



Indirect interactions between a native and a supposedly non-native wasp species (Hymenoptera: Vespidae: Eumeninae: *Anterhynchium*)

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Key words. Alien species, apparent competition, indirect effects, natural enemies, prey use, resource competition, trap nests

Abstract. Non-native species pose a threat to native organisms. When non-native and native species are closely related, the former can often competitively exclude the latter. Many studies have focused on competitive exclusion of native insect species by non-native eusocial hymenopterans, including ants, hornets, paper wasps and bees. Although solitary species of wasps have been introduced in many regions, few studies have investigated the effects of these insects on their native congeners. We investigated competitive interactions between native and non-native solitary wasps belonging to the same genus (Hymenoptera: Vespidae: Eumeninae: *Anterhynchium*). Specifically, we compared resource use and natural enemies of the native *Anterhynchium flavomarginatum* and supposedly non-native *A. gibbifrons* at a forest edge in Takasago, Hyogo, Japan, in June–October 2019, using trap nests (bamboo canes). Of 950 bamboo canes, 70 (7.4%) and 50 (5.3%) were used as nests by *A. flavomarginatum* and *A. gibbifrons*, respectively. *Anterhynchium flavomarginatum* produced two generations over the period studied, whereas *A. gibbifrons* produced only one. Although *A. gibbifrons* began nesting two weeks after *A. flavomarginatum*, the nesting period of *A. gibbifrons* overlapped that of the first nesting period of *A. flavomarginatum*. Nest architecture and the inner diameter of the canes used by both species were similar, suggesting potential competition for nesting resources. *Anterhynchium flavomarginatum* used larvae of 14 species of moths (Lepidoptera: Crambidae, Pyralidae, Tortricidae) as food for their larval offspring, whereas *A. gibbifrons* used only a single species, *Demobotys pervulgalis* (Lepidoptera: Crambidae). Prey species were exclusive to each wasp species, indicating no competition for this resource. Three parasitoid species, *Macrosiagon nasutum* (Coleoptera: Ripiphoridae), *Amobia distorta* (Diptera: Sarcophagidae) and *Megaselia* sp. (Diptera: Phoridae), attacked both *Anterhynchium* species. The percentage parasitism by *Amobia distorta* was higher for the native *A. flavomarginatum*. *Anterhynchium gibbifrons* may indirectly affect *A. flavomarginatum* via shared parasitoids.

INTRODUCTION

Non-native species can negatively affect native species by both direct and indirect pathways (Elton, 1958; Mack et al., 2000; Sugiura, 2016; David et al., 2017). Direct interactions include consumption and interference (Snyder & Evans, 2006; Sugiura, 2010, 2016) and indirect interactions are mediated through shared resources, i.e. food or space (Thomson, 2004; Snyder & Evans, 2006) and enemies (predators, parasitoids and pathogens; Holt & Bonsall, 2017). When combined, these interactions can lead to the exclusion and displacement of native species (Reitz & Trumble, 2002; Gao & Reitz, 2017). When non-native and native species are closely related, the former can competitively exclude or displace the latter, given that congeners are more likely to share resource needs and natural enemies (Reitz & Trumble, 2002).

The negative effects of non-native insect species on native species and biota are widely reported (Snyder & Evans, 2006; Kenis et al., 2009). In a review of 403 research publications focused on the ecological effects of invasive insects, 55% focused on non-native eusocial hymenopterans such as ants, hornets, paper wasps, bumblebees and honeybees (Kenis et al., 2009). Although solitary wasps are more diverse than eusocial wasps (Aguiar et al., 2013; Peters et al., 2017), few studies have focused on non-native solitary wasps, excluding parasitoid species (Kenis et al., 2009). Although some solitary species of wasps have been introduced in many areas (Beggs et al., 2011; Fateryga et al., 2014; Ravoet et al., 2017), Beggs et al. (2011) suggest that their ecological effects may be overlooked because they are of less concern for human health. However, native solitary wasps play a crucial ecological role in controlling herbivorous insects (Losey & Vaughan, 2006; Tylaniakis

et al., 2007; Brock et al., 2021) and non-native species can threaten both their populations and the ecosystem services they provide. Clarifying the potential effects of non-native solitary wasp introductions improves our understanding of the wider pattern of ecological effects of non-native hymenoptera on native biota.

We aimed to understand the resource use and natural enemies of two solitary wasp congeners (Hymenoptera: Vespidae: Eumeninae: *Anterhynchium*). In central Japan, *Anterhynchium flavomarginatum* (Smith, 1852) is commonly found in agricultural fields, secondary forests and urban areas (Iwata, 1975). The congener *Anterhynchium gibbifrons* Yamane & Murota, 2015 was recently described on the basis of specimens obtained from Fukui Prefecture, also located in central Japan (Yamane & Murota, 2015). Several lines of evidence indicate that *A. gibbifrons* has only recently invaded Japan (Watanabe et al., 2020) and is thus considered here as a non-native species (see the subsection ‘Species studied’ in the Materials and Methods). Wasps in the genus *Anterhynchium* de Saussure, 1863 nest in pre-existing cavities in wood and bamboo canes (Iwata, 1975; Endo, 2017). *Anterhynchium gibbifrons* frequently occurs in the same habitat as *A. flavomarginatum* in central Japan (Yamane & Murota, 2015; Endo, 2017). If *A. gibbifrons* shares resource needs and natural enemies with *A. flavomarginatum*, it may outcompete *A. flavomarginatum* via direct or indirect competition, but these relationships have never been investigated.

To understand the interactions between these two species, we used trap nests to compare resource use and natural enemies under field conditions in Hyogo Prefecture, Japan. Trap nests are artificial nesting resources (e.g., bamboo canes) set out by researchers for solitary bees and wasps that nest in cavities (Fig. 1), which are appropriate for investigating their life histories, prey resources and parasitoids (Krombein, 1967; Staab et al., 2018). This approach is well suited to these congeners given their abundance and known use of trap nests in Hyogo Prefecture (Endo, 2017). We aimed to determine whether these congeners share nest and prey resources and parasitoid species.

MATERIALS AND METHODS

Study site

The study sites were located in Kitaike, Amida-cho, Takasago, Hyogo, Japan (34°47'N, 134°47'E, above sea level 15–20 m) and monitored in June–October 2019 (Tsujii, 2020). Average monthly temperature ranged from 19.6 to 28.1°C, average monthly humidity ranged from 74 to 83%, and total precipitation was 717 mm during the period studied (Himeji Meteorological Station; 34°50'N, 134°40'E, above sea level 38.2 m). The study site included paddy fields and secondary forest and the surveys were carried out along a 700-m-long forest edge. The secondary forest was dominated by oaks (e.g., *Quercus variabilis* Blume and *Q. glauca* Thunb.) and bamboos [*Phyllostachys edulis* (Carrière) Houz. and *P. nigra* (Lodd. ex Loud.) Munro var. *henonis* (Mittford) Stapf ex Rendle].

Species studied

Three species of *Anterhynchium*: *A. flavomarginatum*, *A. melanopterum* Yamane, 1981 and *A. gibbifrons*, are recorded in



Fig. 1. Trap nests used to study two species of *Anterhynchium* in central Japan. Each trap box contained 12 bamboo canes.

Japan (Yamane, 1990; Yamane & Murota, 2015). *Anterhynchium flavomarginatum* is the most abundant of the three and also occurs throughout East and Southeast Asia (Yamane, 1990; Yamane & Terayama, 2016). *Anterhynchium flavomarginatum* has been frequently collected in our study area (Endo, 2017). *Anterhynchium melanopterum* is a rare species in Japan and is also found in South Korea and China (Yamane, 1990; Yamane & Murota, 2015; Yamane & Terayama, 2016). This species has never been recorded in our study area. *Anterhynchium gibbifrons* was described based on specimens obtained from central Japan (Yamane & Murota, 2015) and initially considered as endemic (Murota & Yamane, 2015). However, multiple lines of evidence indicate that *A. gibbifrons* has recently been unintentionally introduced to Japan (Watanabe et al., 2020). Specifically, Ohkusa (2019) discovered a specimen of *A. gibbifrons* collected from South Korea in 1974, substantially predating the oldest specimen recorded in Japan, collected in 2007 (Endo, 2017). In addition, records of this species have been increasing across a wide area in southwestern Japan since 2015 (Ohkusa, 2015; Kawashima, 2016; Komeda, 2016; Nakamura, 2020; Watanabe et al., 2020; Ito et al., 2021), following the publication of the species description (Yamane & Murota, 2015). Finally, at least four other bamboo-associated insects, *Xylocopa tranquebarorum tranquebarorum* (Swederus, 1787) (Hymenoptera: Apidae), *Sinibotys butleri* (South, 1901) (Lepidoptera: Crambidae), *Platylomia pieli* Kato, 1938 (Hemiptera: Cicadidae) and *Hierodula* sp. (Mantodea: Mantidae), have been unintentionally introduced to Japan via bamboo products (Okabe et al., 2010; Mano & Takasaki, 2011; Hayashi & Usui, 2017; Sakurai et al., 2018). Given that *A. gibbifrons* typically nests in dead bamboo canes (Murota & Yamane, 2015; Endo, 2017), it is possible that it was introduced via bamboo products. An extensive trap nest survey was conducted in our study area in 2005, with no detections of *A. gibbifrons* (T. Endo & Y. Nishimoto, unpubl. data). However, the species has been collected frequently in the area studied since 2011 (T. Endo & N. Ijiri, unpubl. data). Thus, *A. gibbifrons* presumably invaded the study area during 2005–2011.

The cavity nesting behaviour of *A. flavomarginatum* and *A. gibbifrons* (Figs 2 and 3) is described by Iwata (1975) and Murota & Yamane (2015), respectively. First, the female wasp lays an egg

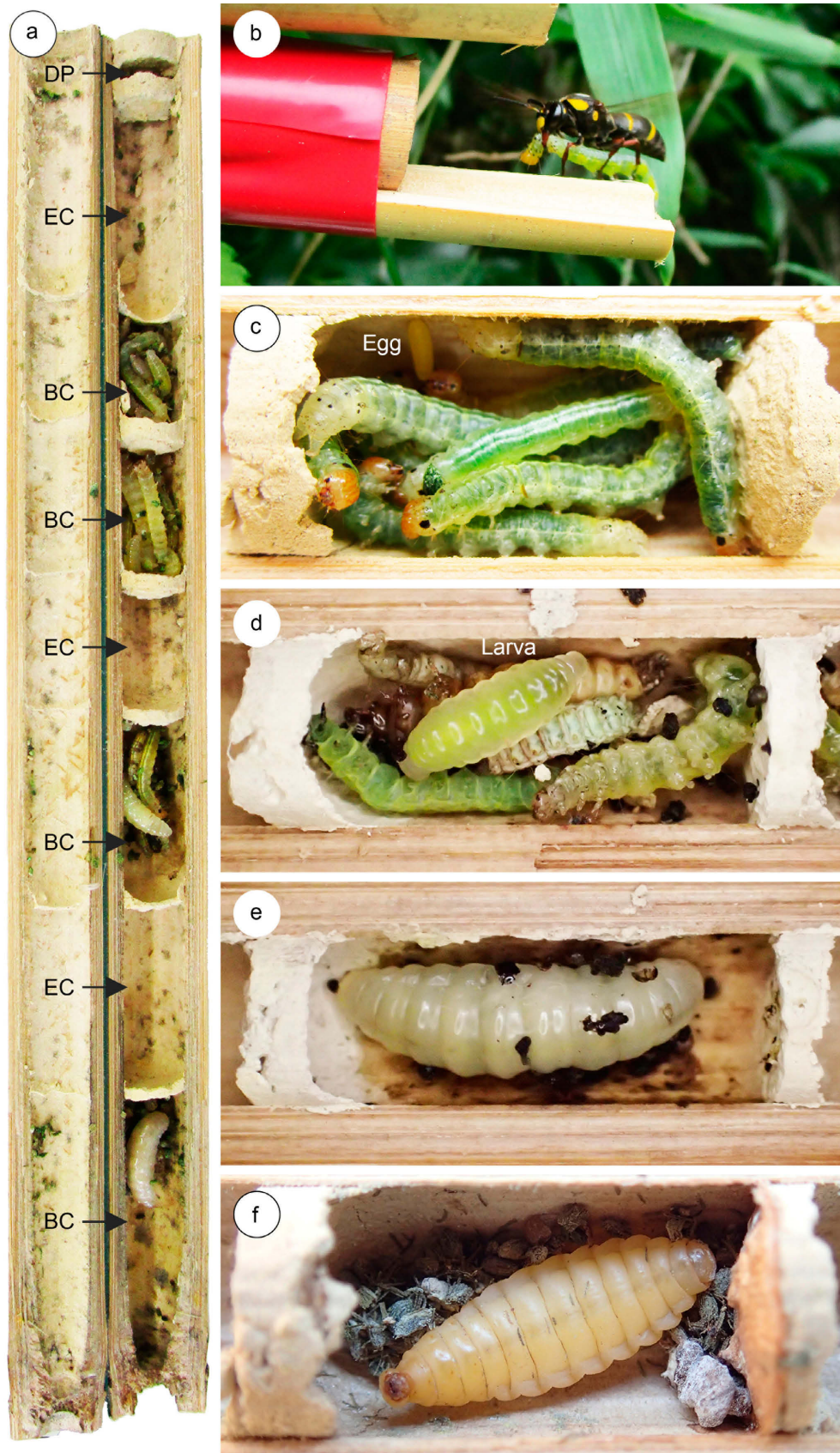


Fig. 2. The nests, developmental stages and prey of *Anterhynchium flavomarginatum*. (a) Representative architecture of a nest of *A. flavomarginatum* constructed in a bamboo cane (cross section). Bamboo canes were always placed horizontally in the trap boxes (see Fig. 1; this photograph is rotated through 90° counter-clockwise). This nest is composed of four brood cells (BC) and three empty cells (EC). All cells are separated by mud walls and the cavity entrance is typically sealed with a double mud plug (DP). (b) An adult female wasp carrying a caterpillar into a bamboo cane. (c) An egg hanging from the ceiling of the brood cell and caterpillars provided by the mother wasp. (d) A middle instar wasp larva feeding on caterpillars in a brood cell. (e) A late-instar wasp larva in a brood cell. (f) A wasp prepupa in a brood cell.



Fig. 3. The nests, developmental stages and prey of *Anterhynchium gibbifrons*. (a) Representative architecture of a nest of *A. gibbifrons* (cross section; see Fig. 2 for a description of cane orientation). This nest is composed of four brood cells (BC) and four empty cells (EC). All cells are separated by mud walls and the cavity entrance is typically sealed with a double mud plug (DP). (b) An adult female wasp carrying a caterpillar into a bamboo cane. (c) An egg hanging from the ceiling of a brood cell and caterpillars provided by the mother wasp. (d) A middle instar wasp larva feeding on caterpillars in a brood cell. (e) A late-instar wasp larva consuming prey in a brood cell. (f) A wasp prepupa in a brood cell.

within a cavity, such as a tunnel created by wood-boring insects or a hollow plant stem (Iwata, 1975; Murota & Yamane, 2015). Next, she hunts for lepidopteran larvae, permanently paralyzes them using her ovipositor and carries them to the cavity (Figs 2b and 3b; Iwata, 1975; Murota & Yamane, 2015). Once 3–21 larvae have been stored within the cavity, she seals the entrance using mud, at which point the cavity is referred to as a ‘brood cell’ (Fig. 2; Iwata, 1975). Female wasps typically create multiple brood cells separated by mud partitions (i.e., a nest; Figs 2a and 3a; Iwata, 1975; Murota & Yamane, 2015). Typically, intercalary and vestibular cells are also created, which are empty (Figs 2a and 3a; Krombein, 1967; Iwata, 1975; Murota & Yamane, 2015). Eggs of both *A. flavomarginatum* and *A. gibbifrons* (Figs 2c and 3c) hatch within a few days and the larvae consume the stored lepidopteran larvae and grow rapidly (Figs 2d, 2e, 3d and 3e). Although *A. flavomarginatum* prey on the larvae of several species of leaf-rolling caterpillars (Lepidoptera: Crambidae, Pyralidae and Tortricidae; Iwata, 1975; Itino, 1992), the prey species of *A. gibbifrons* are unknown. Immature forms of both species are hosts for multiple parasitoid species (Coleoptera, Diptera and Hymenoptera; Iwata, 1975; Endo, 2017), but the percentage parasitism by both species has not been compared.

Trap nests

A total of 12 bamboo canes (four replicates of each for three inner diameter classes: 5–7, 8–12 and 13–16 mm) were placed inside a plastic box (a ‘trap box’; 250 × 130 × 330 mm) to protect them from rain (Fig. 1; Tsujii, 2020). All trap nests (bamboo canes) were 200 mm in length, with one end open and the other closed at a node. Prior to placing the canes inside the trap boxes, each cane was split into two halves longitudinally and taped back together. This allowed easy examination of the contents of brood cells by simply opening the canes in the field. Each trap box was fixed to the trunk of a tree by string 1.5 m above the ground. In total, 48 trap boxes, each with 12 canes, were placed in a line along the forest edge at the study site on June 9 and 15 2019, spaced at 10-m intervals. No trap boxes were placed within 10 m of a residential area.

Field surveys

Traps were checked twice weekly from June to October 2019 (Tsuji, 2020). We first checked for the presence of insects or nests in each cane by probing with a thin grass stem. When canes were found to be occupied, they were opened to allow for insect identification. When canes were occupied by either species of *Anterhynchium*, we photographed the nests using a digital camera (IXY210, Canon) and recorded the number of brood and empty cells, larval developmental stage and presence of parasitoids. Number of brood cells and developmental stages of larvae were only recorded once the cavity entrance had been sealed with mud or nesting activity had otherwise ceased. We also measured the fresh weight of the prey stored in the brood cells to the nearest 0.01 g using a portable electronic scale (MH-500, Zime). The weights of consumed prey, parasitoids and wasp larvae were not measured. In addition, we photographed prey for species identification. The lepidopteran and wasp larvae in each brood cell were counted.

Any ant colonies found within the trap nests were removed, as *Anterhynchium* are known to avoid ants (Miyano & Yamaguchi, 2001). Once a cane was used for nesting by *Anterhynchium* or another species of cavity-nesting bee or wasp, a new cane of identical diameter was added to the box. Thus, nesting resources were kept constant over the period of the study. If nesting females were present upon trap box inspection, we waited until the insect had left to avoid disruption.

Identification of wasps, prey and parasitoids

Anterhynchium species were identified based on prepupal body colour; *A. gibbifrons* are more orange than *A. flavomarginatum* (Tsuji & Endo, 2019). The sex of individuals of both species was determined based on the number of spots on the ventral abdomen of the prepupae; males have two spots on the 9th abdominal segment and females have a total of six spots (two each on the 7th, 8th and 9th segments; K. Gôukon, personal communication). Lepidopteran larvae were identified using field photographs. They were first sorted into morphological species based on external characters, including the size and colour of patterns on the head and body. They were then identified to the family, subfamily, genus or species level based on morphology, for example the presence of spots and number of spines (Solis, 2006; Yasuda, 2010; Komai et al., 2011; Yasuda, 2012; Passoa, 2014; Yasuda, 2014). Lepidopteran larvae on plants at the study site were also collected for comparison with the prey. Female moths were also collected at the study site and their larvae were reared from eggs obtained from females kept in the laboratory at 25°C. Both collected and reared specimens were compared with the prey.

In addition, partial sequences of the mitochondrial COI gene were used to identify the prey of *A. gibbifrons* (i.e., DNA barcoding). DNA was extracted from prey (n = 6), a crambid species found on bamboo leaves at the study site (n = 2) and an adult *Demobotys pervulgalis* (Hampson, 1913) (Lepidoptera: Crambidae) collected at the study site (n = 1) and from a different location (n = 1). Given that this species of moth was common at the study site, it was assumed to be the prey of *A. gibbifrons*. Whole larvae and a leg of adults were immersed in propylene glycol and stored at 4°C until subsequent DNA extraction. The methodology used for DNA extraction, PCR amplification and sequencing is described in Matsui et al. (2021). All obtained DNA sequences were deposited in the GenBank database (<https://www.ncbi.nlm.nih.gov/genbank/>; accession number: LC652646–LC652655). The scientific names of Crambidae species followed Nuss et al. (2021). Finally, parasitoids were identified to species level based on the morphology of larvae, pupae or adults (Kurahashi, 1970; Liu et al., 1995; Makino et al., 2006, 2011).

Data analyses

Generalised linear models (GLMs) with a Poisson error distribution and log link function were used to assess the relationships of wasp species and nesting period with nest architecture, specifically the number of brood and empty cells within a nest. Wasp species and nesting period were fixed effects, and the total number of cells and number of brood and empty cells were response variables. GLMs with a Gaussian error distribution and identity link were then used to assess relationships among species, nesting period and nest inner diameter. Wasp species and nesting period were fixed effects, and the inner diameter of the cane was used as the response variable. P-values were adjusted for multiple comparisons using the Benjamini-Hochberg procedure (Benjamini & Hochberg, 1995) in emmeans (ver. 1.5.3) and multcomp (ver. 1.4.15) R packages.

Generalised linear mixed models (GLMMs) with a Poisson error distribution and log link function were used to assess relationships among species, nesting period, wasp sex and number of prey. Species, nesting period and sex were fixed effects and the number of prey larvae and species per brood cell were response variables. Individual bamboo canes were random effects. GLMMs with a Gaussian error distribution and identity link were then used to assess relationships between the same fixed effects and prey weight. GLMMs were constructed using the packages lme4 (ver. 1.1.26) and lmerTest (ver. 3.1.3). P-values were adjusted for multiple comparisons using the Benjamini-Hochberg pro-

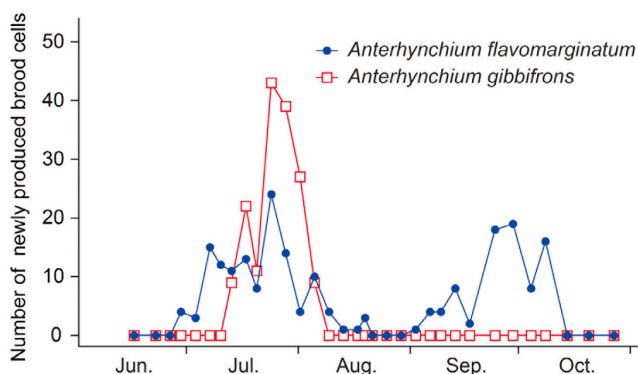


Fig. 4. Seasonal changes in the number of newly produced brood cells. Blue circles and red squares indicate *Anterhynchium flavomarginatum* and *A. gibbifrons*, respectively.

cedure (Benjamini & Hochberg, 1995) in emmeans (ver. 1.5.3) and multcomp (ver. 1.4.15) R packages.

Fisher’s exact tests were used to compare the percentage of brood cells of the two wasps attacked by parasitoids. P-values were adjusted for multiple comparisons using the Benjamini-Hochberg procedure (Benjamini & Hochberg, 1995). Binomial tests were also used to compare the observed wasp sex ratio (the proportion of males) with a 1 : 1 ratio.

All analyses were performed using R statistical analysis software (ver. 4.0.3; R Core Team, 2020).

RESULTS

Seasonal patterns in nesting activity

Of the 950 bamboo canes, 31.3% were used by cavity-nesting bees (3 species) and wasps (10 species). *Anterhynchium flavomarginatum* nested in 70 canes (total of 207 brood cells) and *A. gibbifrons* nested in 50 canes (160 brood cells). *Anterhynchium flavomarginatum* produced two generations over the period of the study (first nesting period, late June–mid August, 127 brood cells in 48 nests; second nesting period, early September–early October, 80 cells in 22 nests; Fig. 4), whereas *A. gibbifrons* produced only one generation (nesting period, mid July–early August; Fig. 4). Although *A. gibbifrons* began nesting two weeks after *A. flavomarginatum* started, the nesting period of *A. gibbifrons* overlapped that of the first nesting period of *A. flavomarginatum* (Fig. 4). In *A. flavomarginatum*, 12.6% of the larvae (16 of 127 cells) produced during the first nesting period pupated and emerged during July–August 2019, whereas 28.3% (36 of 127 cells) from the first nesting period overwintered as prepupae. The remaining larvae were killed by parasitoids or other factors. The larvae produced during the second nesting period overwin-

tered as prepupae and emerged as adults in May–June 2020. In *A. gibbifrons*, no larvae pupated or emerged during July–August 2019, but overwintered as prepupae and adults emerged in May–June 2020. Therefore, *A. flavomarginatum* and *A. gibbifrons* showed partial bivoltinism and univoltinism, respectively.

The sex ratio (proportion of males) among the prepupae produced in the first and second nesting periods of *A. flavomarginatum* was 0.87 (n = 62) and 0.62 (n = 60), respectively. The sex ratio in *A. gibbifrons* was 0.80 (n = 103). The sex ratio in the first nesting period of *A. flavomarginatum* and *A. gibbifrons* was male-biased and significantly different from a 1 : 1 ratio (binomial tests, p < 0.001). The sex ratio in the second nesting period of *A. flavomarginatum* was not significantly different from the 1 : 1 ratio (p > 0.05).

Nest architecture and prey

There were no significant differences in the number of brood cells, empty cells or inner diameter of the canes used by the two species (Table 1). In both species, daughters (female offspring) were provisioned with a greater weight and number of prey than sons (male offspring) (Table 2). The diversity of prey species per brood cell did not differ significantly between species or sex, although the number of prey species was significantly different for sons in the first nesting period of *A. flavomarginatum* and sons of *A. gibbifrons* (Table 2).

Anterhynchium flavomarginatum collected the larvae of 14 species of moths (Lepidoptera: Crambidae, Pyralidae, Tortricidae) as prey for their larvae (Table 3). The prey composition of the first nesting period was different from that of the second nesting period; *Circobotys* sp. (Lepidoptera: Crambidae) were used exclusively in the first nesting period but not in the second nesting period (Table 3). *Anterhynchium gibbifrons* used the larvae of a single moth species in the family Crambidae (subfamily Pyraustinae). This species is morphologically identical to a crambid species that was observed rolling or tying bamboo leaves together at the study site. These larvae were morphologically identical to those reared from eggs obtained from female adults of *Demobotys pervulgalis*. Furthermore, a 562 base pair sequence of the COI obtained from *A. gibbifrons* prey in the nests was identical to the sequences obtained from the field-collected larvae (99.8–100.0% matched) and *D. pervulgalis* adults (99.8–100.0% matched). Therefore, *A. gibbifrons* exclusively used the larvae of *D. pervulgalis* as prey and did not share any prey species with *A. flavomarginatum*.

Table 1. The nest architecture of *Anterhynchium flavomarginatum* and *A. gibbifrons*. First – first nesting period; Second – second nesting period. n – the number of canes used by *Anterhynchium* wasps for nesting. * – p < 0.05 (GLMs); n.s. – p > 0.05 (GLMs). Different letters indicate significant differences between wasp species and generations (GLMs with the Benjamini-Hochberg procedure, p < 0.05).

	<i>A. flavomarginatum</i>		<i>A. gibbifrons</i> (n = 50)	Statistical test
	First (n = 48)	Second (n = 22)		
Total number of cells [median (range)]	6 (1–9)	5 (3–9)	6 (1–9)	n.s.
Number of brood cells [median (range)]	2 (1–6)	4 (1–9)	3 (1–5)	n.s.
Number of empty cells [median (range)]	3 (0–5) a	2 (0–3) b	3 (0–5) a	*
Inner diameter of used canes [mean ± SE]	10.0 ± 0.3	9.5 ± 0.4	10.3 ± 0.3	n.s.

Table 2. The total weight and number of prey per brood cell for *Anterhynchium flavomarginatum* and *A. gibbifrons*. n – the number of brood cells. The same letters indicate no significant difference (GLMMs, $p > 0.05$). The total weight and number of prey were determined for brood cells containing wasp eggs and early instars. For such cells, data only on those for which the sex of the wasp offspring could be identified at the prepupal stage were used in the analyses.

	<i>A. flavomarginatum</i>				<i>A. gibbifrons</i>	
	First nesting period		Second nesting period		Daughter (n = 21)	Son (n = 76)
	Daughter (n = 5)	Son (n = 44)	Daughter (n = 22)	Son (n = 30)		
Total weight of prey (mg) [mean ± SE]	798.0 ± 31.5 ab	424.0 ± 17.1 d	745.7 ± 23.5 b	406.3 ± 17.6 d	880.8 ± 42.4 a	595.4 ± 19.8 c
Number of prey [median (range)]	12 (8–15) p	5.5 (3–13) q	10 (6–19) p	6 (3–12) q	11 (6–15) p	7 (4–17) q
Number of species of prey [median (range)]	1 (1–3) xy	1 (1–5) x	1 (1–3) xy	1 (1–3) xy	1 (1–1) xy	1 (1–1) y

Parasitoids

One coleopteran, three dipteran and one hymenopteran species parasitized the *Anterhynchium* wasps (Table 4). Larvae of *Macrosiagon nasutum* (Thunberg, 1784) (Coleoptera: Ripiphoridae) parasitized wasp prepupae. Larvae of *Amobia distorta* (Allen, 1926) (Diptera: Sarcophagidae) were found feeding on wasp larvae and larvae of *Anthrax aygulus* Fabricius, 1805 (Diptera: Bombyliidae) parasitized wasp prepupae. Adults and larvae of *Megaselia* sp. (Diptera: Phoridae) fed on wasp eggs and larvae, respectively. Larvae of *Meliittobia* sp. (Hymenoptera: Eulophidae) parasitized wasp prepupae. Larvae of *Amobia distorta* and *Megaselia* sp. fed on moth larvae, as well as wasp larvae in brood cells. Among the six species, *Amobia distorta* was the most abundant (Table 4). *Macrosiagon nasutum*, *Amobia distorta* and *Megaselia* sp. attacked both *A. flavomarginatum* and *A. gibbifrons* (Table 4). The total percentage parasitism was higher in *A. flavomarginatum* than *A. gibbifrons* (Fisher’s exact test, $p < 0.05$; Table 4). The percentage parasitism by *Amobia distorta* was also higher in *A. flavomarginatum* than *A. gibbifrons* ($p < 0.05$), but those of *M. nasutum* and *Megaselia* sp. did not significantly differ between the two species ($p > 0.05$; Table 4).

DISCUSSION

We compared resource use and natural enemies of a native and supposedly non-native species of *Anterhynchium*. We found overlap in nesting period between the two, similar nest architecture and inner cane diameter preference, but a completely independent use of prey. Therefore, *A. gibbifrons* potentially competes with *A. flavomarginatum* for nesting resources, but not prey, in the area studied. Three parasitoid species attacked both *Anterhynchium* species, suggesting that *A. gibbifrons* could indirectly affect *A. flavomarginatum* via shared parasitoids.

Nest architecture and provision of prey

Nests in terms of the inner diameter of the bamboo cane and number of brood and empty cells were similar for the two species. Although we ensured a constant and ample supply of nesting material at the study site, suitable natural nesting resources, such as wood cavities, are generally limited under natural conditions (Krombein, 1967). Therefore, it is reasonable to assume that these species may compete for nest sites under natural conditions.

Adult females are larger than males in both species (*A. flavomarginatum* body length: female, 15.0–20.5 mm, male, 11.0–15.5 mm; *A. gibbifrons*: female, 18–20 mm,

Table 3. Prey species and composition for *Anterhynchium flavomarginatum* and *A. gibbifrons*. n – number of brood cells in which the prey were examined. * – indicates specimens that could not be identified. Data for prey consumed by wasps and parasitoids were excluded.

Prey		<i>A. flavomarginatum</i>				<i>A. gibbifrons</i>	
		First nesting period (n = 116)		Second nesting period (n = 73)		(n = 153)	
		Number of prey	Number of brood cells	Number of prey	Number of brood cells	Number of prey	Number of brood cells
Crambidae	<i>Anania vicinalis</i> (South, 1901)	1	1	0	0	0	0
	<i>Circobotys</i> sp.	362	57	0	0	0	0
	<i>Demobotys pervulgalis</i> (Hampson, 1913)	0	0	0	0	1264	153
	<i>Diaphania indica</i> (Saunders, 1851)	0	0	13	8	0	0
	<i>Haritalodes derogata</i> (Fabricius, 1775)	57	14	39	10	0	0
	<i>Herpetogramma luctuosalis</i> (Guenée, 1854)	134	30	307	45	0	0
	<i>Herpetogramma rudis</i> (Warren, 1892)	31	9	0	0	0	0
	<i>Mecyna tricolor</i> (Butler, 1879)	92	20	0	0	0	0
	<i>Palpita nigropunctalis</i> (Bremer, 1864)	9	6	74	19	0	0
	<i>Pyrausta</i> sp.	8	2	0	0	0	0
	<i>Spoladea recurvalis</i> (Fabricius, 1775)	63	12	153	14	0	0
	Pyraustinae sp. A	49	13	10	2	0	0
	Pyraustinae unidentified spp.*	2	1	0	0	0	0
	Pyralidae	Phycitinae sp.	9	2	0	0	0
Tortricidae	Tortricidae sp. A	15	9	0	0	0	0
	Tortricidae sp. B	1	1	0	0	0	0

Table 4. Parasitoids of *Anterhychium flavomarginatum* and *A. gibbifrons*. First – first nesting period; Second – second nesting period. n – the number of brood cells. A – adult; L – larva; HE – host egg; HL – host larva; HPP – host prepupa; ML – moth larva. * – $p < 0.05$ (Fisher's exact tests); n.s. – $p > 0.05$ (Fisher's exact tests). The same letters indicate no significant difference (Fisher's exact tests with the Benjamini-Hochberg procedure, $p > 0.05$).

Parasitoid	Order	Family	Species	Stage	Food	Percentage parasitism (%)			Statistical test
						<i>A. flavomarginatum</i>		<i>A. gibbifrons</i> (n = 160)	
						First (n = 127)	Second (n = 80)		
Coleoptera	Ripiphoridae	<i>Macrosiagon nasutum</i> (Thunberg, 1784)	L	HPP	3.9	0	0.6	n.s.	
Diptera	Sarcophagidae	<i>Amobia distorta</i> (Allen, 1926)	L	HL, ML	10.2 a	17.5 a	3.1 b	*	
	Bombyliidae	<i>Anthrax aygulus</i> Fabricius, 1805	L	HPP	0.8	0	0	n.s.	
	Phoridae	<i>Megaselia</i> sp.	A/L	HE, HL, ML	3.1	1.3	3.1	n.s.	
Hymenoptera	Eulophidae	<i>Melittobia</i> sp.	L	HPP	4.7 p	0 pq	0 q	*	
Total						22.8 x	18.8 x	6.9 y	*

male, 14–19 mm; Yamane & Terayama, 2016). Female offspring were provided with a greater amount of prey than male offspring by both species. Cowan (1991) suggests that the amount of prey provided is determined primarily by memory of the sex of the deposited egg in eumenine wasps. Like other eumenine species, *A. flavomarginatum* and *A. gibbifrons* may also adjust the amount of prey provided according to the sex of the offspring.

Prey use

Generally, most eumenine wasps are generalists; few are specialists (Krombein, 1967; Cowan, 1991). These wasps generally prey on the larvae of moths or beetles (Cowan, 1991). For example, many species of the genus *Symmorphus* Wesm., 1836 prey on the larvae of several weevil and leaf beetle species (i.e., generalists; Gathmann & Tschamtké, 1999; Budriené, 2003), whereas *Symmorphus decens* (Kostylev, 1940) exclusively hunts the larvae of a single leaf beetle species (i.e., specialists; Hamanishi, 1996). Species in other genera, such as *Ancistrocerus* Wesm., 1836 and *Discoelius* Latreille, 1809, typically prey on the larvae of several moth species (Itino, 1992; Harris, 1994; Dang & Nguyen, 2019). We identified the larvae of 14 and 1 moth species as prey of *A. flavomarginatum* and *A. gibbifrons*, respectively. Larvae of the moth families Crambidae, Pyralidae and Tortricidae are reported as prey of *A. flavomarginatum* (Iwata, 1975; Itino, 1992). Although the prey of *A. gibbifrons* was unknown, our results indicate it is a specialist and that *A. flavomarginatum* is a generalist in the area studied.

The composition of prey *A. flavomarginatum* differed in the two nesting periods. This indicates that females use the most abundant prey during each nesting period. Although these females used the larvae of 14 species of moth as prey, they also showed a tendency to provide several larvae of only a few or one species within a single brood cell. Therefore, individuals of *A. flavomarginatum* may select for particular species, based on prey availability in order to increase foraging efficiency around nest sites. This type of specialist behaviour within a generalist species is reported in other wasp and bumblebee species (Heinrich, 1976; Cowan, 1991; Powell & Taylor, 2017).

When two species share a potential resource, both or either species can shift their diet niche and so partition the

resource (Begon et al., 2006; Kishi & Tsubaki, 2014). For example, *A. flavomarginatum* may avoid the prey used exclusively by *A. gibbifrons*, and/or *A. gibbifrons* may have narrowed its range of prey use. However, given how recently *A. gibbifrons* is believed to have invaded the study site, it is unlikely that enough time has passed to drive a shift in diet between these two species. Rather, it seems more likely that *A. gibbifrons* simply utilizes prey that is not used by the native generalist species, i.e., it occupied an empty niche. To test if *A. gibbifrons* has indeed occupied an empty niche, further investigations are required in areas where *A. gibbifrons* does not co-occur with *A. flavomarginatum*; alternatively, the prey preferences of *A. flavomarginatum* and *A. gibbifrons* could be tested in a laboratory setting.

Parasitoids

Nine and four parasitoid species are reported parasitizing *A. flavomarginatum* and *A. gibbifrons*, respectively (Iwata, 1975; Itino, 1986; Yamane, 1990; Makino et al., 2006; Endo, 2017; Maeta & Gôkon, 2019). Although the percentage parasitism of the former species is known (Itino, 1986), this is not the case for the latter species. Here, five and three species were found to parasitize these species, respectively. No species was found to exclusively attack *A. gibbifrons*. Because three parasitoid species (*M. nasutum*, *Amobia distorta* and *Megaselia* sp.) attacked both species at the study site, *A. gibbifrons* could indirectly affect the native *A. flavomarginatum* via shared parasitoids (i.e., apparent competition). For example, *A. gibbifrons* may have increased the population of *Amobia distorta* prior to the second nesting period of *A. flavomarginatum*, thereby contributing to the observed increase in parasitism between the first and second nesting periods (from 10.2% to 17.5%). However, we note that the total percentage parasitism did not differ significantly between the first and second nesting periods of *A. flavomarginatum*. Therefore, any potential competition between these species via shared parasitoids may currently be relatively minor.

CONCLUSIONS

The solitary wasp *A. gibbifrons* may have been unintentionally introduced to Japan (Watanabe et al., 2020), although there is no strong evidence for such an introduction.

The distribution of *A. gibbifrons* is increasing throughout Japan (Ohkusa, 2015; Kawashima, 2016; Komeda, 2016; Nakamura, 2020; Watanabe et al., 2020; Ito et al., 2021). We demonstrated exclusive use of bamboo-feeding caterpillars by *A. gibbifrons* in an area in central Japan. We note that the non-native bamboo *P. edulis* present at our study site has been spreading throughout Japan (Someya et al., 2010; Shinohara et al., 2014), which could be aiding the spread of *A. gibbifrons*. We found that *A. gibbifrons* may indirectly affect *A. flavomarginatum* via shared nesting resources and enemies, but there is no evidence of competition for prey resources in the area studied. It is possible that *A. gibbifrons* may further interfere with *A. flavomarginatum* via disrupting nesting or reproductive behaviour, but we did not consider these direct interactions in this study. Further field observations could provide a more holistic understanding of both direct and indirect interactions between these two species.

ACKNOWLEDGEMENTS. This study was partially supported by a grant from the School of Human Sciences at Kobe College. We thank N. Ijiri and Y. Nishimoto for providing information on *A. gibbifrons*. We thank K. Utaka and K. Okuda for providing access to the study location. We are grateful to K. Gōkun for assistance in sexing immature wasps and thank M. Shibata, A. Nobori, Y. Goto, A. Iwai, H. Mochizuki, Y. Mori and T. Yoshimura for their assistance with field work.

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Received October 26, 2021; revised and accepted January 7, 2022
Published online February 14, 2022