inverse proportion to the distance from Osaka Nanko Central Park, though the numbers were comparatively high in Kobe (Fig. 2). The number of aestivating adults increased from late May. The density of aestivating adults was also highest at Osaka Nanko Central Park and decreased in inverse proportion to the distance from Osaka Nanko Central Park (Fig. 3).

Interspecific relationships with native ladybird beetles

On the trees observed, *A. bipunctata*, *H. axyridis*, *M. sexmaculatus* and *C. septempunctata* individuals were found, but the numbers of observed *Propylea japonica*, *Calvia muiri*, *Chilocorus rubidus* and *Chilocorus kuwanae* found were very small.

The ratio of the number of *A. bipunctata* individuals (larvae, pupae and active adults) to all ladybird beetles in every area observed was high at Osaka Nanko Central Park, the ferry terminal and Suminoe Park (Fig. 4). At most observation points, the dominant species of ladybird beetles was *H. axyridis*. *H. axyridis* occurred later in the season than *A. bipunctata*; preying behavior toward pre-pupae of *A. bipunctata* by *H. axyridis* larvae was observed, though the frequency was very low. The frequency of predation toward larvae and pupae of *H. axyridis* by *A. bipunctata* adults that developed earlier than *H. axyridis* was very low (Table 2). The ratio of the number of aestivating adults of *A. bipunctata* to all ladybird beetles was high at Osaka Nanko Central Park, the ferry terminal, Hirabayashi and Port Island (Fig. 5). In Osaka Nanko Central Park especially, many adults were aestivated in leaf shelters of trees such as *Q. glauca* and *C. sinensis*. Aestivating and over-wintering adults of *A. bipunctata* were also found together with adult native ladybird beetles, *H. axyridis*, *M. sexmaculatus* and

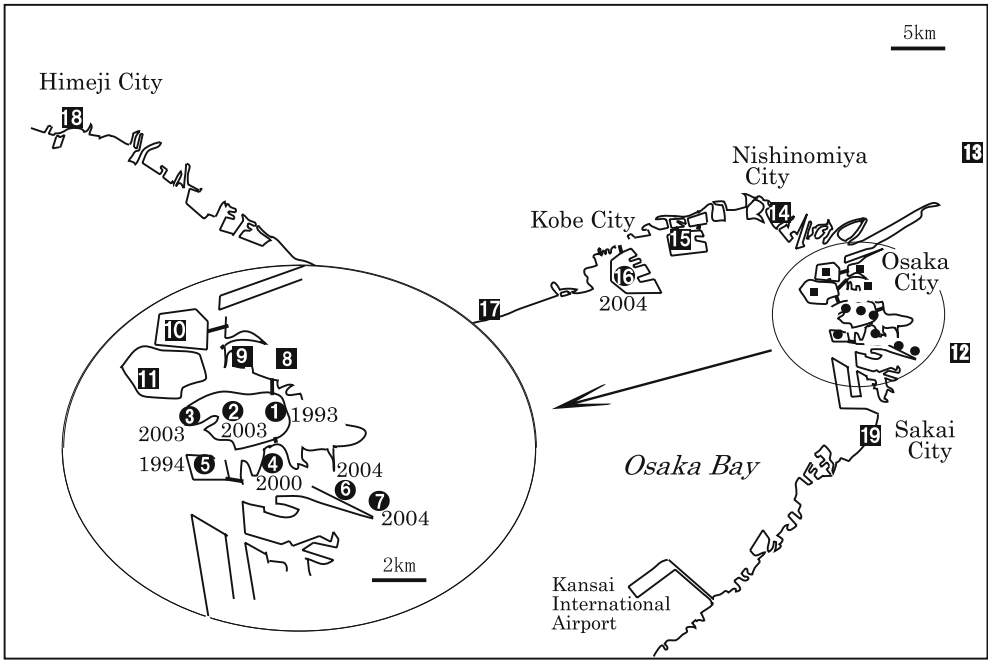

Fig. 1 Distribution map of *Adalia bipunctata* in Japan. *Filled circles* Observation points where *A. bipunctata* had been found as of 2004, *filled squares* observation points where *A. bipunctata* had not been found as of 2004. *1* Osaka Nanko Central Park, *2* Trade Center, *3* Wild Bird Sanctuary, *4* Ferry Terminal, *5* El City, *6* Hirabayashi, *7* Suminoe Park, *8* Tempozan, *9* Yahataya Park, *10* Hokko Yacht Harbor, *11* Maishima, *12* Nagai Park, *13* Tsurumi Park, *14* Hamakoshien, *15* Rokko Island, *16* Port Island, *17* Sumaura Park, *18* Hamate Park, *19* Hamadera Park. *Years* indicate the first year *A. bipunctata* was recorded at each observation point

C. muiri in the same leaf shelter. In summer, aestivating adults of *A. bipunctata* utilized approximately 3–5% of all leaf shelters checked. Thus, these leaf shelters are important aestivating sites for adults of *A. bipunctata*. *H. axyridis* had the highest rate of cohabitation with adults of *A. bipunctata*, nevertheless, the maximum rate was only 6%, and the most frequently found aestivating and over-wintering adults occurred alone in a leaf shelter (Fig. 6).

Rate of adult emergence

The rate of adult emergence from the pupae of *A. bipunctata* was 73% for *A. buergerianum* and 85% for *R. umbellata*. The combined rates of pupae that had been preyed upon (individuals with a hole in the abdomen from predation) and adults that failed to emerge, were 23% in *A. buergerianum* and 13% in *R. umbellata*. The total combined rate of emergence of *A. bipunctata* on *A. buergerianum* and *R. umbellata* was 75%, the combined rate of predation was 18%, and the remaining 3% of the individuals died from unknown causes (Table 3). No parasites emerged from the pupae of *A. bipunctata*, and the main mortality factor appears to have been predation by the native ladybird beetles. In addition, a few cases of cannibalism within *A. bipunctata* were observed.

Changes in habitat and feeding habits

In the year after the initial record of *A. bipunctata*, this species was found to be univoltine, and fed on aphids on *A. buergerianum*, *R. umbellata* and *H. syriacus* in spring. Table 4 shows the changes in the plant species used by *A. bipunctata* for feeding on aphids, aestivation and over-wintering for 3- or 4-year periods. From 1994–1996, this species was abundant on the trees listed above, but was not found on other types of trees or grasses. In autumn of 2000 and 2003, some active adults and larvae were observed on *Quercus serrata*, and in autumn of 2002 and 2004, only active adults were observed. In the most recent 4 years of the study, 2001–2004, all active stages (larvae, pupae and active adults) of *A. bipunctata* were found on 17 plant species, including four species of grass, *S. altissima*, *Rumex japonicus*, *Erigeron annus* and *Artemisia princeps*. In 2003, some active adults preyed on aphids, *Aphis oenotherae*, on *Oenothera stricta*, which had not been investigated before 2000. From 2001–2004, at least nine species of plants were newly added to the habitat plant list of this species during the active season. From 1994–1996, leaf shelters of only three tree species were utilized as aestivating sites by *A. bipunctata*, but in the next 4 years (1997–2000), 11 species, and during 2001–2004, 18 species were utilized. From 1994–1996, only one tree species was utilized for over-wintering of *A. bipunctata*.

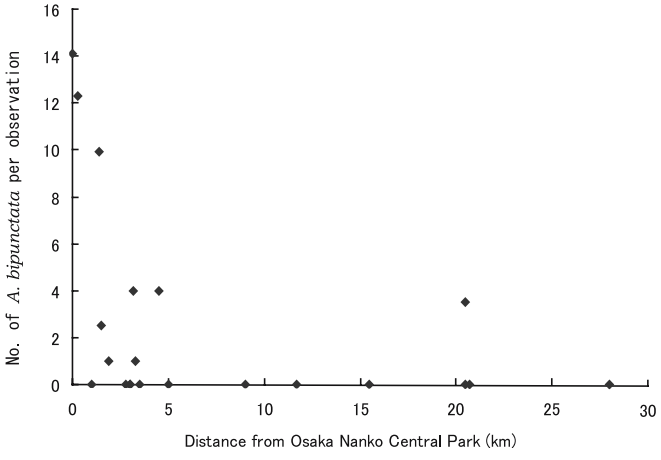

Fig. 2 Relationship between distance from Osaka Nanko Central Park and the mean density (active adults) of *Adalia bipunctata* at each observation point during the active season (spring) in 2004

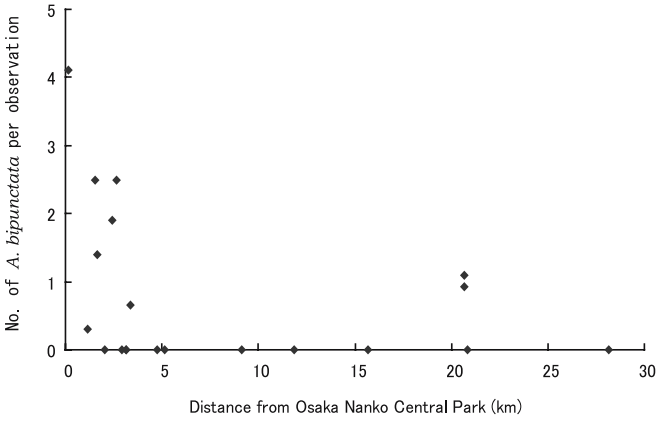

Fig. 3 Relationship between distance from Osaka Nanko Central Park and the mean density (aestivating adults) of *Adalia bipunctata* at each observation point during the aestivating season in 2003

Table 2 Frequency of predation between *Adalia bipunctata* and *Harmonia axyridis* on *Rhaphiolepis umbellata* (totals from 29 April, 3 May and 8 May in 2004)

Stage	Number of *A. bipunctata*		Number of *H. axyridis*	
	Total	Preyed on (%)	Total	Preyed on (%)
Larva	24	2 (8.3)	60	1 (1.7)
Pupa	231	2 (0.9)	42	0 (0)
Adult	27	0 (0)	4	0 (0)
Total	282	4 (1.4)	106	1 (0.9)

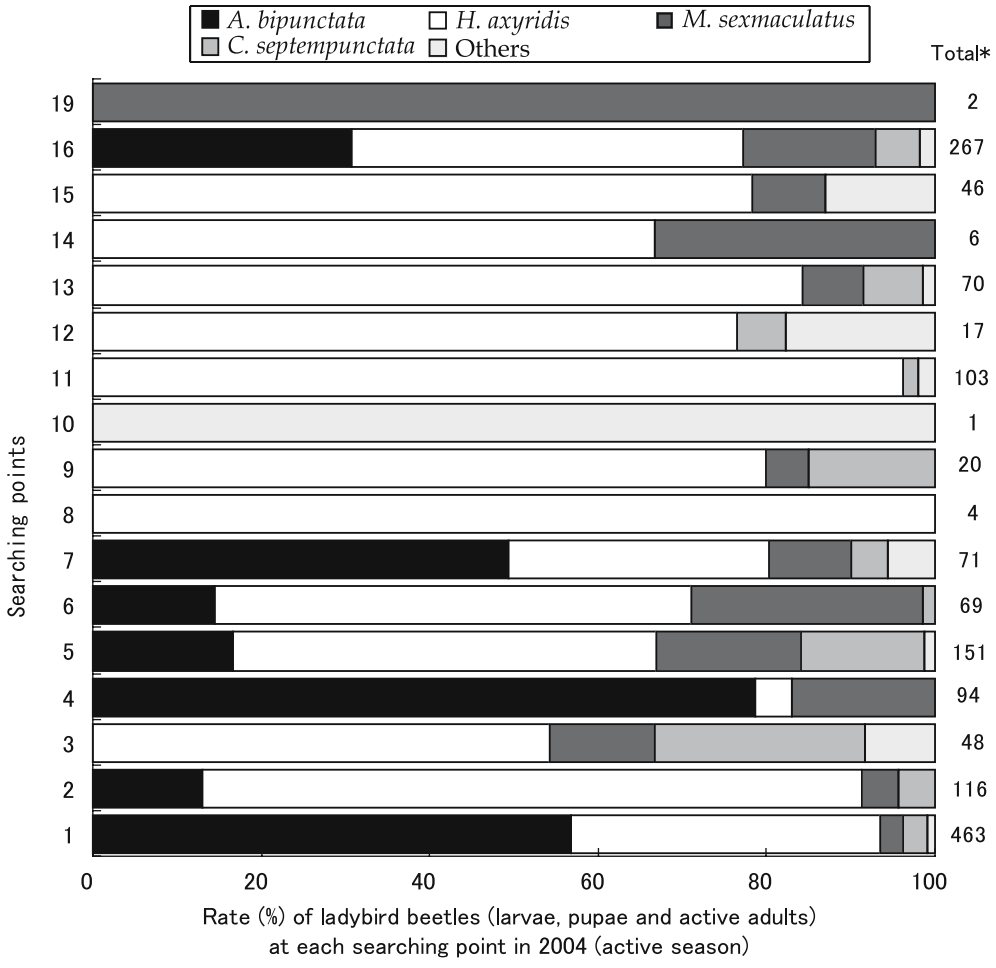

Fig. 4 The percentage of individuals of each ladybird beetle species at each observation point during the active season (spring) in 2004. Each *row* represents an observation point (see Fig. 1). *Right hand column* indicates total number of individuals of all ladybird beetle species

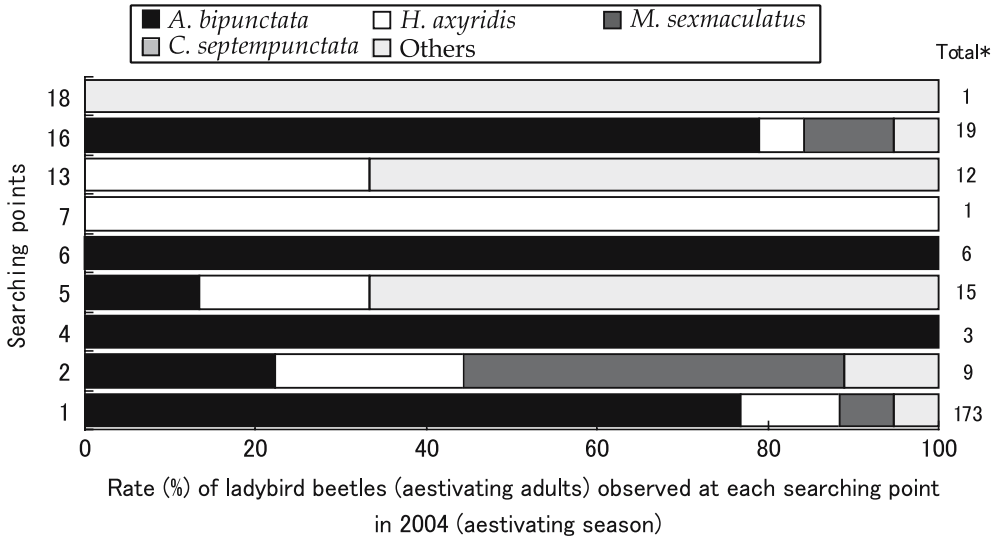

Fig. 5 The percentage of individuals of each ladybird beetle species at each observation point during the aestivating season in 2004. Each *row* represents an observation point (see Fig. 1). The *right hand column* indicates total number of individuals of all ladybird beetle species

However, during 1997–2000 six tree species, and during 2001–2004, 12 tree species were utilized. Only four species of aphid were fed on by *A. bipunctata*: *Periphyllus californiensis*, *Nippolachnus piri*, *Aphis gossypii* and *Aphis rumicis* from 1994–1996 (Table 4). However, from 1997–2000, four new species of aphid, *Uloreucon nigro-tuberculatum*, aphid species C, D and G were added to the menu. Moreover, during 2001–2004, seven species of aphid, *Aphis citricola*, *Aphis craccivora*, *Aphis spiraecola* and aphid species A, B, E and F, were newly recorded.

Thus, the species of plants utilized by *A. bipunctata* for habitat during the active, aestivating and over-win-

Table 3 Rate of adult emergence of *Adalia bipunctata* of 100 pupae collected from *Acer buergerianum* tree and *Rhaphiolepis umbellata* tree

Plant	Emerged (%)	Failed to emerge (%)	
		Preyed upon	Other
A. buergerianum	73 (73.0)	23 (23.0)	4 (4.0)
R. umbellata	84 (84.0)	14 (14.0)	2 (2.0)

tering seasons have increased with the passage of time. The diet of *A. bipunctata* has also expanded, and this ladybird beetle is becoming more of a generalist.

Discussion

There are several processes for expansion of the geographical distribution of alien species (Shigesada 1992; Shigesada and Kawasaki 1997). The first process is establishment, during which distribution scarcely expands. The second process is dispersion over several years or decades. In some species of insects, the dispersion occurs at an accelerating pace (Kiritani and Morimoto 2004). *A. bipunctata* was first recorded in 1993 (Sakuratani 1994), and the establishment period of this species may take about 10 years (1990s–ca. 2000). Dispersion of this species might have begun over the last several years.

The foods of *A. bipunctata* are several species of aphid and psylla. The larvae and adults of *A. bipunctata* have been able to dominate use of these food items in competition with the native ladybird beetles that occur sympatrically with *A. bipunctata* (Sakuratani et al. 2000). Furthermore, the number of food species of *A. bipunctata* has recently increased. Whereas in Europe, *A. bipunctata* is a generalist, and feeds on about 45 species of aphid prey (Banks 1955; Iperti 1965; Smith 1965; Blackman 1965, 1967; Semyanov 1970; Heathcote 1969; Mills 1981; Hodek and Honěk 1996), in Japan *A. bipunctata* feeds on only a few species of aphid and psylla, such as *P. californiensis*, *N. piri* and *Psylla satumensis*. *A. bipunctata* preys on aphids growing on potato and cereal fields in Europe (Skuhravý and Novák 1957; Kiekhefer and Miller 1967), but it does not utilize these food items in Japan. The number of species of aphids and plants utilized by *A. bipunctata* in Japan has tended to increase (Table 4), thus, it is possible that the habitat of *A. bipunctata* will spread to that of the grassland-growing aphids. The wide distribution of the trees it inhabits and the continued increase in its food menu may cause the distribution expansion of *A. bipunctata* to accelerate.

The population density of *A. bipunctata* in the active stage was highest at Osaka Nanko Central Park where the occurrence of this species was observed continuously from the first record, and the density decreased inversely with increasing distance from

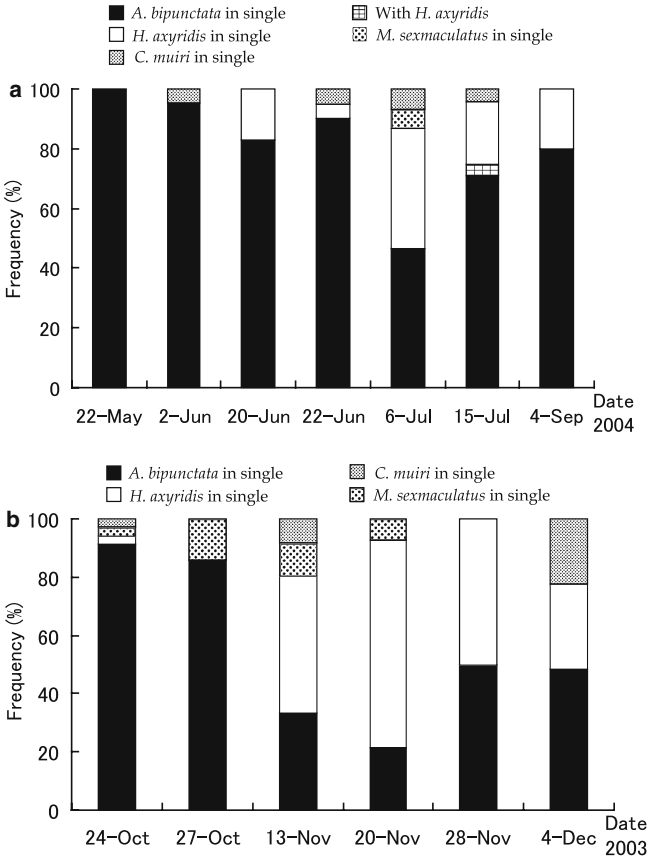

Fig. 6 The percentage of individuals of each ladybird beetle species in each leaf shelter on observation days, Osaka Nanko Central Park. **a** Aestivating season (2004), **b** over-wintering season (2003)

Osaka Nanko Central Park (Fig. 2). Thus, the first place of invasion of *A. bipunctata* is inferred to have been Osaka Nanko Central Park, which may be the epicenter of the outbreak. The distribution might expand from this epicenter. In Osaka City, *A. buergerianum* and *R. umbellata*, on which *A. bipunctata* is often found, are planted widely in the park and along the roadside (Osaka City Environmental Research Center 2000). Thus, the distribution of *A. bipunctata* is considered to have expanded continuously along these trees with aphids and psyllas. However, in Port Island of Kobe City, this species is believed to be have a patchy distribution, probably caused by trucks loading cargo carrying *A. bipunctata*. *Monochamus alternatus* spread by continuous diffusion and hitchhikers (Kiritani and Morimoto 2004). The food distribution assists the spread of exotic insects such as *Lissorhoptrus oryzophilus* (Kiritani and Morimoto 2004).

At most observation points, the habitat of *A. bipunctata* overlapped not only with that of *H. axyridis* but also with that of *M. sexmaculatus*, and thus there were interspecific relationships for both food and habitat. The native species in the most intensive interspecific relationship with *A. bipunctata* in Japan may be *H. axyridis*. In Europe and North America, the population densities of the native ladybird beetle, *A. bipunctata*, decreased

Table 4 Periodic changes in habitat plant and prey species in *Adalia bipunctata*

Plant family	Plant species	Aphid species	Year		
			1994–1996	1997–2000	2001–2004
Active season					
Aceraceae	*Acer buergerianum*	*Periphyllus californiensis*	○	○	○
Rosaceae	*Rhaphiolepis umbellata*	*Nippolachnus piri*	○	○	○
		Psylla satumensis	○	○	○
	Prunus lannesiana	aphid A	×	×	○
	P. persica	aphid B	×	–	○
	Spiraea thumbergii	*Aphis spiraecola*	×	×	○
Fagaceae	*Quercus serrata*	aphid C	–	○	○
	Q. acutissima	aphid D	×	○	○
Ulmaceae	*Celtis sinensis*	–	×	×	○
Malvaceae	*Hibiscus syriacus*	*Aphis gossypii*	○	×	○
Leguminosae	*Robinia pseudo-acacia*	*Aphis craccivora*	×	–	○
Pittosporaceae	*Pittosporum tobira*	*Aphis citricola*	×	×	○
Caprifoliaceae	*Weigela coraeensis*	aphid E	×	–	○
Compositae	*Solidago altissima*	*Uloreucon nigrotuberculatum*	×	○	○
	Erigeron annus	aphid F	×	–	○
	Artemisia princeps	aphid G	×	○	○
Polygonaceae	*Rumex lupulina*	*Aphis rumicis*	○	–	○
Aestivating season					
Aceraceae	*A. buergerianum*		○	○	○
Rosaceae	*P. lannesiana*		×	×	○
Fagaceae	*Quercus glauca*		○	○	○
	Q. myrsinaefolia		–	×	○
	Pasania edulis		○	○	○
	Q. serrata		–	○	○
	Q. acutissima		×	○	○
	Q. phillyraeoides		×	○	○
	Castanopsis cuspdata		–	×	○
Ulmaceae	*C. sinensis*		×	×	○
	Ulmus parvifolia		×	×	○
	Zelkova serrata		–	○	○
Malvaceae	*H. syriacus*		×	×	○
Magnoliaceae	*Magnolia liliflora*		–	○	○
Lauraceae	*Cinnamomum camphora*		×	○	○
Aquifoliaceae	*Ilex rotunda*		×	○	○
Theaceae	*Camellia japonica*		×	○	○
Carprifroliaceae	*W. coraeensis*		×	–	○
Over-wintering season					
Aceraceae	*A. buergerianum*		×	○	○
Rosaceae	*R. umbellata*		×	×	○
	P. lannesiana		×	×	○
Fagaceae	*Q. glauca*		○	○	○
	Q. myrsinaefolia		–	○	○
	P. edulis		×	○	○
	Q. serrata		×	×	○
	Q. acutissima		×	○	○
Ulmaceae	*C. sinensis*		×	×	○
	U. parvifolia		×	×	○
	Z. serrata		×	○	○
Malvaceae	*H. syriacus*		×	×	○

Aphid A–G Species not classified, × not found, ○ found, – not observed

due to the invasion of *H. axyridis* (Elliott et al. 1996; Brown and Miller 1998; Horn 1999; Brown 2003; Evans 2004; Bazzocchi et al. 2004). However, in Japan the population of *A. bipunctata* is not currently in danger of extinction from competition with *H. axyridis*. The dominant species of predacious ladybird beetle was *A. bipunctata* in some of our observation points. This phenomenon differs from the case in foreign countries where the population density of *A. bipunctata* decreased due to the occurrence of *H. axyridis*.

Though few cases of predation on *A. bipunctata* by native ladybird beetles have been reported in Japan (Sakuratani et al. 2000), some effects of native ladybird beetles on *A. bipunctata* will be expected, because the predation rate on the pupae of *A. bipunctata* collected from the field was 18% (Table 3). With respect to body size, the larger native ladybird beetle, *H. axyridis*, is an intraguild predator of *A. bipunctata* (Kajita et al. 2000; Burgio et al. 2002). Thus, the larger body size will be an advantage for intraguild predation. However, as the

body size of *H. axyridis* is larger than that of both *A. bipunctata* and *M. sexmaculatus*, *H. axyridis* causes disadvantages to both *A. bipunctata* and *M. sexmaculatus* with regard to the amount of predation necessary for its development. As the occurrence of *H. axyridis* is later than that of *A. bipunctata* in Japan (Sakuratani et al. 2000), the utilization of prey by *A. bipunctata* may be disadvantageous to *H. axyridis* in spring. As the population density of the invasive ladybird beetle (in our case, *A. bipunctata*) in a guild increased (Evans 2004), the population density of aphids decreased and the habitat of native ladybird beetles came to be occupied by *A. bipunctata* in early spring in Japan. Local populations of *H. axyridis* will be negatively impacted by these processes of invasion. Thus, the time lag of occurrence between *A. bipunctata* and *H. axyridis* is advantageous to the establishment and dominancy of *A. bipunctata*.

In Japan, including Osaka, another predacious ladybird beetle, *C. septempunctata*, is a common species. This species occurs in early spring like *A. bipunctata* (Sakuratani 1988; Sakuratani et al. 1986; Sakuratani and Nakamura 1997). The occurrences of both species synchronize seasonally. However, *C. septempunctata* tends to inhabit grassland areas (Sakuratani 1998), whereas *A. bipunctata* is often found on trees (Table 4). Thus, interspecific competition of *A. bipunctata* with *C. septempunctata* may rarely occur. *A. bipunctata* adults utilize the leaf shelter for aestivation and over-wintering sites (Sakuratani et al. 2000). *H. axyridis* adults and other ladybird beetles adults also utilized such leaf shelters, and in some cases two or more species of ladybird beetle were observed to utilize one leaf shelter simultaneously. However, most ladybird beetles inhabit single leaf shelter individually (Fig. 6). Another common predacious ladybird beetle, *C. septempunctata*, aestivates and over-winters in weeds such as *Miscanthus sinensis* (Sakuratani 1990; Sakuratani and Kubo 1985).

With regard to aestivation and over-wintering of *A. bipunctata*, interspecific competition for habitat between *A. bipunctata* and native ladybird beetles may rarely occur. Furthermore, Japanese populations of *A. bipunctata* are univoltine (Sakuratani et al. 2000), whereas European populations of this species are multivoltine (Hemptine and Naisse 1988; Hodek and Honěk 1996), and Japanese populations of *H. axyridis* are also multivoltine (Sakurai et al. 1981). Thus, the interspecific competition of *A. bipunctata* with *H. axyridis* may be avoided by time lag and desynchronizing of the occurrence season, and in *C. septempunctata*, habitat segregation may contribute to avoidance of competition with *A. bipunctata*.

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