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Impact of introduced honeybees, *Apis mellifera*, upon native bee communities in the Bonin (Ogasawara) Islands

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Abstract The Bonin (Ogasawara) Islands are oceanic islands located in the northwest Pacific, and have ten native (nine endemic) bee species, all of which are nonsocial. The European honeybee (*Apis mellifera*), which was introduced to the islands for apiculture in the 1880s, became naturalized in a few islands shortly after introduction. To detect the impact of the honeybees upon native bee diversity, we analyzed pollen harvest by honeybees and surveyed the relative abundance of honeybees and native bees on flowers on several islands. Both hived and feral honeybee colonies were active throughout the year, harvesting pollen of both native and alien flowers and from both entomophilous and anemophilous flowers. Honeybees strongly depended on the alien plants, especially during winter to spring when native melittophilous flowers were rare. From June to November, honeybees exhaustively utilized native flowers, which had originally been utilized and pollinated by native bees. On Chichi and Haha Islands, where human disturbance of forests has been severe, both native and alien flowers were dominated by honeybees, and native bees were rare or extinct even in well-conserved forests. In contrast, on Ani Island and Haha's satellite islands where primary forests were well conserved and honeybees were still uncommon or absent, native bees remained dominant. These results suggest that competition for nectar and pollen of the native flowers between honeybees and native bees favors honeybees on the disturbed islands, which are thoroughly invaded by alien nectariferous, sometimes aggressive, weedy plants.

Key words Oceanic island · Bee community · Introduced honeybee · Invasion · Pollination · Bonin Islands

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Introduction

The honeybee produces large colonies, and hence many foragers and a sophisticated communication system (Seeley 1985; Roubik 1991). Their competitive ability in foraging is superior to that of any solitary bee and even surpasses most social bees. The Africanized honeybee, which was introduced to tropical America, became the potential competitor of Neotropical bees, and shifts in resource use caused by colonizing Africanized honeybees may have led to a population decline in some Neotropical pollinators (Roubik 1978, 1991). The impact of the introduced honeybee upon native pollinators appears to have been more severe on oceanic islands, probably because native pollinator faunas on oceanic islands lack social bee species, which are frequently abundant pollinators on the continent. For example, Hawaii has 64 native bee species, all of which are solitary endemic colletid bees of the genus *Hylaeus* (Perkins 1901; Howarth and Mull 1992). The ancestor of the Hawaiian *Hylaeus* arrived in Hawaii probably by means of the simultaneous drifting of nesting sites and bees, and then radiated to form 64 species. A large proportion of the endemic entomophilous plants of Hawaii are thought to have coevolved with these small native bees. The absence of social bees on oceanic islands results from the low oversea dispersibility of social bee colonies. European honeybees were introduced into Hawaii for apiculture in 1857, and their offspring became naturalized throughout the islands (Messing 1991). After the introduction of the honeybees, the native bees have dramatically decreased (Cuddihy and Stone 1990), although competition between the feral honeybee and native bees has not yet been investigated in detail.

The Bonin Islands are oceanic islands, located 1000 km south of the mainland of Japan, and are endowed with a rich endemic flora and fauna. The flora of the Bonin Islands is composed of 260 flowering plant species, containing 112 endemic species and 2 endemic genera (Toyoda 1981). These islands have 10 native bee species, all of which are nonsocial and 9 of which are endemic (Hirashima 1989; Kato 1992). Adaptive radiation with characteristic speciation in plants is found in *Pittosporum* (4 species, Pittosporaceae), *Symplocos* (3 species, Symplocaceae), *Callicarpa* (3 species, Verbenaceae) and *Crepidiastrum* (3 species, Compositae) (Ono 1985; Nagamasu 1987; Kawakubo 1990; Ito and Ono 1990; Soejima et al. 1994; Ito 1998). Most of these endemic entomophilous plant species are thought to have coevolved with these endemic bees. The endemic plant genus, *Dendrocacalia*, was recently found to be dioecious, and its evolution may be related to pollination by endemic solitary bees (Kato and Nagamasu 1995).

The unique bee pollinator community of the Bonin Islands, however, is now endangered by the invasion of European honeybees, which were first introduced into the islands for apiculture in 1880 (Funakoshi 1990). Probably because of the absence of honeybee-hunting *Vespa* spp. (Matsuura and Sakagami 1973), European honeybees escaped from apiaries and naturalized even in primary forest in the Bonin Islands. A preliminary survey suggested that native bees have drastically declined on the islands where cultivated and feral honeybee colonies were abundant (Kato 1992). To detect the impact of honeybees upon the native bee community, we studied honeybee' pollen/nectar foraging and relative abundances of honeybees and native bees on flowers during a 1-year period on several islands in the Bonins. Measurements of pollen harvest by cultivated and feral honeybee colonies suggested seasonal changes in their dependence on pollen of alien and native plant species. Quantitative observations of flower-visiting bees on islands that have undergone different amounts of biological invasion demonstrated a clear density compensation between honeybees and native bees. Analyzing these data, we discuss how and when the honeybees compete with the native bees, and how the native bee fauna as well as the original plant–pollinator interactions can be conserved.

Materials and methods

Site

The Bonin (Ogasawara) Islands are located about 1000 km south of Tokyo (26°40′N–27°45′N) in the northwest Pacific Ocean (Fig. 1). The islands are typical oceanic islands that originated from early tertiary volcanic activity in the Izu–Ogasawara–Mariana Arc. They emerged above sea level at least 1 million years ago. The Bonin Islands are divided into three groups, the Muko, Chichi, and Haha Island groups (listed from north to south). These islands have a monsoon climate, with a long, dry summer and a mild winter. The increased rainfall in May and October–November is the result of a seasonal rain front. The warmth index (Kira 1976) is 215.0 (warmth index >180 and <240 refers to subtropical), with the lowest winter temperature seldom below 10°C (Shimizu 1983).

The Bonin Islands have a rich endemic flora. Among 309 native vascular plant species (71 ferns and 238 seed plants), 124 (2 ferns and 112 seed plants) are endemic species, and total endemics are 40.1% of the flora (Toyoda 1981). The islands have two endemic plant genera, *Dendrocacalia* (Asteraceae) and *Boninia* (Rutaceae), the latter of which is closely related to *Melicope* (including *Pelea*, a genus endemic to Hawaii). The number of native plant species that flower from October to February is small, and peaks from April to July (Shimizu 1983; Fig. 2).

Before human colonization in the 1880s, the Bonin Islands were originally covered with two types of primary forests, dry and wet forests (Shimizu 1989). A large area of primary forest, however, was cut for wood and for the cultivation of sugarcane from the 1880s to the 1940s. The remaining natural forests are now fragmentarily distributed on each island (Fig. 1). The wet forests remain only at high altitudes (>400 m) of Haha Island, and are dominated by *Elaeocarpus photiniifolius* and accompanied by *Ardisia sieboldii* and an endemic genus, *Dendrocacalia*. The dry forests, usually formed on rocky habitats, are found on both the Chichi and Haha Island groups. The dry forests on the Chichi Island group are well conserved in Ani Island, and are dominated by *Distylium lepidotum* and *Schima mertensiana*, both of which are associated with many endemic plant species (Shimizu 1992). On Chichi Island, only fragmented areas of primary dry forest remain. Dry forests in the Haha Island group can be found mainly on the satellite islands around Haha Island, and are dominated by *Rhaphiolepis wrightiana* and *Livistona chinensis* var. *boninensis* (Shimizu 1994). Other parts of the Bonin Islands that experienced human disturbance such as cutting and cultivation from 1880 to 1945 to a greater or lesser degree are now regenerating as secondary forests dominated by alien trees such as *Pinus luchuensis, Leucaena leucocephala*, *Bishofia javanica*, *Ficus microcarpa*, and *Casuarina equisetifolia* or native trees such as *Schima mertensiana* (Shimizu 1989). Currently, only the islands of Chichi and Haha are inhabited by humans.

Ten bee species are indigenous to the Bonin Islands, of which nine are endemic to the islands (Table 1). All native bees are solitary and nest in shoot/wood cavities (Kato 1992). In 1880, three colonies of European (Italian) honeybees, *Apis mellifera*, were introduced from America to Chichi Island (Funakoshi 1990). These colonies reproduced there, and their offspring increased rapidly on Chichi and Haha. Apiculturists introduced nectar and pollen plants such as *Leucaena leucocephala*, *Thunbergia alata*, and *Mimosa* sp. in the 1880s, and other nectariferous plants were also introduced at a later date. Some of these alien plants have become naturally established on these islands. Now, many honeybee colonies are cultivated on Chichi and Haha Islands, and feral honeybee colonies are found in the forest on Chichi, Haha, and Ani Islands.

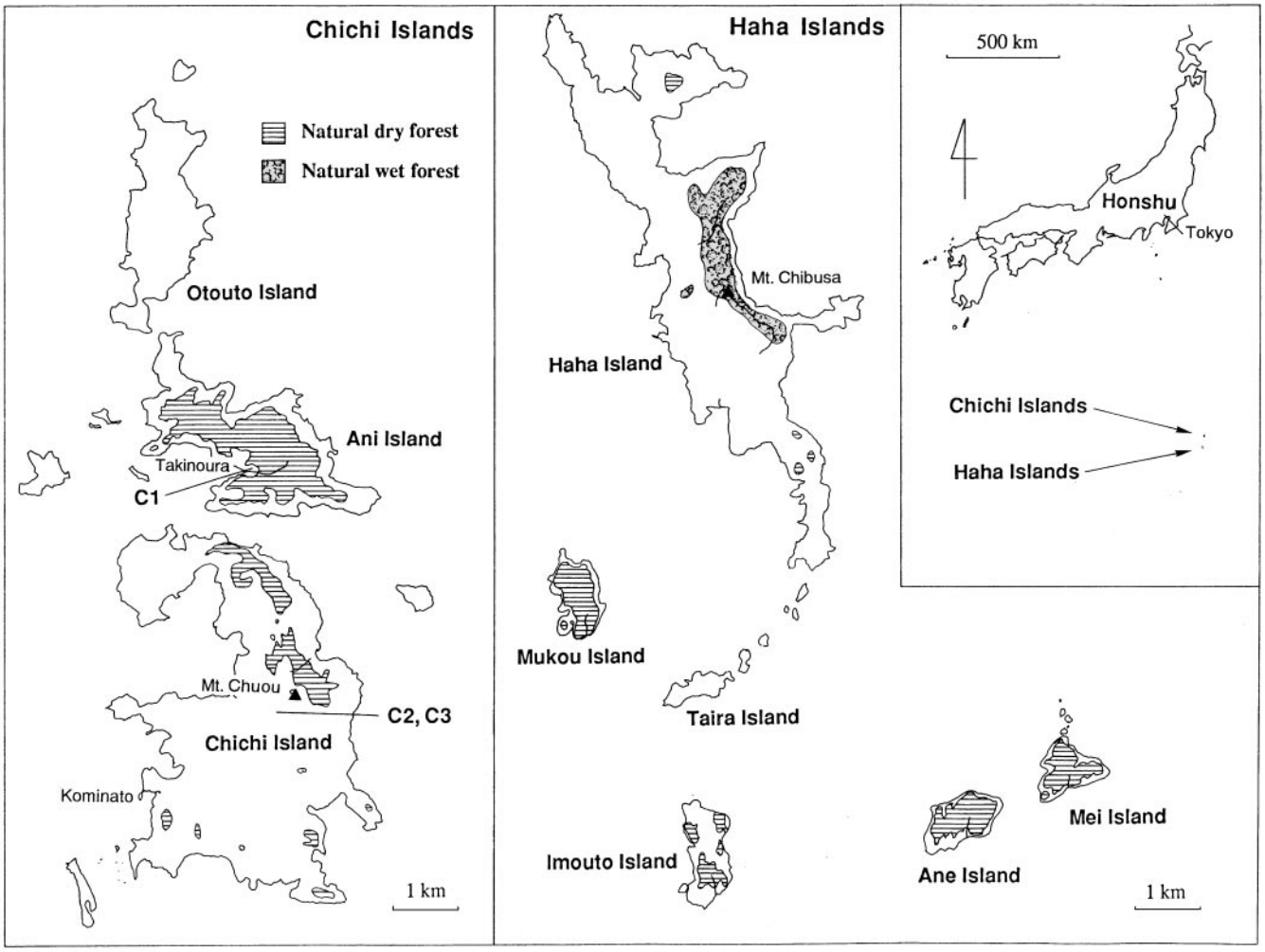


Fig. 1. Map of the Bonin Islands shows the location of Chichi and Haha Islands (*right inset*), the distribution of natural forests within Chichi (*left*) and Haha Island (*middle*) groups, and the sites of honeybee colonies studied for pollen harvest (C1, C2, and C3). Routine routes of flower visitor survey are also shown

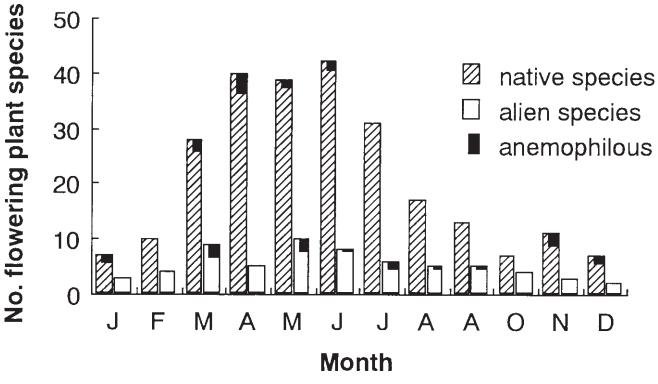


Fig. 2. Flowering phenology of native and alien plant species (excluding Graminae and Cyperaceae) in the Bonin Islands. (After Toyoda 1981)

Honeybee pollen and nectar foraging

The seasonal changes in species composition of honeybee pollen loads were studied for a feral colony on Ani Island and for two managed colonies on Chichi Island. The colony on Ani Island (C1) was found in the trunk hollow of a live tree (*Hernandia sonora*) in a coastal forest at Takinoura (see Fig. 1). The colony was found in July 1991 and remained until at least 1997. The two colonies studied on Chichi Island (C2, C3) had been established in a mango orchard (about 0.5 ha) near Mt. Chuou for apiculture by a farmer, Mr. Tanaka. Among the honeybee colonies cultivated on Chichi Island, these two colonies were located nearest to natural dry forests. C2 and C3 were destroyed by pyralid wax moths (*Galleria* sp.) in July 1995 and December 1996, respectively. The pollen harvest data for C2 and C3 were combined for analyses.

The number of worker bees leaving and returning per minute was recorded once at approximately 0900 (and also

Table 1. List of bee species on Bonin Islands, with their status, nest sites, range of body length (mm) and tongue length (mm), active period, and distribution records

Family	Species	Code	Status[a]	Nest site[b]	Body length (N)	Tongue length[c] (N)	Active period	Records[d]			
								A	C	H	S
Colletidae	*Hylaeus boninensis*	H1	e	s	5.5–7.0[e]	?	May–Aug.	?/−	+/−	+/−	−/−
	H. incomitatus	H2	e	s	4.5–5.3 (3)	1.5–1.6 (3)	Apr.–Sep.	+/+	+/−	+/−	+/+
	H. yasumatsui	H3	e	s	4.1–5.4 (3)	1.1–1.2 (3)	Apr.–Sep.	+/+	+/−	+/+	?/−
	H. ikedai	H4	e	s	3.0–4.0 (3)	0.9–1.0 (3)	Apr.–Sep.	+/+	+/−	+/+	+/+
Megachilidae	*Lithurge ogasawarensis*	LI	e	s	11.4–13.2 (3)	5.6–8.0 (3)	Jun.–Sep.	+/+	+/−	+/+	+/+
	Megachile asahinai	M1	e	s	10.5–12.1 (2)	4.8–5.0 (2)	Jun.–Nov.	+/+	+/−	+/−	+/+
	M. rixator sakishimana	M2	n (or a)	s	8.4–10.8 (3)	4.5–4.7 (3)	Jun.–Nov.	−/+	−/−	−/−	−/+
	Heriades fulvohispidus	HE	e	s	3.9–6.0 (3)	1.6–2.0 (3)	Jun.–Aug.	+/+	+/−	+/−	?/−
Anthophoridae	*Ceratina boninensis*	CE	e	s	4.8–7.0 (3)	2.3–3.0 (3)	Jun.–Sep.	+/+	+/−	+/+	+/+
	Xylocopa ogasawarensis	X1	e	w	20.5–25.3 (2)	7.1–7.5 (2)	Mar.–Nov.	+/+	+/+	+/+	+/+
	X. sonorana	X2	a	w	22 (1)	4.6 (1)	?	−/−	−/−	−/−	−/+
Apidae	*Apis mellifera*	AP	i	h	12.5–12.8 (3)	5.3–5.4 (3)	Jan.–Dec.	−/+	−/+	−/+	−/−

[a] a, alien; e, endemic, native; n, nonendemic, native; i, introduced
[b] h, tree hollows; s, preexisting cavities such as stem hollows or beetle burrows; w, tree burrows bored by the nesting bee itself
[c] length of glossa + mentum
[d] A, Ani Is.; C, Chichi Is.; H, Haha Is.; S, Haha's satelite islands. Indigenous (Hirashima 1989) and present (our study) distribution records are shown separated by slash (/). + and − denote presence and absence of bee species, respectively
[e] After Ikudome (1989)

at 1500 for C1). Ten returning honeybees, some of which had pollen loads, were collected for analysis. These observations were made at monthly intervals for C1 and at approximately 2-weekly intervals for C2 and C3 from March 1995 to February 1996. One of the two pollen loads of each pollen-foraging worker collected from the nests was detached from the corbicula and dried. Each pollen load was put in a microtube, heated in 10% KOH, and acetolyzed. Acetolysis of pollen grains followed the standard method (Erdtman 1960), and grains were mounted in silicon oil for light microscopy. Pollen was identified by species after Huang (1972).

We monitored flowering phenology of native and alian plants by walking around various trails about once a week on Chichi Island, once a month on Ani Island, and Haha Island throughout the year in 1995. On these field trips, honeybees foraging on flowers and floral host species were observed and recorded. Foraging honeybees with and without pollen loads were regarded as pollen- and nectar-foraging workers, respectively.

Bee communities on flowers

Quantitative observations of flower visitors were made on Ani and Chichi Islands on July 19–26, 1991, on Haha Island on July 27, 1991, and on Haha's satellite islands, i.e., Mei Island, on July 16, Imouto on July 17, Ane on July 18, and Mukou on July 20, 1992. To compare the relative abundance of native bees and honeybees, we recorded all insects visiting flowers during a 15-min period for each native plant species on clement days (generally in the morning). For these observations, flowering stands as large as possible were chosen in natural vegetation in each island. The plant species studied on Ani (A), Chichi (C), Haha (H), Mei (M), Imouto (I), Ane (N), and Mukou (K) Islands are as follows: *Schima mertensiana* (Theaceae) (A, C); *Hibiscus glaber* (Malvaceae) (A, C, H, M); *Terminalia catappa* (Conbretaceae) (H, N); *Syzygium cleyeraefolium* (Myrtaceae) (A); *Ipomoea pes-caprae* (Convoluvulaceae) (A); *Lobelia boninensis* (Campanulaceae) (M, I, N, K); *Callicarpa subpubescens* (Verbenaceae) (H, N); *Vitex rotundifolia* (Verbenaceae) (A, C, H, M, I, N, K); *Psychotria homalosperma* (Rubiaceae) (A); *Hedyotis grayi* (Rubiaceae) (H); *Stachytarpheta jamaicensis* (Verbenaceae) (C); *Scaevola sericea* (Goodeniaceae) (A, C, M, I, N); and *Clinostigma savoryana* (Palmae) (A, H, K).

From March 1995 to February 1996, insects visiting flowers on Ani Island were recorded at monthly intervals along a trail from Takinoura to the central plateau on Ani Island. We collected insects that were visiting flowers by netting for about 8 min at a flowering plant and then by sweeping the flowers with the net. The collected insects were then pinned and identified. Additional observations of flower visitors were made on Chichi and Haha Islands during November 16–22, 1993, March 23–29, 1995, May 26–29, 1996, and September 12–14, 1996.

Results

Honeybee pollen/nectar foraging

Honeybees were active throughout the year. The number of returning/leaving workers per minute peaked from May to

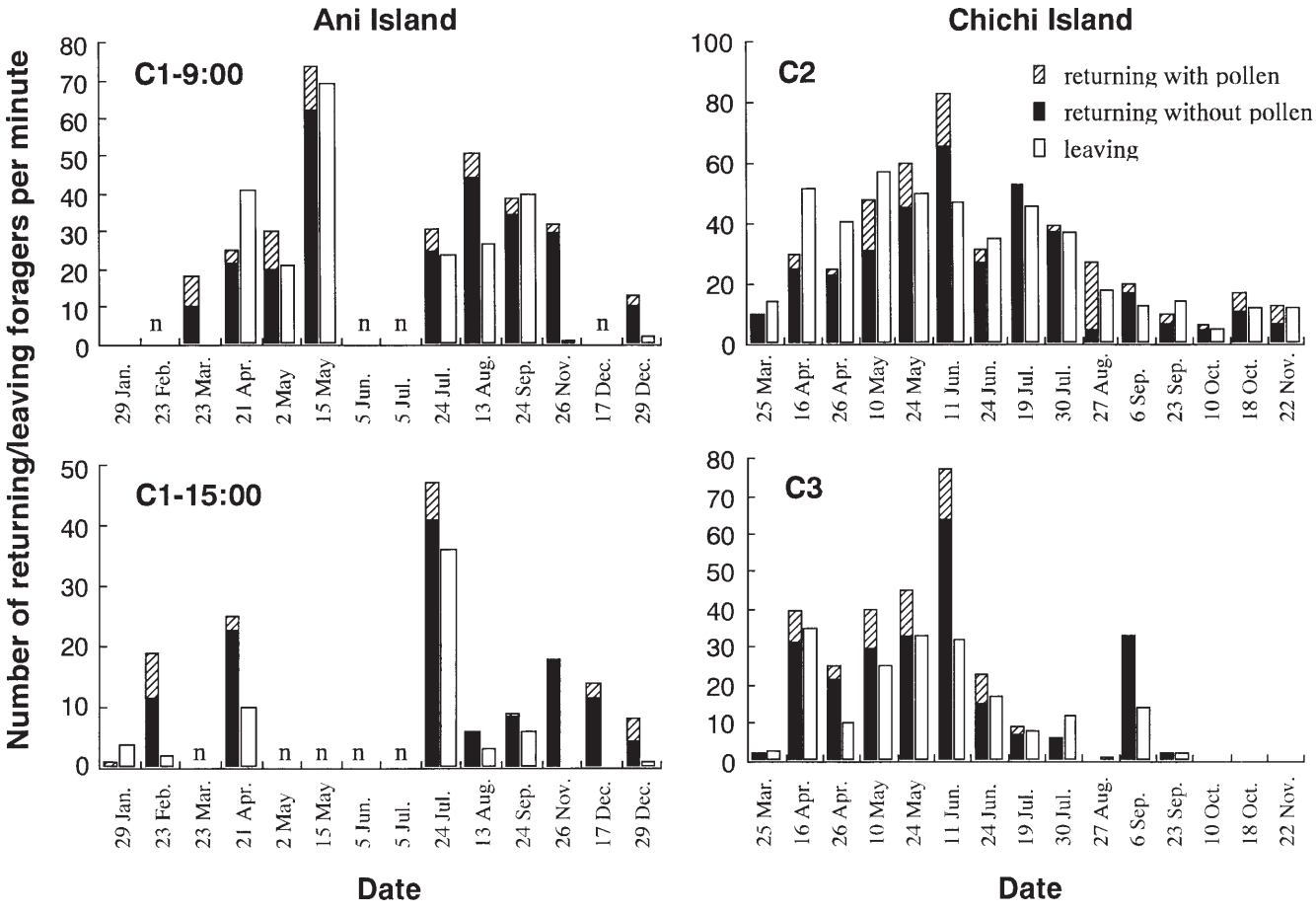


Fig. 3. Seasonal changes of activity of honeybee foragers in a feral colony on Ani Island (*C1*) and two cultivated colonies on Chichi Island (*C2* and *C3*). Activity is shown (*bars*) by number of returning and leaving workers per minute. Returning workers with or without pollen loads were discriminated. On the days labeled as *n*, we obtained pollen load samples but failed to observe honeybee foraging activity

July and was lowest in January on Ani Island (Fig. 3), and also peaked in June then decreased in the two colonies on Chichi Island. Foraging was more active in the morning than in the afternoon, except in July on Ani Island. Among returning workers, the annual mean proportion of pollen-foraging workers was 17.6% in the morning and 16.0% in the afternoon in C1, 21.4% in C2, and 25.6% in C3; 94.5% of pollen loads were composed of only one flower species.

The feral honeybee colony on Ani Island (C1) harvested pollen of 21 plant species, of which 14 were native and 7 were alien (Table 2). The weight proportion of alien plant species in the pollen harvest peaked from April to May and again in December (Fig. 4). The plants utilized as a pollen source were composed of 16 entomophilous and 5 anemophilous species. The proportion of anemophilous flowers in the pollen harvest peaked in February and May (Fig. 4). Some plant species such as the cultivated passion fruit, *Passiflora edulis*, and the alien herb, *Bidens pilosa*, were absent from Ani Island (Yasui 1988), and the pollen of these species is thought to be harvested from neighboring Chichi Island.

The hived colonies on Chichi Island (C2 and C3) harvested pollen of 23 plant species, of which 14 were native and 9 were alien (Table 3). The proportion of alien plants in the pollen harvest was greater than that of native plants throughout most of the year (Fig. 4). The plants were composed of 19 entomophilous and 4 anemophilous species. The proportion of anemophilous plants peaked in March and June. The honeybees frequently harvested pollen of an alien shrub species, *Leucaena leucocephala*, from April to May and from September to October, with a shift to native and other alien flowers from June to August (Table 3).

Plant species observed to be visited by nectar-foraging honeybees are listed in Table 4. Four alien plant species, *Leucaena leucocephala*, *Stachytarpheta jamaicensis*, *Bidens pilosa*, and *Lantana camara*, are nectariferous plants flowering throughout the year and a potential nectar source for honeybees, especially in winter. Nectar of the summer-flowering native plants species were vigorosly harvested by honeybees, especially on Chichi and Haha Islands.

Bee communities on flowers

Native bees observed on flowers were very rare in both disturbed and natural forests on both Chichi and Haha

Table 2. Seasonal changes of flower composition in honeybee pollen loads for a feral colony (C1) on Ani Island

Plant species	#1	#2	Date													Total
			29 Jan.	23 Feb.	24 Mar.	21 Apr.	2 May	15 May	5 Jun.	5 Jul.	24 Jul.	13 Aug.	24 Sep.	26 Nov.	17 Dec.	29 Dec.	
Rhaphiolepis indica	n	e	0.83											1.00	0.50		2.33
Pinus luchuensis	a	a	0.17	0.75	0.40												1.32
Ilex mertensii	n	e		0.25													0.25
Osteomeles sp.	n	e			0.20												0.20
Dodonaea viscosa	n	a			0.40												0.40
Passiflora edulis[a]	a	e				0.50											0.50
Lantana camara	a	e				0.50			0.50	0.25	0.14						1.39
Syzygium sp.	n	e					0.13					0.67	0.50				1.30
Casuarina equisetifolia	a	a					0.38	0.89									1.27
Leucaena leucocephala	a	e					0.50						0.10				0.60
Stachytarpheta jamaicensis	a	e						0.11									0.11
Ochrosia nakaiana	n	e							0.50								0.50
Scirpus ternatanus	n	a								0.25							0.25
Trema orientalis	n	a								0.08							0.08
Clinostigma savoryana	n	e								0.42	0.43						0.85
Pandanus boninensis	n	e									0.14						0.14
Terminalia catappa	n	e									0.29		0.10				0.39
Scaevola sericea	n	e										0.33	0.10				0.43
Metrosideros boninensis	n	e											0.20				0.20
Vitex rotundiflora	n	e													0.50		0.50
Bidens pilosa	a	e														1.00	1.00
No. of pollen loads analyzed			3	9	7	2	8	9	2	9	7	3	5	4	2	6	76

#1, distributional status: a, alien; n, native. #2, pollination system: a, anemophilous; e, entomophilous

[a] Absent on Ani Island

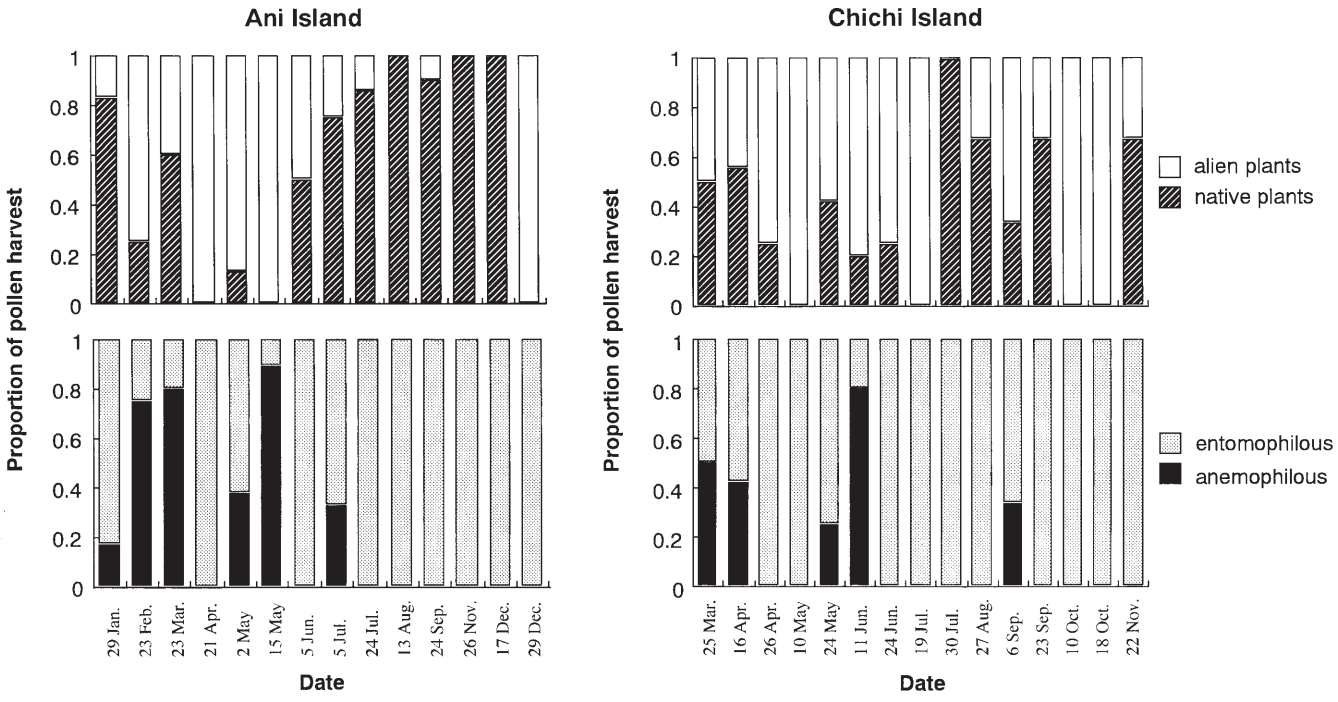


Fig. 4. Seasonal changes of the proportion of pollen source [alien (*white bars*) vs. native (*hatched bars*) plants, and entomophilous (*dotted bars*) vs. anemophilous (*black bars*) plants] for the honeybee colonies on Ani (*left*) and Chichi (*right*) Islands

Islands. In contrast, native bees were frequently observed on flowers from late March to November on Ani Island, although quantitative data are lacking. The native flowers that bloomed from December to February were mainly visited by syrphid, calliphorid, and tephritid flies on Ani Island.

In July, when native bee activity peaked, the relative abundance of bees on flowers differed greatly among islands. On 8 species of flowers on Ani Island, 108 bee individuals of 10 species were observed in July 1991 (Table 5). Among them, 97.2% were native bees and the other 2.8% were honeybees. On 5 species of flowers on Chichi Island, 42 individuals of 2 species were observed. Among them, only 7.1% were native bees and the other 92.9% were honeybees. The bee–flower network on Ani Islands was much more complicated than that on Chichi Island (Fig. 5; the number of connectance was 27 on Ani Island and 7 on Chichi Island). For example, flowers of a native entomophilous plant, *Vitex rotundifolia*, were visited only by honeybees on Chichi Island but by 4 native bee species on Ani Island. The mean number of native bee species per flower species was 3.0 and 0.4 on Ani and Chichi Islands, respectively.

On Haha Island, 52 bee individuals of 6 species were observed on 6 species of flowers in July 1992 (Table 6). Among them, 21.2% were native bees and the other 78.8% were honeybees. On Haha's satellite islands, 148 individuals of 8 species were observed on 7 species of flowers. On these islands, only native bees were seen and no honeybees were found. The mean number of native bee species per flower species was 1.0, 1.8, 2.0, 3.0, and 2.0 on Haha, Mei, Imouto, Ane, and Mukou Islands, respectively. The bee–flower network on Haha's satellite islands (data of Ane, Imouto, Mei, and Mukou Island were combined) was more complicated than that on Haha Island (Fig. 5; the number of connectance was 12 on Haha Island and 18 on its satellite islands). Flowers of a native entomophilous shrub species, *Callicarpa subpubescens*, were visited only by honeybees on Haha Island but by 3 native bee species on Haha's satellite islands. Flowers of an endemic palm, *Clinostigma savoryana*, were visited predominantly by small colletid bees, *Hylaeus yasumatsui* or *Hylaeus incomitatus* on Ani Island and Haha's satellite islands, but only by honeybees on Haha Island. We could not observe flower visitors of *C. savoyana* on Chichi Island where the plant is now rare.

Relative abundance of bee foragers on flowers in July varied among the islands (Fig. 6). The dominance of honeybees and the rarity of native bees on Chichi and Haha Islands contrasted with the dominance of native bees and the rarity of honeybees on Ani Island and Haha's satellite islands. The year-round dominance of honeybees on flowers on Chichi and Haha Islands was confirmed throughout the period of observation (see Table 4). Alien nectariferous plants such as *Leucaena, Stachytarpheta, Bidens, Lantana, Alpinia, Acacia, Bryophyllum*, and *Thunbergia* were visited only by honeybees. Almost all native plant species were also dominated by honeybees on Chichi and Haha Islands in May, September, and November. Endemic plant species such as *Dendrocacalia crepidifolia*, *Crepidiastrum* spp., and *Elaeagnus rotundata*, which bloomed in November in primary mountain forests on Haha Island, were visited only by honeybees.

Table 3. Seasonal changes of flower composition in honeybee pollen loads for two hived colonies (C2 and C3) on Chichi Island

Plant species	#1	#2	Date														Total
			25 Mar.	16 Apr.	26 Apr.	10 May	24 May	11 Jun.	24 Jun.	19 Jul.	30 Jul.	27 Aug.	6 Sep.	23 Sep.	10 Oct.	18 Oct.	22 Nov.	
Rivina humilis	a	e	0.50														0.50
Myrsine okabeana	n	a	0.50	0.28													0.78
Leucanea leucocephala	a	e		0.43	0.50	0.83							0.33	0.33	0.75	0.75	3.92
Boninia sp.	n	e		0.14													0.14
Fimbristylis sp.	n	a		0.14													0.14
Lantana camara	a	e			0.25							0.33					0.58
Photinia wrightiana	n	e			0.25												0.25
Stachytarpheta jamaicensis	a	e				0.17	0.33		0.50				0.33				1.33
Casuarina equisetifolia	a	a					0.25	0.80									1.05
Pandanus boninensis	n	e					0.42										0.42
Callicarpa subpubescens	n	e						0.20									0.20
Terminalia catappa	n	e							0.25								0.25
Acacia confusa?	a	e							0.25								0.25
Lagerstroemia indica	a	e								0.33							0.33
Psidium sp.	a	e								0.67							0.67
Schima mertensiana	n	e									0.33						0.33
Clematis terniflora	n	e									0.33						0.33
Scaevola sericea	n	e									0.33						0.33
Hernandia sonora	n	e										0.67					0.67
Trema orientalis	n	a											0.33				0.33
Fagara boninsimae	n	e												0.67			0.67
Thunbergia alata	a	e													0.25	0.25	0.33	0.83
Rhaphiolepis indica	n	e															0.67	0.67
No. pollen loads analyzed			6	6	4	6	6	5	4	3	3	3	3	3	3	4	3	62

#1, distributional status: a, alien; n, native. #2, pollination system: a, anemophilous; e, entomophilous

Table 4. Plant species observed to be visited by honeybees in the Bonin Islands, with the months when flowering and honeybee visits were observed

Flower species	Family	Status[a]	Honeybees (month)												Native bees (islands)			
			J	F	M	A	M	J	J	A	S	O	N	D	A	C	H	S
Leucaena leucocephala	Leguminosae	a	+	+	+	+	+	+	+	+	c	+	+	+		−	−	
Stachytarpheta jamaicensis	Verbenaceae	a	+	+	+	+	+	c	c	c	c	+	+	+		−	−	
Bidens pilosa	Asteraceae	a	+	+	+	+	+	+	+	c	ch	+	h	+		−	−	
Lantana camara	Acanthaceae	a	+	+	+	+	+	+	+	a	+	+	+	+	−	−	−	
Rhaphiolepis indica	Rosaceae	n	a	+	+								+	+		−	−	
Peucedanum boninense	Apiaceae	n			h	+										−	−	
Zanthoxylum arnottianum	Rutaceae	n			c	+										−		
Eurya boninensis	Theaceae	n			c	+										−		
Osteomeles spp.	Rosaceae	n				c										−		
Callicarpa spp.	Verbenaceae	n					c	+	+	+	+	+	c		+	−	−	+
Alpinia speciosa	Zingiberaceae	a					c	+								−		
Photinia wrightiana	Rosaceae	n					c								+	−		
Acacia confusa	Leguminosae	a					c	+								−		
Bryophyllum pinnatum	Crassulaceae	a					+	+	c	+						−		
Vitex rotundifolia	Verbenaceae	n					+	+	ac	+	a	+	+		+	−	−	+
Scaevola sericea	Goodeniaceae	n						+	ac	+					+		−	
Schima mertensiana	Theaceae	n						+	ac	+	+				+	+		
Hibiscus glaber	Malvaceae	n						+	h	+	+	+			+	+	+	+
Syzygium buxifolium	Myrtaceae	n							a	a					+	−		
Terminalia catappa	Conbretaceae	n							h							−	−	+
Hedyotis spp.	Rubiaceae	n							h	h	c	+	h		+		+	+
Clinostigma savoryana	Palmae	n							h	+	a				+	−	−	+
Thunbergia alata	Acanthaceae	a							c	+	+	+				−		
Metrosideros boninensis	Myrtaceae	n								c						−		
Dendrocacalia crepidifolia	Asteraceae	n											h				−	
Elaeagnus rotundata	Elaeagnaceae	n											h				−	
Crepidiastrum spp.	Asteraceae	n											h				−	
Number of flowering alien plant species		8	4	4	4	4	7	7	6	6	5	5	4	4				
Number of flowering native plant species		19	1	1	4	4	3	5	9	9	5	3	6	0				

+, flowering observed but honeybee visits not observed; a, c, h, honeybee visits observed on Ani, Chichi, and Haha Is., respectively. Records of native bee visits to these flowers are also shown in the last four columns; + and − indicate presence and absence of flower visits on Ani (A), Chichi (C), Haha (H), and Haha's satellite Islands (S); and no symbol, lack of observation

[a] a, alien; n, native

Table 5. Relative abundance of bees on 9 species of flowers on Ani and Chichi Islands in July

Site Bee species	Flower species									Total
	Sc	Hi	Sy	Ip	Vi	Ps	St	Sc	Cl	
Ani Island										
Hylaeus incomitatus			2						30	32
H. yasumatsui									9	9
H. ikedai			1		3					4
Megachile asahinai					2					2
M. rixator sakishimana				1	3			3		7
Heriades fulvohispidus	2	1	3							6
Lithurge ogasawarensis		2			1					3
Ceratina boninensis		2	1	9	13	2		4	2	33
Xylocopa ogasawarensis	4	2						3		9
Apis mellifera[a]			1			1		1		3
Total number of individuals	6	7	8	10	22	3	−	11	41	108
Chichi Island										
Xylocopa ogasawarensis	1	2								3
Apis mellifera[a]	4	2			8		11	14		39
Total number of individuals	5	4	−	−	8	−	11	14	−	42

Sc, *Schima mertensiana*; Hi, *Hibiscus glaber*; Sy, *Syzygium cleyeraefolium*; Ip, *Ipomoea pes-caprae*; Vi, *Vitex rotundifolia*; Ps, *Psychotria homalosperma*; St, *Stachytarpheta jamaicensis*; Sc, *Scaevola sericea*; Cl, *Clinostigma savoryana*. −, absence of flowers studied

[a] Introduced species

Table 6. Relative abundance of bees on 8 species of flowers on Haha Island and its satellite islands in July

Site Bee species	Flower species								Total
	Te	Hi	Lo	Ca	Vi	He	Sc	Cl	
Haha Island									
Hylaeus incomitatus						1			1
H. yasumatsui						2			2
Lithurge ogasawarensis		2							2
Ceratina boninensis		1				3			4
Xylocopa ogasawarensis		2							2
Apis mellifera[a]	5	1		2	7	1		26	42
Total number of individuals	5	6	–	2	7	7	–	26	53
Haha's satellite islands									
Mei Island									
Hylaeus ikedai		1	2		12				15
Lithurge ogasawarensis		1							1
Ceratina boninensis			2		10		7		19
Total number of individuals	–	2	4	–	22	–	7	–	35
Imouto Island									
Hylaeus ikedai					1		1		2
Heriades fulvohispidus	1								1
Megachile rixator sakishimana							1		1
Ceratina boninensis	6						3		9
Xylocopa ogasawarensis			1				1		2
Total number of individuals	–	–	1	–	1	–	6	–	15
Ane Island									
Hylaeus ikedai			9	1	7		7		24
Megachile rixator sakishimana					1		3		4
Lithurge ogasawarensis				1					1
Ceratina boninensis			1	1	20		22		44
Xylocopa ogasawarensis			2						2
Total number of individuals	–	–	12	3	28	–	32	–	75
Mukou Island									
Hylaeus incomitatus								7	7
H. ikedai			2		1				3
Ceratina boninensis			2		2				4
Xylocopa ogasawarensis			1						1
Total number of individuals	–	–	5	–	3	–	–	7	15

Te, *Terminalia catapa*; Hi, *Hibiscus glaber*; Lo, *Lobelia boninensis*; Ca, *Callicarpa subpubescens*; Vi, *Vitex rotundifolia*; Sc, *Scaevola sericea*; He, *Hedyotis grayi*; Cl, *Clinostigma savoryana*. –, absence of flowers studied

[a] Introduced species

Discussion

The original bee fauna in the Bonin Islands was characterized by a dominance of small solitary endemic bees and by the absence of social bees (see Table 1). All native bee species have the habit of nesting in wood or shoot cavities, suggesting that they may have arrived on the islands by nest drifting (Kato 1992). After the introduction of honeybees in the 1880s, honeybees naturalized even in natural forests on these islands, probably because of the absence of the predaceous *Vespa* spp., which have prevented the naturalization of European honeybees on mainland Japan (Matsuura and Sakagami 1973).

The honeybees in the Bonin Islands foraged on flowers throughout the year and utilized both native and alien plants as nectar and pollen sources. Species composition of honeybee pollen harvest demonstrated the importance of alien plants as a pollen source (Fig. 4). If there were not these alien plants, some of which had been introduced as a nectar source for apiculture, honeybees would not be able to maintain their colonies throughout the year on these islands. The fact that they utilize pollen of anemophilous plants suggests that pollen is a limited resource for honeybees during these periods. Honeybee dependence on alien plants decreased from June to December on Ani Island (Fig. 4). During this period, honeybees were found harvesting nectar and pollen of native flowers, which would have been harvested by the native bees.

Relative abundance of bee foragers on flowers differed strikingly between neighboring islands (that is, between Ani and Chichi Island and between Haha Island and its satellite islands). In general, native bees were rare on islands where honeybees were dominant (Tables 5, 6). One reason for the rarity of native bees on Chichi and Haha Islands may be habitat fragmentation resulting from disturbance of primary forests (Fig. 1). However, the reason is not thought to be only the extent of habitat disturbance, because Haha's small satellite islands, which had smaller areas of natural vegetation than Chichi and Haha Islands, fostered many

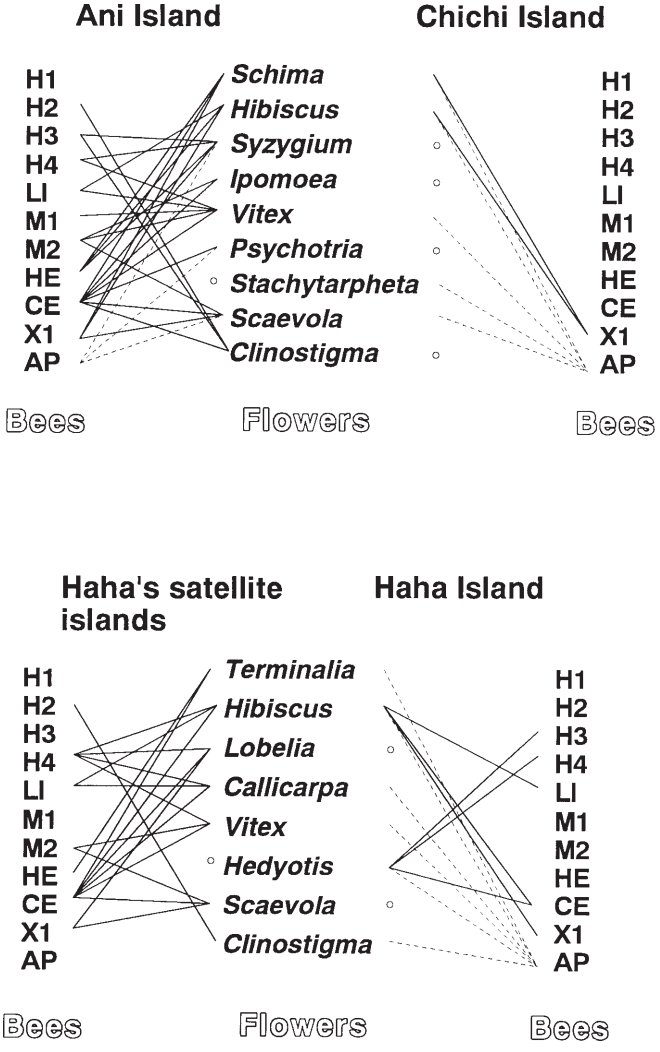


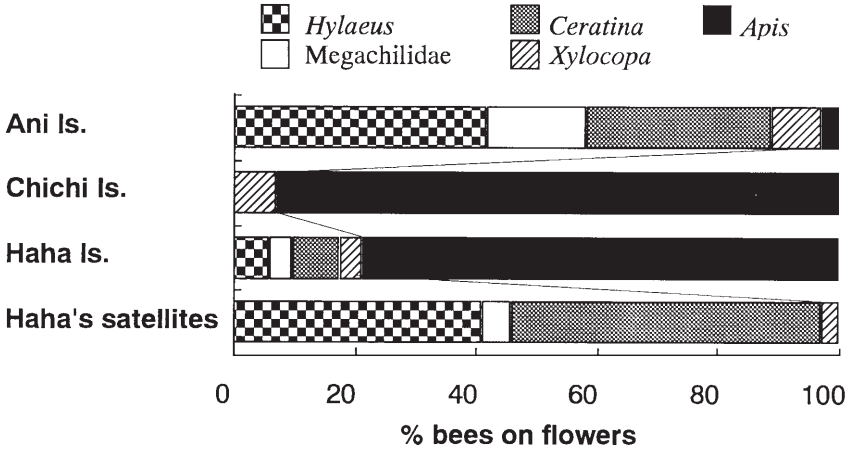
Fig. 5. Flower utilization by bee species observed in July on Ani, Chichi, Haha, and Haha's satellite islands in July. For Haha's satellite islands, data of Mei, Imouto, Ane, and Mukou Is. are combined. *Solid* and *broken lines* show native bee and honeybee visits to flowers, respectively (See Table 1 for bee species codes). *Open circles* indicate absences of flowering plants during the observations

native bees. Accordingly, the rarity of native bees on Chichi and Haha islands is hypothesized to result directly from resource competition with honeybees. The apparent overlap of nectar and pollen source between native bees and honeybees and the sophisticated and superior foraging ability of the honeybee over that of the native solitary bees support this hypothesis (Roubik 1980).

The abundance of honeybees on flowers on Chichi Island resulted not only from apiculture but also from the abundance of feral colonies, which we suggest are sustained by the abundance of nectariferous, alien plants. The honeybees, in turn, appeared to promote selectively the pollination of these nectariferous, sometimes aggressively competitive and weedy, plant species such as *Leucaena leucocephala*, *Lantana camara*, *Stachytarpheta jamaicensis*, and *Bidens pilosa*. On Ani Island, the density of feral honeybee colonies seemed to be low because of a scarcity of nectariferous alien plants. Analysis of the pollen harvest of the honeybee colony on Ani Island suggests that the honeybees collected nectar and pollen of some cultivated plant species such as passion fruits from neighboring Chichi Island in April (Table 2). Because the distance between the nest site on Ani Island and the passion fruit orchard on Chichi Island is less than 2 km (Fig. 1), this is quite possible. The absence of honeybees on Haha's satellite islands is also thought to result from a scarcity of nectariferous alien plant species, which provide them with enough nectar and pollen throughout the year. These small satellite islands are more than 3 km away from Haha Island, and this distance seems sufficient to prevent interisland foraging expeditions by the honeybees.

Relatively large proportions of dioecious species on oceanic islands have been reported in Hawaii (27.7%; Carlquist 1974), New Zealand (12%–13%; Godley 1975), and the Bonin Islands (9%; Kawakubo 1990). Some of these dioecious plants are thought to have evolved dioecy within the islands from hermaphroditic ancestors by reducing the costs of geitonogamy (Thomson and Brunet 1990; de Jong et al. 1993). An endemic shrub on Haha Island, *Dendrocacalia crepidifolia*, is such a case (Kato and Nagamasu 1995). The two factors that result in increased geitonogamy on oceanic

Fig. 6. Relative abundance of foraging bees by species on flowers on Ani, Chichi, Haha, and Haha's satellite islands in July



islands are an increased woodiness of herbaceous plants accompanied by an increase in the number of flowers per plant (Carlquist 1974) and the dependence on native, small, solitary bees for pollination (Bawa and Opler 1975; Bawa 1980). Although the original pollinators of *D. crepidifolia* are unknown because of the monopoly of these flowers by honeybees, the pollinators are most likely to have been the small, less hairy, solitary bees of the genera *Hylaeus*, *Ceratina*, or *Megachile*, which are thought to increase geitonogamy. *Callicarpa subpubescens* is another example of a tree that evolved dioecy in the Bonin Islands (Kawakubo 1990). This species was pollinated by these native solitary bees on Haha's satellite islands (see Table 6), whereas on Haha Island it was only visited by honeybees. The recent expansion of feral honeybees and the drastic decrease of native bees may have changed pollen flow among native plants, and as a consequence the breeding systems of endemic plants may also be changing.

Our data suggest a strong impact of honeybees upon native bee communities and a probable impact upon plant–pollinator interactions in the Bonin Islands. The status of these native bees in the Bonin Islands is vulnerable or endangered, and all these native bees should be listed in the Red Data Book. The native bee communities on Chichi and Haha Islands may have already been permanently altered by the high population level of managed and feral honeybees, while the native bee community on Haha's satellite islands is well conserved.

The native bee community on Ani Island is now endangered. To conserve this community, the following steps are recommended: (1) conserve the natural dry forests, which provide the native bees with their main food resource; (2) eradicate feral honeybee colonies, which are competitively superior to the native solitary bees; and (3) prevent invasions of nectariferous, aggressive, weedy, alien plants that provide honeybees with nectar and pollen, especially from winter to spring, thus supporting their colonies.

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