

Arboreal ant fauna of Joyama Park, Kagoshima Prefecture, southern Japan

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ABSTRACT. Five tree species (*Prunus x yedoensis*, *Prunus jamasakura*, *Prunus lannesiana*, *Quercus acutissima* and *Acer palmatum*) and the associated ant fauna were surveyed in Joyama Park, Hioki City, Kagoshima Prefecture, southern Kyushu, Japan. Ants were found on 206 (92%) of 224 trees surveyed. Fifteen ant species were collected from trees; the three most frequent ant species were *Pristomyrmex punctatus* (on 92 trees), *Crematogaster matsumurai* (65 trees) and *Formica hayashi* (49 trees). The number of ant species found per tree ranged from 0 to 6, with a mean of 1.83 ± 1.11 species. Seven species, *Tetramorium nipponense*, *P. punctatus*, *Cr. matsumurai*, *Cr. vagula*, *Ochetellus glaber*, *Lasius japonicus* and *Camponotus vitosus*, nested in trees: in decayed parts. A total of 87 nests were found, on 84 trees (37.5% of all trees surveyed). The nests of *Cr. matsumurai* were found on 47 (21%) trees. Only three trees had two species nesting together: the respective combinations were *Cr. matsumurai* and *C. vitosus*, *T. nipponense* and *P. punctatus*, and *C. vitosus* and *Cr. vagula*. Among the 15 ant species found on the trees, only four (26.7%) were principally arboreal nesters, and two of the most frequent species (*P. punctatus* and *F. hayashi*) were principally ground nesters.

Keywords: arboreal ant, foraging site, nesting site, Formicidae, Hymenoptera

INTRODUCTION

Ants are important players in the forest ecosystem. Numerous ant species inhabit the canopy of tropical rainforests, and many species can be found from a single tree (Huxley 1980; Wilson 1987; Fiala *et al.* 1990; Hölldobler & Wilson 1990; Joliver 1996; Erwin 2001; Schulz & Wagner 2002; Malsch *et al.* 2003). Erwin (1983) studied the insect fauna in the canopy of tropical rainforests for the first time, in Panama, and pointed out the huge biomass of ants present. In a study of a canopy in the east-Amazon, ants comprised 70 percent of arthropods individuals (Tobin 1991).

In the temperate zone, the fauna and ecology of arboreal ants have been studied mainly in Europe (e.g., Punttila 1996; Alvarado 2000;

Dolek *et al.* 2009; for review, see Seifert 2008). Seifert (2008) pointed out that only 8 percent (14 spp.) are real canopy dwellers and 10 percent (18 spp.) are truly arboricolous among the 51 central-European ant species. He also discussed nest density and biomass of ants on the trees.

In Japan, the species composition, nesting biology and species interaction of arboreal ants were studied in Honshu by Morisita (1939, 1941), Yamaoka (1978, 1979, 1983) and Terayama (2005). Some studies of arboreal ants were also made on mainland Kyushu, in Kagoshima (Kawahara *et al.* 1998; Iwata *et al.* 2005). However, in these studies, tree ants were not categorized according to their foraging ranges and nesting sites as has been done for European arboreal ants by Seifert (2008). In order to analyze the ecological characteristics of "arboreal" ants in

the warm temperate region, foraging and nesting by ants on trees were investigated in Joyama Park, Kagoshima, southern Japan. The coexistence of particular sets of ant species on single trees is also analyzed in relation to ant species diversity in a habitat.

MATERIALS AND METHODS

The study site was Joyama Park (total area: 0.11 km², highest point: 142 m asl.), Hioki City, Kagoshima Prefecture (31°38'N, 130°26'E), southern mainland Kyushu, Japan. It is in the warm temperate region (Fig. 1) with an average annual rainfall of approximately 2000 mm (Kagoshima Local Meteorological Observatory: <http://www.jma-net.go.jp/kagoshima/>). Seasonality is seen in both temperature and precipitation, but the winter is not severe, having light snow and weak frost several times a year. Rainfall is concentrated in the summer (June–September), but there are usually no completely dry months.

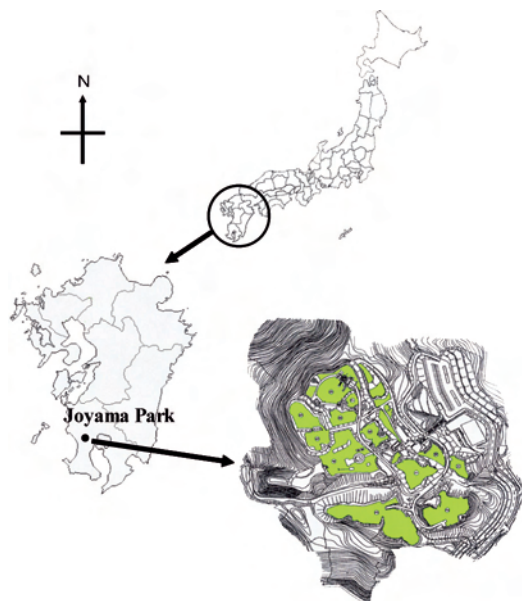
The park has several types of vegetation: secondary evergreen forests (original forest type: broad-leaved evergreen forest), forest edges, a *Quercus acutissima* plantation, grassland and

playground with surrounding patches of planted trees. The survey was conducted in these patches of trees and in the *Q. acutissima* plantation (Fig. 2). Of approximately 300 trees, 224 trees with more than 4 cm in diameter at breast height (DBH) were surveyed for ant species composition and ant nests. Trees less than 4 cm DBH were not surveyed because generally such small trees are not suitable for ant nesting. The trees surveyed comprised five species: *Prunus x yedoensis* (135), *Q. acutissima* (40), *Acer palmatum* (25), *P. jamasakura* (12) and *P. lannesiana* (12) (Table 1). The largest and smallest trees were *P. x yedoensis* (40.8 cm DBH) and *Q. acutissima* (4.1cm), respectively.

Foraging ants were collected on the tree trunk, without using baits, in the daytime, from 10 cm to 200 cm above the ground. In the study site no truly nocturnal species occurs so that the survey in the daytime could cover the activity of all species. On *Prunus* trees, ants collecting nectar from extrafloral nectaries were frequently observed. Furthermore, many replete ants were seen on the tree trunk, suggesting that they were carrying homopteran honeydew and nectar. Solid foods, mainly aphids, were also collected by workers from the tree (Harada 2005).

The survey was conducted from March to June in 2001. As Joyama Park is a public park managed strictly by Hioki City, we were not permitted to damage any tree in the park during the survey. Foraging by ants on the canopy was observed and the presence/absence of nests checked on each tree for ten minutes with a telescope (VIXEN, ALICE M6×16SL) in the absence of a canopy observatory system. In most cases, entrances of the nests made in tree trunks were confirmed with the naked eyes. In the remaining cases, to confirm nesting by ants in higher parts of the tree, ascending ants were checked to see whether they had solid objects in their mandibles or liquid food in their crops.

Scientific names of ants, and identification and arrangement of ant species, follow the Myrmecological Society of Japan (1989, 1991, & 1992) and Yamane *et al.* (2010). We used Fisher's Exact test (McDonald 2009) to test for the association of ant species.



The green areas are the grasslands. There are many trees planted around the grasslands.

Fig. 1. Location and topographical map of Joyama Park.



Fig. 2. View of Joyama Park, the study site.

Table 1: Number of trees of each species with mean and range of DBH

Tree species	Number of trees	DBH in cm	
		Mean	Range
<i>Prunus x yedoensis</i> Matsumura	135	14.1	4.5–27.1
<i>Quercus acutissima</i> Carruthers	40	14.8	4.1–28.3
<i>Acer palmatum</i> Thunb. var. <i>matsumurae</i> Makino	25	7.8	7.0–24.5
<i>Prunus jamasakura</i> Siebold et Zuccarini	12	9.2	6.1–18.5
<i>Prunus lannesiana</i> Wilson var. <i>speciosa</i> Makino	12	15.4	6.1–29.9
Total	224	12.3	

RESULTS

Foragers

Fifteen ant species belonging to 11 genera in three subfamilies were observed foraging on 206 (92%) of the 224 trees (Table 2). The number of ant species found per tree ranged from 0 to 6, with a mean of 1.83 ± 1.11 (SD) species. The average species richness for each tree species ranged from 1.25 ± 0.97 for *P. jamasakura* to 2.02 ± 0.98 for *P. x yedoensis*. On most trees of *P. x yedoensis* (98.5%) and *P. lannesiana* (91.7%), at least one ant species was observed. On the other hand, on around 20 percent of *P. jamasakura*, *Q. acutissima* and *A. palmatum* trees, ants were not found. The three dominant ant species (measured by frequency of occurrence on trees) were

Pristomyrmex punctatus Mayr, 1886 (found on 92 trees), *Crematogaster matsumurai* Forel, 1901 (on 65 trees) and *Formica hayashi* Terayama et Hashimoto, 1996 (on 49 trees), each species being collected from all the tree species surveyed.

Cr. matsumurai was the species most frequently found nesting on the trees surveyed (see Fig. 4). On 33 selected *P. x yedoensis* trees the ant species found foraging together with this species were recorded (Fig. 3). *Formica hayashi* was most frequently observed with *Cr. matsumurai* (n=19), followed by *P. punctatus* (n=12) and *Tapinoma melanocephalum* (Fabricius, 1793) (n=10).

Foragers of *Cr. matsumurai* were observed on 33 *P. x yedoensis* trees, of which only two were shared with *Cr. vagula* foragers. Statistical analysis proved that this pattern did not differ from random association (Fisher's Exact test

$\chi^2 = 2.0$, $p_{\text{two-sided}} = 0.239$). On the other hand, on eight of these 33 trees, *Camponotus vitosus* and *Cr. matsumurai* were observed foraging together, demonstrating a positive association (Fisher's Exact test $\chi^2 = 6.42$, $p_{\text{two-sided}} = 0.025$) (Fig. 3).

Nests

Seven ant species, *P. punctatus*, *Cr. matsumurai*, *Cr. vagula* Wheeler, 1928, *Tetramorium*

nipponense Wheeler, 1928, *Ochetellus glaber* (Mayr, 1862), *Lasius japonicus* Santschi, 1941 and *Camponotus vitosus* F. Smith, 1874, nested in the trees. Their nests were mostly seen in decayed parts of the trunk. A total of 87 nests were found on 84 trees (37.5% of all trees surveyed) (Fig. 4, Table 2). The ratio of trees inhabited by ants varied between 33.3% and 44.0% among the five tree species.

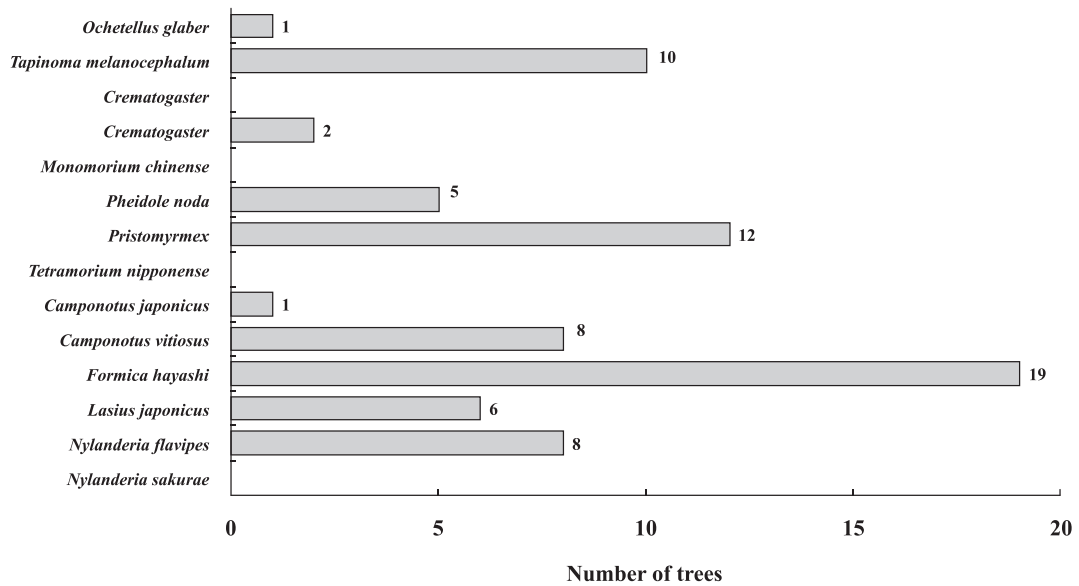


Fig. 3. Ant species found with *C. matsumurai* on 33 *Prunus x yedoensis* trees.

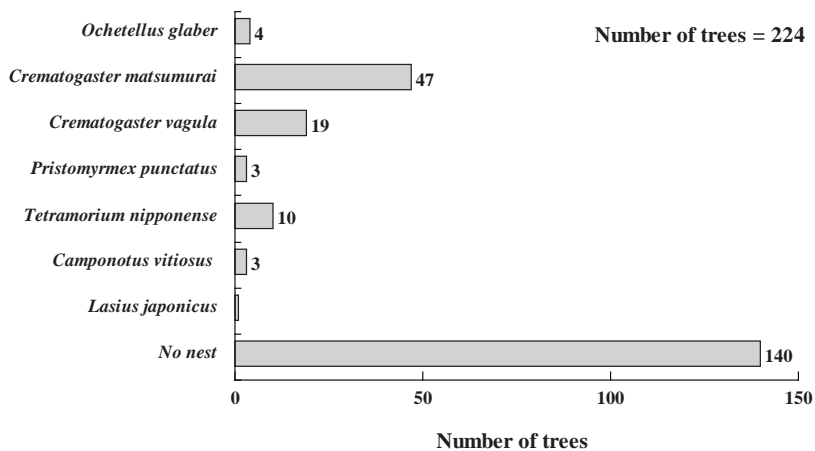


Fig. 4. Ant species nesting on trees.

Table 2: Number of trees on which foraging ants were observed and ant nests were found

Ant species	Tree species																																																																																																																																																																																																																																																																																																																																			
	<i>P. x. yedoensis</i> (135)		<i>Q. acutissima</i> (40)		<i>A. palmatum</i> (25)		<i>P. jamaokura</i> (12)		<i>P. lannesiana</i> (12)																																																																																																																																																																																																																																																																																																																											
	Foraging	Nest	Foraging	Nest	Foraging	Nest	Foraging	Nest	Foraging	Nest	Foraging	Nest																																																																																																																																																																																																																																																																																																																								
Dolichoderinae													<i>Ochetellus glaber</i>	19	2	0	0	2	0	2	0	3	0	3	2	<i>Tapinoma melanocephalum</i>	9	0	11	0	2		0	0	2		2	0	Myrmicinae													<i>Crematogaster matsumurai</i>	33	28	20	8	7	8	2	2	3	1	3	1	<i>C. osakensis</i>	1	0	2	0	0	0	0	0	0	0	0	0	<i>C. vagula</i>	18	11	2	1	3	3	2	2	3	2	3	2	<i>Monomorium chinense</i>	5	0	1	0	0	0	0	0	1	0	1	0	<i>Pheidole noda</i>	26	0	1	0	0	0	0	0	1	0	1	0	<i>Pristomyrmex punctatus</i>	69	2	11	1	8	0	2	0	2	0	2	0	<i>Tetramorium nipponense</i>	23	7	3	3	1	0	0	0	0	0	0	0	Formicinae													<i>Camponotus japonicus</i>	0	0	1	0	0	0	0	0	0	0	0	0	<i>C. vittosus</i>	16	2	4	0	7	1	4	0	0	0	0	0	<i>Formica hayashi</i>	34	0	6	0	3	0	4	0	2	0	2	0	<i>Lasius japonicus</i>	10	0	8	1	2	0	1	0	0	0	0	0	<i>Nyländeria flavipes</i>	3	0	0	0	0	0	0	0	0	0	0	0	<i>Nyländeria sakurai</i>	9	0	0	0	0	0	0	0	0	0	0	0	Number of trees with ants	133/135		33/40		20/25		10/12		10/12		10/12		Ratio (%) of trees without ants	1.5		17.5		20.0		16.7		8.3		8.3		Total number of ant species	14		12		9		7		8		8		Species number per tree	2.02±0.98		1.73±1.41		1.44±1.16		1.25±0.97		1.42±1.00		1.42±1.00		Range	0–5		0–6		0–4		0–3		0–3		0–3		Total number of ant-nested trees	51		13		11		4		5		5		Ratio (%) of ant-nested trees	37.8		32.5		44.0		33.3		41.7		41.7	
<i>Ochetellus glaber</i>	19	2	0	0	2	0	2	0	3	0	3	2	<i>Tapinoma melanocephalum</i>	9	0	11	0	2		0	0	2		2	0	Myrmicinae													<i>Crematogaster matsumurai</i>	33	28	20	8	7	8	2	2	3	1	3	1	<i>C. osakensis</i>	1	0	2	0	0	0	0	0	0	0	0	0	<i>C. vagula</i>	18	11	2	1	3	3	2	2	3	2	3	2	<i>Monomorium chinense</i>	5	0	1	0	0	0	0	0	1	0	1	0	<i>Pheidole noda</i>	26	0	1	0	0	0	0	0	1	0	1	0	<i>Pristomyrmex punctatus</i>	69	2	11	1	8	0	2	0	2	0	2	0	<i>Tetramorium nipponense</i>	23	7	3	3	1	0	0	0	0	0	0	0	Formicinae													<i>Camponotus japonicus</i>	0	0	1	0	0	0	0	0	0	0	0	0	<i>C. vittosus</i>	16	2	4	0	7	1	4	0	0	0	0	0	<i>Formica hayashi</i>	34	0	6	0	3	0	4	0	2	0	2	0	<i>Lasius japonicus</i>	10	0	8	1	2	0	1	0	0	0	0	0	<i>Nyländeria flavipes</i>	3	0	0	0	0	0	0	0	0	0	0	0	<i>Nyländeria sakurai</i>	9	0	0	0	0	0	0	0	0	0	0	0	Number of trees with ants	133/135		33/40		20/25		10/12		10/12		10/12		Ratio (%) of trees without ants	1.5		17.5		20.0		16.7		8.3		8.3		Total number of ant species	14		12		9		7		8		8		Species number per tree	2.02±0.98		1.73±1.41		1.44±1.16		1.25±0.97		1.42±1.00		1.42±1.00		Range	0–5		0–6		0–4		0–3		0–3		0–3		Total number of ant-nested trees	51		13		11		4		5		5		Ratio (%) of ant-nested trees	37.8		32.5		44.0		33.3		41.7		41.7														
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<i>Crematogaster matsumurai</i>	33	28	20	8	7	8	2	2	3	1	3	1	<i>C. osakensis</i>	1	0	2	0	0	0	0	0	0	0	0	0	<i>C. vagula</i>	18	11	2	1	3	3	2	2	3	2	3	2	<i>Monomorium chinense</i>	5	0	1	0	0	0	0	0	1	0	1	0	<i>Pheidole noda</i>	26	0	1	0	0	0	0	0	1	0	1	0	<i>Pristomyrmex punctatus</i>	69	2	11	1	8	0	2	0	2	0	2	0	<i>Tetramorium nipponense</i>	23	7	3	3	1	0	0	0	0	0	0	0	Formicinae													<i>Camponotus japonicus</i>	0	0	1	0	0	0	0	0	0	0	0	0	<i>C. vittosus</i>	16	2	4	0	7	1	4	0	0	0	0	0	<i>Formica hayashi</i>	34	0	6	0	3	0	4	0	2	0	2	0	<i>Lasius japonicus</i>	10	0	8	1	2	0	1	0	0	0	0	0	<i>Nyländeria flavipes</i>	3	0	0	0	0	0	0	0	0	0	0	0	<i>Nyländeria sakurai</i>	9	0	0	0	0	0	0	0	0	0	0	0	Number of trees with ants	133/135		33/40		20/25		10/12		10/12		10/12		Ratio (%) of trees without ants	1.5		17.5		20.0		16.7		8.3		8.3		Total number of ant species	14		12		9		7		8		8		Species number per tree	2.02±0.98		1.73±1.41		1.44±1.16		1.25±0.97		1.42±1.00		1.42±1.00		Range	0–5		0–6		0–4		0–3		0–3		0–3		Total number of ant-nested trees	51		13		11		4		5		5		Ratio (%) of ant-nested trees	37.8		32.5		44.0		33.3		41.7		41.7																																																					
<i>C. osakensis</i>	1	0	2	0	0	0	0	0	0	0	0	0	<i>C. vagula</i>	18	11	2	1	3	3	2	2	3	2	3	2	<i>Monomorium chinense</i>	5	0	1	0	0	0	0	0	1	0	1	0	<i>Pheidole noda</i>	26	0	1	0	0	0	0	0	1	0	1	0	<i>Pristomyrmex punctatus</i>	69	2	11	1	8	0	2	0	2	0	2	0	<i>Tetramorium nipponense</i>	23	7	3	3	1	0	0	0	0	0	0	0	Formicinae													<i>Camponotus japonicus</i>	0	0	1	0	0	0	0	0	0	0	0	0	<i>C. vittosus</i>	16	2	4	0	7	1	4	0	0	0	0	0	<i>Formica hayashi</i>	34	0	6	0	3	0	4	0	2	0	2	0	<i>Lasius japonicus</i>	10	0	8	1	2	0	1	0	0	0	0	0	<i>Nyländeria flavipes</i>	3	0	0	0	0	0	0	0	0	0	0	0	<i>Nyländeria sakurai</i>	9	0	0	0	0	0	0	0	0	0	0	0	Number of trees with ants	133/135		33/40		20/25		10/12		10/12		10/12		Ratio (%) of trees without ants	1.5		17.5		20.0		16.7		8.3		8.3		Total number of ant species	14		12		9		7		8		8		Species number per tree	2.02±0.98		1.73±1.41		1.44±1.16		1.25±0.97		1.42±1.00		1.42±1.00		Range	0–5		0–6		0–4		0–3		0–3		0–3		Total number of ant-nested trees	51		13		11		4		5		5		Ratio (%) of ant-nested trees	37.8		32.5		44.0		33.3		41.7		41.7																																																																		
<i>C. vagula</i>	18	11	2	1	3	3	2	2	3	2	3	2	<i>Monomorium chinense</i>	5	0	1	0	0	0	0	0	1	0	1	0	<i>Pheidole noda</i>	26	0	1	0	0	0	0	0	1	0	1	0	<i>Pristomyrmex punctatus</i>	69	2	11	1	8	0	2	0	2	0	2	0	<i>Tetramorium nipponense</i>	23	7	3	3	1	0	0	0	0	0	0	0	Formicinae													<i>Camponotus japonicus</i>	0	0	1	0	0	0	0	0	0	0	0	0	<i>C. vittosus</i>	16	2	4	0	7	1	4	0	0	0	0	0	<i>Formica hayashi</i>	34	0	6	0	3	0	4	0	2	0	2	0	<i>Lasius japonicus</i>	10	0	8	1	2	0	1	0	0	0	0	0	<i>Nyländeria flavipes</i>	3	0	0	0	0	0	0	0	0	0	0	0	<i>Nyländeria sakurai</i>	9	0	0	0	0	0	0	0	0	0	0	0	Number of trees with ants	133/135		33/40		20/25		10/12		10/12		10/12		Ratio (%) of trees without ants	1.5		17.5		20.0		16.7		8.3		8.3		Total number of ant species	14		12		9		7		8		8		Species number per tree	2.02±0.98		1.73±1.41		1.44±1.16		1.25±0.97		1.42±1.00		1.42±1.00		Range	0–5		0–6		0–4		0–3		0–3		0–3		Total number of ant-nested trees	51		13		11		4		5		5		Ratio (%) of ant-nested trees	37.8		32.5		44.0		33.3		41.7		41.7																																																																															
<i>Monomorium chinense</i>	5	0	1	0	0	0	0	0	1	0	1	0	<i>Pheidole noda</i>	26	0	1	0	0	0	0	0	1	0	1	0	<i>Pristomyrmex punctatus</i>	69	2	11	1	8	0	2	0	2	0	2	0	<i>Tetramorium nipponense</i>	23	7	3	3	1	0	0	0	0	0	0	0	Formicinae													<i>Camponotus japonicus</i>	0	0	1	0	0	0	0	0	0	0	0	0	<i>C. vittosus</i>	16	2	4	0	7	1	4	0	0	0	0	0	<i>Formica hayashi</i>	34	0	6	0	3	0	4	0	2	0	2	0	<i>Lasius japonicus</i>	10	0	8	1	2	0	1	0	0	0	0	0	<i>Nyländeria flavipes</i>	3	0	0	0	0	0	0	0	0	0	0	0	<i>Nyländeria sakurai</i>	9	0	0	0	0	0	0	0	0	0	0	0	Number of trees with ants	133/135		33/40		20/25		10/12		10/12		10/12		Ratio (%) of trees without ants	1.5		17.5		20.0		16.7		8.3		8.3		Total number of ant species	14		12		9		7		8		8		Species number per tree	2.02±0.98		1.73±1.41		1.44±1.16		1.25±0.97		1.42±1.00		1.42±1.00		Range	0–5		0–6		0–4		0–3		0–3		0–3		Total number of ant-nested trees	51		13		11		4		5		5		Ratio (%) of ant-nested trees	37.8		32.5		44.0		33.3		41.7		41.7																																																																																												
<i>Pheidole noda</i>	26	0	1	0	0	0	0	0	1	0	1	0	<i>Pristomyrmex punctatus</i>	69	2	11	1	8	0	2	0	2	0	2	0	<i>Tetramorium nipponense</i>	23	7	3	3	1	0	0	0	0	0	0	0	Formicinae													<i>Camponotus japonicus</i>	0	0	1	0	0	0	0	0	0	0	0	0	<i>C. vittosus</i>	16	2	4	0	7	1	4	0	0	0	0	0	<i>Formica hayashi</i>	34	0	6	0	3	0	4	0	2	0	2	0	<i>Lasius japonicus</i>	10	0	8	1	2	0	1	0	0	0	0	0	<i>Nyländeria flavipes</i>	3	0	0	0	0	0	0	0	0	0	0	0	<i>Nyländeria sakurai</i>	9	0	0	0	0	0	0	0	0	0	0	0	Number of trees with ants	133/135		33/40		20/25		10/12		10/12		10/12		Ratio (%) of trees without ants	1.5		17.5		20.0		16.7		8.3		8.3		Total number of ant species	14		12		9		7		8		8		Species number per tree	2.02±0.98		1.73±1.41		1.44±1.16		1.25±0.97		1.42±1.00		1.42±1.00		Range	0–5		0–6		0–4		0–3		0–3		0–3		Total number of ant-nested trees	51		13		11		4		5		5		Ratio (%) of ant-nested trees	37.8		32.5		44.0		33.3		41.7		41.7																																																																																																									
<i>Pristomyrmex punctatus</i>	69	2	11	1	8	0	2	0	2	0	2	0	<i>Tetramorium nipponense</i>	23	7	3	3	1	0	0	0	0	0	0	0	Formicinae													<i>Camponotus japonicus</i>	0	0	1	0	0	0	0	0	0	0	0	0	<i>C. vittosus</i>	16	2	4	0	7	1	4	0	0	0	0	0	<i>Formica hayashi</i>	34	0	6	0	3	0	4	0	2	0	2	0	<i>Lasius japonicus</i>	10	0	8	1	2	0	1	0	0	0	0	0	<i>Nyländeria flavipes</i>	3	0	0	0	0	0	0	0	0	0	0	0	<i>Nyländeria sakurai</i>	9	0	0	0	0	0	0	0	0	0	0	0	Number of trees with ants	133/135		33/40		20/25		10/12		10/12		10/12		Ratio (%) of trees without ants	1.5		17.5		20.0		16.7		8.3		8.3		Total number of ant species	14		12		9		7		8		8		Species number per tree	2.02±0.98		1.73±1.41		1.44±1.16		1.25±0.97		1.42±1.00		1.42±1.00		Range	0–5		0–6		0–4		0–3		0–3		0–3		Total number of ant-nested trees	51		13		11		4		5		5		Ratio (%) of ant-nested trees	37.8		32.5		44.0		33.3		41.7		41.7																																																																																																																						
<i>Tetramorium nipponense</i>	23	7	3	3	1	0	0	0	0	0	0	0	Formicinae													<i>Camponotus japonicus</i>	0	0	1	0	0	0	0	0	0	0	0	0	<i>C. vittosus</i>	16	2	4	0	7	1	4	0	0	0	0	0	<i>Formica hayashi</i>	34	0	6	0	3	0	4	0	2	0	2	0	<i>Lasius japonicus</i>	10	0	8	1	2	0	1	0	0	0	0	0	<i>Nyländeria flavipes</i>	3	0	0	0	0	0	0	0	0	0	0	0	<i>Nyländeria sakurai</i>	9	0	0	0	0	0	0	0	0	0	0	0	Number of trees with ants	133/135		33/40		20/25		10/12		10/12		10/12		Ratio (%) of trees without ants	1.5		17.5		20.0		16.7		8.3		8.3		Total number of ant species	14		12		9		7		8		8		Species number per tree	2.02±0.98		1.73±1.41		1.44±1.16		1.25±0.97		1.42±1.00		1.42±1.00		Range	0–5		0–6		0–4		0–3		0–3		0–3		Total number of ant-nested trees	51		13		11		4		5		5		Ratio (%) of ant-nested trees	37.8		32.5		44.0		33.3		41.7		41.7																																																																																																																																			
Formicinae													<i>Camponotus japonicus</i>	0	0	1	0	0	0	0	0	0	0	0	0	<i>C. vittosus</i>	16	2	4	0	7	1	4	0	0	0	0	0	<i>Formica hayashi</i>	34	0	6	0	3	0	4	0	2	0	2	0	<i>Lasius japonicus</i>	10	0	8	1	2	0	1	0	0	0	0	0	<i>Nyländeria flavipes</i>	3	0	0	0	0	0	0	0	0	0	0	0	<i>Nyländeria sakurai</i>	9	0	0	0	0	0	0	0	0	0	0	0	Number of trees with ants	133/135		33/40		20/25		10/12		10/12		10/12		Ratio (%) of trees without ants	1.5		17.5		20.0		16.7		8.3		8.3		Total number of ant species	14		12		9		7		8		8		Species number per tree	2.02±0.98		1.73±1.41		1.44±1.16		1.25±0.97		1.42±1.00		1.42±1.00		Range	0–5		0–6		0–4		0–3		0–3		0–3		Total number of ant-nested trees	51		13		11		4		5		5		Ratio (%) of ant-nested trees	37.8		32.5		44.0		33.3		41.7		41.7																																																																																																																																																
<i>Camponotus japonicus</i>	0	0	1	0	0	0	0	0	0	0	0	0	<i>C. vittosus</i>	16	2	4	0	7	1	4	0	0	0	0	0	<i>Formica hayashi</i>	34	0	6	0	3	0	4	0	2	0	2	0	<i>Lasius japonicus</i>	10	0	8	1	2	0	1	0	0	0	0	0	<i>Nyländeria flavipes</i>	3	0	0	0	0	0	0	0	0	0	0	0	<i>Nyländeria sakurai</i>	9	0	0	0	0	0	0	0	0	0	0	0	Number of trees with ants	133/135		33/40		20/25		10/12		10/12		10/12		Ratio (%) of trees without ants	1.5		17.5		20.0		16.7		8.3		8.3		Total number of ant species	14		12		9		7		8		8		Species number per tree	2.02±0.98		1.73±1.41		1.44±1.16		1.25±0.97		1.42±1.00		1.42±1.00		Range	0–5		0–6		0–4		0–3		0–3		0–3		Total number of ant-nested trees	51		13		11		4		5		5		Ratio (%) of ant-nested trees	37.8		32.5		44.0		33.3		41.7		41.7																																																																																																																																																													
<i>C. vittosus</i>	16	2	4	0	7	1	4	0	0	0	0	0	<i>Formica hayashi</i>	34	0	6	0	3	0	4	0	2	0	2	0	<i>Lasius japonicus</i>	10	0	8	1	2	0	1	0	0	0	0	0	<i>Nyländeria flavipes</i>	3	0	0	0	0	0	0	0	0	0	0	0	<i>Nyländeria sakurai</i>	9	0	0	0	0	0	0	0	0	0	0	0	Number of trees with ants	133/135		33/40		20/25		10/12		10/12		10/12		Ratio (%) of trees without ants	1.5		17.5		20.0		16.7		8.3		8.3		Total number of ant species	14		12		9		7		8		8		Species number per tree	2.02±0.98		1.73±1.41		1.44±1.16		1.25±0.97		1.42±1.00		1.42±1.00		Range	0–5		0–6		0–4		0–3		0–3		0–3		Total number of ant-nested trees	51		13		11		4		5		5		Ratio (%) of ant-nested trees	37.8		32.5		44.0		33.3		41.7		41.7																																																																																																																																																																										
<i>Formica hayashi</i>	34	0	6	0	3	0	4	0	2	0	2	0	<i>Lasius japonicus</i>	10	0	8	1	2	0	1	0	0	0	0	0	<i>Nyländeria flavipes</i>	3	0	0	0	0	0	0	0	0	0	0	0	<i>Nyländeria sakurai</i>	9	0	0	0	0	0	0	0	0	0	0	0	Number of trees with ants	133/135		33/40		20/25		10/12		10/12		10/12		Ratio (%) of trees without ants	1.5		17.5		20.0		16.7		8.3		8.3		Total number of ant species	14		12		9		7		8		8		Species number per tree	2.02±0.98		1.73±1.41		1.44±1.16		1.25±0.97		1.42±1.00		1.42±1.00		Range	0–5		0–6		0–4		0–3		0–3		0–3		Total number of ant-nested trees	51		13		11		4		5		5		Ratio (%) of ant-nested trees	37.8		32.5		44.0		33.3		41.7		41.7																																																																																																																																																																																							
<i>Lasius japonicus</i>	10	0	8	1	2	0	1	0	0	0	0	0	<i>Nyländeria flavipes</i>	3	0	0	0	0	0	0	0	0	0	0	0	<i>Nyländeria sakurai</i>	9	0	0	0	0	0	0	0	0	0	0	0	Number of trees with ants	133/135		33/40		20/25		10/12		10/12		10/12		Ratio (%) of trees without ants	1.5		17.5		20.0		16.7		8.3		8.3		Total number of ant species	14		12		9		7		8		8		Species number per tree	2.02±0.98		1.73±1.41		1.44±1.16		1.25±0.97		1.42±1.00		1.42±1.00		Range	0–5		0–6		0–4		0–3		0–3		0–3		Total number of ant-nested trees	51		13		11		4		5		5		Ratio (%) of ant-nested trees	37.8		32.5		44.0		33.3		41.7		41.7																																																																																																																																																																																																				
<i>Nyländeria flavipes</i>	3	0	0	0	0	0	0	0	0	0	0	0	<i>Nyländeria sakurai</i>	9	0	0	0	0	0	0	0	0	0	0	0	Number of trees with ants	133/135		33/40		20/25		10/12		10/12		10/12		Ratio (%) of trees without ants	1.5		17.5		20.0		16.7		8.3		8.3		Total number of ant species	14		12		9		7		8		8		Species number per tree	2.02±0.98		1.73±1.41		1.44±1.16		1.25±0.97		1.42±1.00		1.42±1.00		Range	0–5		0–6		0–4		0–3		0–3		0–3		Total number of ant-nested trees	51		13		11		4		5		5		Ratio (%) of ant-nested trees	37.8		32.5		44.0		33.3		41.7		41.7																																																																																																																																																																																																																	
<i>Nyländeria sakurai</i>	9	0	0	0	0	0	0	0	0	0	0	0	Number of trees with ants	133/135		33/40		20/25		10/12		10/12		10/12		Ratio (%) of trees without ants	1.5		17.5		20.0		16.7		8.3		8.3		Total number of ant species	14		12		9		7		8		8		Species number per tree	2.02±0.98		1.73±1.41		1.44±1.16		1.25±0.97		1.42±1.00		1.42±1.00		Range	0–5		0–6		0–4		0–3		0–3		0–3		Total number of ant-nested trees	51		13		11		4		5		5		Ratio (%) of ant-nested trees	37.8		32.5		44.0		33.3		41.7		41.7																																																																																																																																																																																																																														
Number of trees with ants	133/135		33/40		20/25		10/12		10/12		10/12																																																																																																																																																																																																																																																																																																																									
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Range	0–5		0–6		0–4		0–3		0–3		0–3																																																																																																																																																																																																																																																																																																																									
Total number of ant-nested trees	51		13		11		4		5		5																																																																																																																																																																																																																																																																																																																									
Ratio (%) of ant-nested trees	37.8		32.5		44.0		33.3		41.7		41.7																																																																																																																																																																																																																																																																																																																									

The total number of observed trees is given in brackets

The nests of *Cr. matsumurai* were found on 47 (21%) trees out of 224 (Table 2). While in most cases we observed only one nest per three trees, one of each of *P. x yedoensis*, *Q. acutissima* and *A. palmatum* were inhabited by two ant colonies. The combinations of ant species on these trees were *Cr. matsumurai* and *C. vitiosus*, *T. nipponense* and *P. punctatus*, and *C. vitiosus* and *Cr. vagula*, respectively. *Cr. matsumurai* and *Cr. vagula* nests were not observed together on any tree. On 135 *P. x yedoensis* trees with ant nests, 65 percent of the nests were found in the DBH classes 10–15 cm and 15–20 cm (Table 3). On these 135 *Prunus x yedoensis* trees, 28 nests of *Cr. matsumurai* and 11 nests of *Cr. vagula* were found, though nests of these two species were never observed together on single trees, the presence and absence of the nests were not differing on trees with and without the corresponding species (Fisher's Exact test $\chi^2 = 3.13$, $p_{\text{two-sided}} < 0.12$).

DISCUSSION

In the present study, 15 ant species belonging to 11 genera were observed on trees. These species figure corresponds to 50 percent of the total number of ant species (30) so far recorded from Joyama Park (Harada 2008). Iwata *et al.* (2005) reported 18 species belonging to 11 genera (46.2% of the 39 recorded species) from trees in Nanatsujima Park, Kagoshima City. The mean number of species per tree was also not distinctly different between Joyama Park and Nanatsujima

Park (both in Kagoshima Prefecture): 1.87 with a range from 0 to 6, and 2.07 with a range from 1 to 7, respectively. These figures thus represent the approximate number of species found on trees and number of species per tree in parks of this region.

Of the 15 species, seven (46.7%) nested on trees, but only three species (20%), *Cr. matsumurai*, *Cr. vagula* and *C. vitiosus*, are considered principally arboreal nesters (roughly corresponding to truly arboricolous species *sensu* Seifert, 2008), while the other four nested mainly on the ground surface or in soil. For the remaining eight species, although nests were not located for all of them in the study site, in other parts of Kyushu all these nest in soil, with two species *T. melanocephalum* and *Nylanderia flavipes* F. Smith, 1874, found to nest also on the ground surface (e.g., in rotting wood and other spaces) and rarely on trees. Of the most common ant species, that is, *P. punctatus*, *Cr. matsumurai* and *F. hayashi*, only *Cr. matsumurai* was a principal arboreal nester.

The 30 ant species from the whole Joyama Park (Harada 2008) are grouped into two categories with respect to nesting site (principally arboreal nesters and principally ground nesters) based on Yamane *et al.* (2010) (Table 4). Only four were principally arboreal nesters, but of the 26 principally ground nesters, as many as 11 species climbed trees, probably to forage. This means we should be careful when the term “arboreal” ant is used for ants found on trees (Yamane 2002, Hashimoto *et al.* 2010). In Kagoshima University Arboretum, of the 27 species recorded, 16

Table 3: Number of nests of different ant species on 135 *P. x yedoensis* trees of different DBH classes

Ant species	DBH in cm					
	4–5	5–10	10–15	15–20	20–25	25
<i>Ochetellus glaber</i>	0	1	1	0	0	0
<i>Crematogaster matsumurai</i>	0	2	9	10	6	1
<i>Crematogaster vagula</i>	0	4	3	3	1	0
<i>Pristomyrmex punctatus</i>	0	1	0	0	1	0
<i>Tetramorium nipponense</i>	0	0	2	4	1	0
<i>Camponotus vitiosus</i>	0	0	1	1	0	0
Total number of ant nests	0	8	16	18	9	1
Number of trees	5	25	46	43	14	2
Ratio (%) of ant-nested trees	0	32.0	34.8	41.9	64.3	50.0

Table 4: Number of ant species nesting on trees and on/in the ground

Subfamily	species mainly nesting	
	on the tree	on/in the ground
Ponerinae	0 (0%)	3 (10%)
Dolichoderinae	0 (0%)	2 (6.7%)
Myrmicinae	3 (10%)	15 (50%)
Formicinae	1 (3.3%)	6 (20%)
Total	4 (13.3%)	26 (86.7%)

foraged in trees including nine for which arboreal nests were confirmed (Yunoki Miho, unpubl. data 2001). Of these nine species, only three are considered to be principally arboreal nesters (Yamane 2002). On the other hand, in forests of central Europe (23°51'N, 51°14'E), 51 ant species were observed regularly or occasionally foraging in tree canopies, of which 18 can be considered truly arboricolous and 14 of these real canopy dwellers (Seifert 2008). In the present study, the distinction of arboricolous ants from real canopy dwellers is not made; both are included as principally arboreal nesters, in which nests are principally constructed on trees (foraging also tends to be done on trees).

Pristomyrmex punctatus was the most frequent species among the ants found on foraging trees in the study site, followed by *Cr. matsumurai* and *F. hayashi*. Among them, only *Cr. matsumurai* is a principally arboreal nester, the others being principally ground nesters. In Nanatsujima Park, Kagoshima City, among the 18 ant species observed on trees, the most frequent was the dolichoderine *Technomyrmex brunneus* Forel, 1895 [referred to as *T. albipes* (F. Smith 1861), 60.4% of all baits], followed by *Tetramorium bicarinatum* Nylander, 1846 (18.3%) and *Camponotus japonicus* Mayr, 1866 (9.1%) (Iwata *et al.* 2005). No overlap is seen in numerically dominant species between Joyama Park and Nanatsujima Park. This can be explained by the fact that the famous tramp species *T. brunneus* (Bolton 2007; Shimana & Yamane 2009) had not been observed in Joyama Park when the survey was conducted. The occurrence of this species may have modified the whole ant fauna in Nanatsujima Park.

On 20 (8.9%) of 224 trees surveyed in the study site, no foraging ants were observed. Of 135 *Prunus x yedoensis* trees, only two (1.5%) lacked foraging ants. *Prunus x yedoensis*, *P. jamasakura* and *P. lannesiana* have extra-floral nectaries on the petiole near the base of their leaves, and their trunks tend to decay around the junctions of branches after the latter fall off. Thus, the trees of the genus *Prunus* may provide both food and nest sites for arboreal nesters. This may explain the frequent occurrence of ants on *Prunus* trees compared with other tree species. For the ants found on trees, there was no species-specific relationship between ants and tree species, although *Cr. matsumurai* seems to prefer *P. x yedoensis* and *A. palmatum* (this study: Harada *et al.*, in prep.).

The arboreal nester *Cr. matsumurai* forages both on trees and on the ground in Joyama Park. On the trees, aphids are the main solid food, and plant nectar and secretions of aphids are liquid food (Harada 2005). In a tropical rainforest in Borneo, for most ant colonies nesting in tree canopies, foraging areas were limited to the vicinities of nests and within the same type of microhabitat (within-tree position) (Tanaka *et al.* 2010). This is not the case in the temperate forests of southwest Japan, where foraging areas of tree-nesting species are often very large, and include nearby trees and the ground.

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REFERENCES

- Alvarado M, 2000. Habitat correlates of ant assemblages in different forests of the south pannonian plain. *TISCIA* 32:35–42.
- Bolton B, 2007. Taxonomy of the dolichoderine ant genus *Technomyrmex* Mayr (Hymenoptera: Formicidae) based on the worker caste. *Contributions of the American Entomological Institute* 35:1–150.
- Dolek M, Freese-Hanger A, Bussler H, Floren A, Liegl A and Schmidl J, 2009. Ants on oaks: effects of forest structure on species composition. *Journal of Insect Conservation* 13(4): 367 - 375.
- Erwin TL, 1983. Tropical forest canopies, the last biotic frontier. *Bulletin of the Entomological Society of America* 29:14–19.
- Erwin TL, 2001. Forest canopies, animal diversity. In: Levin SA (ed.) *Encyclopedia of Biodiversity* 3:19–25.
- Fiala B, Jakob A, Maschwitz U and Linsenmair K, 1990. Diversity, evolutionary specialization and geographic distribution of a mutualistic ant-plant complex: *Macaranga* and *Crematogaster* in South East Asia. *Biological Journal of the Linnean Society* 66:305–331.
- Harada Y, 2005. Diel and seasonal patterns of foraging activity in the arboreal ant *Crematogaster matsumurai* Forel. *Entomological Science* 8:167–172.
- Harada Y, 2008. Ant fauna of Joyama Park, Ijuincho, Kagoshima-Ken, southern Japan. *The Biogeographical Society of Japan* 63:87–96. (In Japanese)
- Hashimoto Y, Morimoto Y, Widodo ES, Mohamed M and Fellowes JR, 2010. Vertical habitat use and foraging activities of arboreal and ground ants (Hymenoptera: Formicidae) in a Bornean tropical rainforest. *Sociobiology* 56(2): 435–438.
- Hölldobler B and Wilson EO, 1990. *The Ants*. The Belknap Press of Harvard University Press, Cambridge, Massachusetts.
- Huxley CR, 1980. Symbiosis between ants and epiphytes. *Biological Reviews of the Cambridge Philosophical Society* 55:321–430.
- Iwata K, Eguchi K and Yamane SK, 2005. A case study on urban ant fauna of southern Kyusyu, Japan, with Notes on a New Monitoring Protocol. *Journal of Asia-Pacific Entomology* 83:263–272.
- Jolivet P, 1996. *Ants and Plants*. Backhuys Publishers, Leiden, p304.
- Kawahara Y, Hosoyamada S and Yamane Sk, 1998. Ant fauna of the Terayama station for education and research on nature, Kagoshima University. *Bulletin of the Faculty of Education, Kagoshima University, Natural Science* 50:147–156. (In Japanese)
- Malsch AKN, Rosciszewski K and Maschwitz U, 2003. The ant species richness and diversity of a primary lowland rain forest, the Pasoh Forest Reserve, West-Malaysia. In: *Pasoh Ecology of a Lowland Rain Forest in Southeast Asia* (Okuda T, Manokaran N, Matsumoto Y, Niiyama K, Thomas SC and Ashton P, eds), Springer, 347–373.
- McDonald JH, 2009. *Handbook of Biological Statistics*. 2nd edition. Sparky House Publishing, Baltimore, Maryland. Downloaded at <http://udel.edu/~mcdonald/statfishers.html> on 29.01.2011.
- Morisita M, 1939. Interactions of several ants on a tree. *Journal of Kansai Entomological Society* 9:22–42. (In Japanese)
- Morisita M, 1941. Interactions of *Formica japonica* and other ants. *Entomological Science* 15:1–9. (In Japanese)
- Myrmecological Society of Japan, 1989. *A Guide for the Identification of Japanese Ants* (I). Ponerinae, Cerapachyinae, Pseudomyrmecinae, Dorylinae and Leptanillinae, p42. (In Japanese)
- Myrmecological Society of Japan, 1991. *A Guide for the Identification of Japanese Ants* (II). Dolichoderinae and Formicinae, p56. (In Japanese.)
- Myrmecological Society of Japan, 1992. *A Guide for the Identification of Japanese Ants* (III). Myrmicinae and supplement to Leptanillinae, p94. (In Japanese)
- Punttila P, 1996. Succession, forest fragmentation, and the distribution of wood ants. In *Oikos* 75:291–298.
- Schulz A and Wagner T, 2002. Influence of forest type and tree species on canopy ants (Hymenoptera: Formicidae) in Budongo Forest, Uganda. *Oecologia* 133:224–232.
- Seifert B, 2008. The ants of Central European tree canopies (Hymenoptera: Formicidae)—an underestimated population? In: *Canopy arthropod research in Europe* (Floren A and Schmidl J, eds), Bioform Entomology, Nuernberg, 157–173.

- Shimana Y and Yamane Sk, 2009. Geographical distribution of *Technomyrmex brunneus* Forel (Hymenoptera: Formicidae) in the western part of the mainland of Kagoshima, South Kyushu, Japan. *Ari* 32:9–19.
- Tanaka H, Yamane Sk and Itioka T, 2010. Within-tree distribution of nest sites and foraging areas of ants on canopy trees in a tropical rainforest in Borneo. *Population Ecology* 52:147–157.
- Terayama M, 2005. Ants from the Akasaka Imperial Gardens, Tokyo. *Memoirs of the National Science Museum* 39:239–243. (In Japanese)
- Tobin JE, 1991. A neotropical rainforest canopy ant community: some ecological considerations. In: *Ant-Plant Interactions* (Huxley CR and Cutler DF, eds), Oxford University Press, Oxford, UK, 536–538.
- Wilson E O, 1987. The arboreal ant fauna of Peruvian Amazon forest: a first assessment. *Biotropica* 19(3): 245–251.
- Yamane Sk, 2002. The distribution and the diversity of ant in Southeast Asia. In: *Natural History of Social Wasps and Bees* (Sugiura N, Ito F and Maeda Y, eds), Hokkaido University Press, 179–193. (In Japanese)
- Yamane Sk, Harada Y and Eguchi K, 2010. *Natural History of Ants in South Kyushu, Japan*. Nanpo-sinsha, Kagoshima, p200. (In Japanese)
- Yamaoka H, 1978. Arboreal ants in Chiba-ken, ant fauna and colony composition, No. 3. *Chiba-seibutsuchi* 28(1): 14–18. (In Japanese)
- Yamaoka H, 1979. Dead twigs as nesting spaces for ants. *Chiba-seibutsushi* 29:1–9. (In Japanese)
- Yamaoka H, 1983. Arboreal ants of forest of Sakato-jinja. *Chiba-seibutsuchi* 33(1): 26–30. (In Japanese)