Insect. Soc. (2011) 58:417–426
DOI 10.1007/s00040-011-0159-9

Insectes Sociaux

RESEARCH ARTICLE

Feeding habits of Hymenoptera and Isoptera in a tropical rain forest as revealed by nitrogen and carbon isotope ratios

**F. Hyodo · Y. Takematsu · T. Matsumoto ·
Y. Inui · T. Itioka**

Received: 8 October 2010 / Revised: 10 March 2011 / Accepted: 14 March 2011 / Published online: 27 March 2011

Abstract Despite the recognition of the functional role of Hymenoptera (ants, bees and wasps) and Isoptera (termites) in tropical ecosystems, their detailed feeding habits are not well known. To examine the feeding habits of these groups, we measured nitrogen (N) and carbon (C) stable isotope ratios (δ^{15}N and δ^{13}C) of hymenopterans (12 families, ≥16 genera and ≥32 species) and isopterans (one family and 10 species) collected in a tropical rain forest, Sarawak, Malaysia. We compared the isotopic signatures of these insects to those previously reported for other consumers collected in the same forest. The δ^{15}N and δ^{13}C values of these insects overlapped with those of the other consumers, indicating that they have access to diverse C and N sources in the forest. The δ^{15}N values of ants and termites indicated that their feeding habits range along a continuum from herbivory (i.e. dependent on honeydew and nectar) to predation and from wood-feeders to soil-feeders, respectively. In addition, the δ^{15}N values of wasps varied greatly from −0.1‰ (Braconidae sp.) to 8.6‰ (*Bembix* sp.), suggesting that their feeding habits also range from omnivory to predation. The ant species *Camponotus gigas* had δ^{13}C values similar to those of invertebrate detritivores and omnivores rather than to those of invertebrate herbivores, although the diet of this species consists mostly of honeydew. This discrepancy suggests that the ant uses carbohydrates as an energy source, the isotopic signatures of which are not well retained in the body tissues. Values of both δ^{15}N and δ^{13}C of the predatory army ant *Leptogenys diminuta* and the soil-feeding termite *Dicuspiditermes nemorosus* did not differ significantly, indicating that both trophic level and the humification of feeding substrates can increase the isotopic signatures of terrestrial consumers.

Keywords Carbon and nitrogen isotopes · Ants · Bees · Wasps · Termites · Lambir National Park

Introduction

Hymenoptera and Isoptera are highly abundant and diverse insect groups within tropical ecosystems (Brian, 1978; Roubik, 1989; Hölldobler and Wilson, 1990; Abe et al., 2000). In an Amazonian tropical forest, ants and termites comprise one-third of total animal biomass, and together with wasps and bees, they constitute 75% of overall insect abundance (Fittkau and Klinge, 1973). These animals have long been recognised to play major roles in tropical rain forest ecosystems. For example, ants function as scavengers and predators (Hölldobler and Wilson, 1990), and through associations with aphids and homopterans, some ant species can access plant-derived food sources and thus function as herbivores (Blüthgen et al., 2003; Davidson et al., 2003). With the aid of microbial symbionts, termites decompose

---

F. Hyodo (✉)
Research Core for Interdisciplinary Sciences,
Okayama University, 3-1-1, Tsushimanaka,
Okayama 700-8530, Japan
e-mail: fhyodo@cc.okayama-u.ac.jp

Y. Takematsu
Department of Biological Environmental Sciences,
Yamaguchi University, 1677-1, Yoshida,
Yamaguchi 735-5838, Japan

T. Matsumoto · T. Itioka
Graduate School of Human and Environmental Studies,
Kyoto University, Yoshida-Nihonmatsu, Sakyo,
Kyoto 606-8501, Japan

Y. Inui
Department of Arts and Sciences, Osaka Kyoiku University,
4-698-1, Asahigaoka, Kashiwara, Osaka 582-8582, Japan

substantial amounts of organic matter at different stages of decomposition, from fresh plant material to soil organic matter (Breznak and Brune, 1994; Bignell and Eggleton, 2000; Watanabe and Tokuda, 2010). Wasps can function as predators or parasitoids (Richter, 2000), and bees serve as pollinators in tropical rain forests, where many plant species are dependent on bees for pollen transfer (Roubik, 1989; Momose et al., 1998).

Despite their importance in ecosystems, the precise feeding habits of these insects are not well understood. One reason for the lack of information is that the feeding behaviours of some species are difficult to directly observe due to their cryptic lifestyle (e.g. nocturnal foraging or living in canopy layers or below ground). Another reason is that the food sources of these animals consist of several food items, making quantifying the relative contribution of each food source difficult. For example, some ant and wasp species feed on both nectar and animal prey (Hölldobler and Wilson, 1990; Gadagkar, 1991; Matsuura, 1991). In addition, soil organic matter, which is the food source of soil-feeding termites, is highly complex and composed of minerals, decayed plant materials and micro-organisms (Bignell and Eggleton, 2000). Most importantly, estimating the food sources assimilated by insects is extremely difficult using field observations.

Stable isotope techniques have been widely used to determine the feeding habits and trophic positions of consumers within ecosystems (Post, 2002; Fry, 2006). This technique is based on the assumptions that the nitrogen (N) isotope ratios (δ^{15}N) of animals are approximately 3.4‰ higher than those of their diets, whereas the carbon (C) isotope ratios (δ^{13}C) of animals are similar (<1‰) to those of their diets (DeNiro and Epstein, 1978; Minagawa and Wada, 1984). Considering the energy transfer efficiency through the food chain (Lindeman, 1942) and resource partitioning, which could allow species coexistence (Tilman, 1982), the great biomass and diversity of the hymenopterans and isopterans predict that many species are dependent on the most abundant food sources in the ecosystem, such as primary production or dead organic matter, and that they consume a broad spectrum of food resources. Indeed, these predictions have been partly confirmed by the stable isotope technique. For example, the high abundance of ants in canopy layers was once considered a paradox due to the scarcity of potential prey that could support such large ant populations. Nitrogen isotopic studies revealed that most canopy ants are dependent on honeydew and nectar via aphids and homopterans (Blüthgen et al., 2003; Davidson et al., 2003). In termites, the C and N isotopic signatures correspond well to their known feeding habits and vary greatly, indicating the diversification of food resource utilization (Higashi and Abe, 1996; Tayasu et al., 1997; Bourguignon et al., 2009). However, the C and N isotopic signatures of many species of tropical ants and termites, and especially of wasps, are still unexplored.

Here, we measured the δ^{15}N and δ^{13}C values of ants, bees, wasps and termites collected from a tropical rain forest in Sarawak, Malaysia. We then compared their C and N isotopic signatures to those previously reported for other consumers of four trophic groups (detritivores, herbivores, omnivores and predators) in the same forest (Hyodo et al., 2010b). We hypothesised that the isotopic signatures of these insects would indicate diverse feeding habits ranging from herbivory, omnivory (and detritivory for termites) to predatory, which could overlap with the other consumers.

Materials and methods

Study site and sample collection

Sampling was conducted in Lambir National Park (4°02′ N, 113°05′ E, 20–150 m asl), Sarawak, Malaysia, from November 2004 to June 2005. Mean annual rainfall is approximately 2,700 mm, with no distinct dry season. The hymenopterans (12 families, ≥16 genera and ≥32 species) and isopterans (one family and 10 species) used in this study and their known feeding habits are listed in Table 1. These insects were collected randomly from the forest floor or from soil and deadwood. Some individuals were also collected from canopy layers using a walkway and tower crane system (Yumoto and Nakashizuka, 2005). Collected insects were kept in a freezer for 24 h to terminate their activity and were then dried in a drying oven at 60°C for 24 h. The whole bodies of the insects were ground into powder using a mortar and pestle prior to analyses. We also compared the isotopic signatures of the hymenopterans and isopterans to those previously reported for detritivores, herbivores, omnivores and predators (Hyodo et al., 2010b). The data of the fungus-growing termite, *Macrotermes malaccensis* and the soil-feeding termite, *Dicuspiditermes nemorosus* have already been reported (Hyodo et al., 2010b).

Stable N and C isotope analyses

For stable N and C isotope analyses, the samples were placed in tin capsules, and isotope ratios were then measured using a mass spectrometer (Delta^{plus} XP, Germany) coupled with an elemental analyser. The precision of the online procedure was better than ±0.2‰ for both isotope ratios. The natural abundances of ^{15}N and ^{13}C are expressed in per mil (‰) deviation from international standards: δ^{15}N or $\delta^{13}C = (R_{sample}/R_{standard} - 1) \times 1{,}000$, where R in δ^{15}N or δ^{13}C is ^{15}N/^{14}N or ^{13}C/^{12}C, respectively. Atmospheric N and Pee Dee belemnite were used as the international standards for N and C, respectively.

Statistical analyses

To examine whether δ^{15}N or δ^{13}C values differed among species within each group (i.e. ants, wasps and termites), we used one-way analysis of variance (ANOVA) for samples with more than three replicates of individuals (wasps) or colonies (ants and termites). For comparisons of bee species (*Apis* spp. and *Trigona* spp.), we used *t* tests. Some samples of the same genera were treated as one group due to the small sample size, assuming that congeners exhibited similar feeding habits. These species included two species of *Apis* (*A. dorsata* and *A. koschevnikovi*), four species of *Trigona* (*T. itama*, *T. melanocephala*, *T. fimbriata* and one unidentified species) and two species of *Ropalidia* (*R. flavopicta* and an unidentified species). Tukey–Kramer honestly significant difference (HSD) tests were applied to examine differences among species.

We also examined differences in δ^{15}N and δ^{13}C values among all species with more than three replicates using one-way ANOVA. Tukey–Kramer HSD post hoc tests were also applied to test for differences among species. These statistical analyses were performed using JMP statistical software (version 8.0.2 for Macintosh; SAS Institute, Cary, NC, USA).

Results

δ^{15}N of ants, bees, wasps and termites

δ^{15}N values varied significantly among ant species ($F_{5,36} = 34.7$, $P < 0.0001$; Fig. 1; Table 1; Appendix). *Crematogaster borneensis*, which depends on food bodies produced by the myrmetic host plants (*Macaranga trachyphylla*), had lower δ^{15}N than the other species, whereas the predatory army ants *Leptogenys diminuta* had the highest values of δ^{15}N. The δ^{15}N of honey bees (*Apis* spp.) was significantly lower than that of stingless bees (*Trigona* spp.) ($t = 4.80$, $P = 0.00006$). The other bees showed low δ^{15}N values. For wasps, δ^{15}N values varied widely among species ($F_{4,14} = 20.3$, $P < 0.0001$). The paper wasp *Ropalidia* spp. and the nocturnal wasp *Provespa anomala* were significantly depleted in ^{15}N compared to the sand wasp *Bembix* sp., and the parasitoid wasp Ichneumonidae sp. (*Bembecinus* sp.) exhibited δ^{15}N values intermediate between these two groups. The spider-hunting wasps Pompilidae sp. and *Chalybion bengalense* had high values of δ^{15}N, which were similar to those of *Bembix* sp., although the results for these species were not statistically tested due to the lack of replication. The δ^{15}N of termites also varied widely ($F_{6,44} = 197.0$, $P < 0.0001$). The soil-feeding termite *D. nemorosus* had similar δ^{15}N values to those of the soil/wood interface-feeding termite *Prohamitermes mirabilis*, both of which were significantly higher than the other termite species. In addition, the δ^{15}N of *Homallotermes foraminifera*, which was classified as a soil/wood interface feeder, was significantly lower than that of the soil-feeding termite, *D. nemorosus*, but was similar to that of the litter-feeding termite *Longipeditermes longipes*. The lichen-feeding termite *Hospitalitermes hospitalis* had significantly lower δ^{15}N values compared to the other termite species. The wood-feeding termite, *Microcerotermes sabahensis* and the fungus-growing termite (*M. malaccensis* and the other two fungus-growing species) had intermediate δ^{15}N values.

Values of δ^{15}N significantly differed among all the species examined ($F_{19,93} = 64.4$, $P < 0.0001$). *Bembix* sp. was the most enriched in ^{15}N compared to the other insects, with the exceptions of *L. diminuta* and *D. nemorosus*. *Hospitalitermes hospitalis* was significantly more depleted in ^{15}N than the other species, except for *Apis* spp. and the fungus-growing termite *M. malaccensis*. Note that the values of ^{15}N for the termites, *D. nemorosus*, *P. mirabilis* and *Termes rostratus* did not significantly differ from those of the predatory wasps, Pompilidae sp., *C. bengalense* and *Bembix* sp., the parasitoid wasp, Ichneumonidae sp., or the army ant *L. diminuta*.

δ^{13}C of ants, bees, wasps and termites

Values of δ^{13}C significantly differed among ant species ($F_{5,36} = 69.8$, $P < 0.0001$); the δ^{13}C of *C. borneensis* was significantly lower than values for the other ant species. For bees, *Apis* spp. were more enriched in ^{13}C than *Trigona* spp. ($t = 4.795$, $P = 0.0006$). The δ^{13}C values of wasp species did not differ significantly ($F_{4,14} = 2.796$, $P = 0.0698$) and the other bees had variable δ^{13}C values. Values of δ^{13}C for termites differed significantly among species ($F_{6,44} = 13.2$, $P < 0.0001$). Termite species feeding on decomposed organic matter (i.e. *D. nemorosus*, *P. mirabilis*, *H. foraminifera* and *M. malaccensis*) had significantly higher δ^{13}C than other termites feeding on relatively fresh organic matter (i.e. *M. sabahensis*, *H. hospitalis* and *L. longipes*).

δ^{13}C values significantly differed across all species examined ($F_{19,93} = 24.4927$, $P < 0.0001$). *Bembix* sp. and *Apis* spp. had significantly higher δ^{13}C than the termite species, except for *D. nemorosus* and *M. malaccensis*, as well as the arboreal honeydew- and nectar-feeding ant *Tetraponera attenuata* and the plant-ant *C. borneensis*. Of all the species, *C. borneensis* was most depleted in ^{13}C. As observed for δ^{15}N, values of ^{13}C for the soil-feeding termites, such as *D. nemorosus*, were indistinguishable from those of the predatory wasps (e.g. *Bembix* sp.) and army ants (*L. diminuta*).

Table 1 Hymenoptera and Isoptera examined in this study (the feeding habits are also shown)

No.	Species	*n*	Feeding habits[a]
	Hymenoptera		
	Ants		
	Formicidae		
1	*Crematogaster borneensis*	5	Plant-ant of myrmecophytic *Macaranga* plants
2	*Crematogaster difformis*	5	Plant-ant of myrmecophytic epiphytes
3	*Camponotus gigas*	9	Omnivorous ant
4	*Leptogenys diminuta*	3	Predatory army ant
5	*Tetraponera attenuata*	16	Arboreal honeydew- and nectar-feeding ants
6	*Oecophylla smaragdina*	4	Omnivorous weaver ant
	Bees		
	Apidae		
7	*Apis* spp.	3	Nectar and pollen feeding honeybee
8	*Trigona* spp.	10	Nectar and pollen feeding stingless bee
	Anthophoridae		
9	*Amegilla* sp.	1	Nectar and pollen feeding bee
	Halictidae		
10	*Nomia* sp.	1	Nectar and pollen feeding bee
11	Megachilidae sp.	1	Nectar and pollen feeding leaf cutter bee
	Wasps		
12	Braconidae sp.	2	Parasitoid wasp
13	Ichneumonidae sp.	4	Parasitoid wasp
	Nyssonidae		
14	*Bembix* sp.	3	Fly-hunting wasp
15	*Bembecinus* sp.	3	Homopteran-hunting wasp
16	Pompilidae sp.	2	Spider-hunting wasp
17	Scoliidae sp.	1	Scarabidae parasitoid wasp
	Sphecidae		
18	*Chalybion bengalense*	1	Spider-hunting wasp
	Vespidae		
19	*Polybioides pescas*	2	Predatory wasp
20	*Provespa anomala*	6	Predatory wasp
21	*Ropalidia* spp.	3	Predatory wasp
22	*Vespa affinis*	2	Predatory wasp
	Termites		
	Isoptera		
	Termitidae		
23	*Hospitalitermes hospitalis*	4	Lichen-feeding termite
24	*Macrotermes malaccensis*	5	Fungus-growing termite
25	*Odontotermes sarawakensis*	1	Fungus-growing termite
26	*Odontotermes denticulatus*	1	Fungus-growing termite
27	*Microcerotermes sabahensis*	4	Wood-feeding termite
28	*Longipeditermes longipes*	3	Litter-feeding termite
29	*Homallotermes foraminifer*	9	Soil-feeding termite (?)
30	*Prohamitermes mirabilis*	9	Soil/wood interface-feeding termite (?)
31	*Termes rostratus*	2	Soil-feeding termite
32	*Dicuspiditermes nemorosus*	4	Soil-feeding termite

n number of colonies or individuals examined in this study

[a] The feeding habits are based on previous studies on ants (Wilson, 1958; Maschwitz and Mühlenberg, 1975; Buschinger et al., 1994; Pfeiffer and Linsenmair, 2000; Van Mele and Cuc, 2000; Blüthgen and Fiedler, 2002; Inui et al., 2009), bees (Roubik, 1989; Michener, 2000), wasps (Bohart and Menke, 1976; O'Neil, 2001; Klein et al., 2004; Grimaldi and Engel, 2005) and termites (Abe, 1979; Eggleton et al., 1999; Bignell and Eggleton, 2000; Jones and Praestyo, 2002)

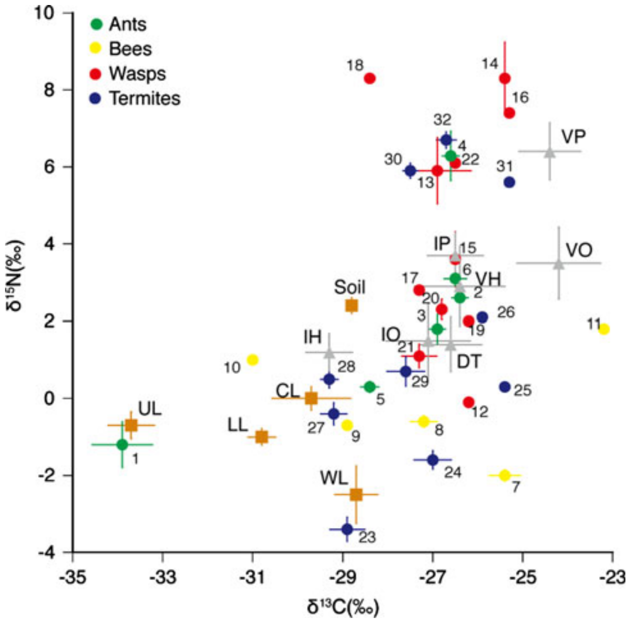

Fig. 1 $\delta^{15}N$ and $\delta^{13}C$ values (means ± SE, *circles*) of ants, bees, wasps, and termites, together with average values (from Hyodo et al., 2010b) for other consumers (*triangles*) and plant material and soil (*squares*) in Lambir National Park. The *numbers on each value* correspond to the species listed in Table 1. *IH* invertebrate herbivores, *IO* invertebrate omnivores, *DT* detritivores, *IP* invertebrate predators, *VH* vertebrate herbivores, *VO* vertebrate omnivores, *VP* vertebrate predators, *UL* understorey leaves, *CL* canopy leaves, *LL* leaf litter, *WL* woody litter, *Soil* soil (0–5 cm)

Comparison of the isotopic values of hymenopterans and isopterans to other consumers in a tropical rain forest

To characterize the isotopic signatures of the hymenopterans and isopterans, we compared their isotopic signatures to those previously reported for other tropical consumers, plants and soil organic matter (Hyodo et al., 2010b). The consumers include detritivores (e.g., cockroach, fungus beetle and pygmy grasshopper), invertebrate herbivores (e.g., leaf beetle, weevil and lepidopteran), vertebrate herbivores (e.g., fruit bat and dove), invertebrate omnivores (e.g., katydid, cricket and darkling beetle), vertebrate omnivores (e.g., squirrel and rat), invertebrate predators (e.g., tiger beetle, praying mantis and spiders) and vertebrate predators (e.g., vampire bat, tree shrew and black-throated babbler). The $\delta^{15}N$ and $\delta^{13}C$ of hymenopterans and isopterans overlapped with those of the other consumers. Among all the consumers examined in the forest, *Bembix* sp. had the highest mean $\delta^{15}N$ value and *H. hospitalis* had the lowest mean $\delta^{15}N$ value, whereas *C. borneensis* had the lowest mean value of $\delta^{13}C$.

The comparison of the isotopic signatures of the specialist predator wasps with those of their prey allows for the estimation of trophic enrichment within this forest ecosystem. The spider-hunting wasps Pompilidae sp. were more enriched in both ^{15}N and ^{13}C (by 3.8 and 1.6‰, respectively) relative to the average for all spiders ($\delta^{15}N$: 3.6 ± 0.3‰; $\delta^{13}C$: −27.0 ± 0.2‰; mean ± SE, $n = 38$). The spider-hunting wasp, *C. bengalense* was enriched in ^{15}N by 5‰ but depleted in ^{13}C by 1.4‰ relative to the average for all spiders. In addition, values of $\delta^{15}N$ and $\delta^{13}C$ of the homopteran-hunting wasp *Bembecinus* sp. were 1.9 and 1.3‰ higher, respectively, than values for all homopterans (Homoptera, $\delta^{15}N$: 1.7 ± 0.6‰ and $\delta^{13}C$: −27.8 ± 0.6‰, $n = 16$).

Discussion

We demonstrated that $\delta^{15}N$ and $\delta^{13}C$ values for hymenopterans and isopterans varied greatly and overlapped among the four groups of insects. Furthermore, as hypothesised, the isotopic signatures of hymenopterans and isopterans overlapped with those of the other consumers belonging to the four trophic groups (i.e., detritivores, herbivores, omnivores and predators). Considering that C and N isotopic signatures are indicative of the flows of energy and material in food webs, our results suggest that these insects use diverse C and N sources, which likely explain their great abundance as well as diversity in tropical ecosystems (Brian, 1978; Hölldobler and Wilson, 1990; Abe et al., 2000).

The observed isotopic patterns of ants and termites were generally consistent with the results of earlier studies. The $\delta^{15}N$ values of ants ranged along a continuum from species associated with canopy plants, such as *T. attenuata*, to those foraging on the ground, such as *L. diminuta* (Blüthgen et al., 2003; Davidson et al., 2003). Termites exhibited higher $\delta^{15}N$ values as their feeding substrates become more humified from wood to soil organic matter (Tayasu et al., 1997). The lichen-feeding termite *H. hospitalis* was the most depleted in ^{15}N among all of the samples. These low values can be explained by the dependence of *H. hospitalis* on "food ball", which is made from lichens (Jones and Gathorne-Hardy, 1995). The food balls have been reported to have low $\delta^{15}N$ values (−3.4 ± 1.59, mean ± SD, $n = 11$: −5.2 ± 0.72, $n = 11$) for the congeners *H. birmanicus* and *H. bicolor*, respectively (Tayasu et al., 2000). The low $\delta^{15}N$ values of lichens likely reflect that N of lichens originated from atmospheric N deposition, which is depleted in ^{15}N (−10 to 0‰; Nadelhoffer and Fry, 1994). The $\delta^{13}C$ values of termites were consistent with earlier studies demonstrating enrichment in ^{13}C when feeding substrates were more humified or included fungal tissues (Tayasu, 1998; Hyodo et al., 2003).

Our results confirmed the previously known feeding habits of *C. borneensis.* This ant species inhabits the hollow stems of its host plant (*Macaranga trachyphylla*) and feeds primarily on food bodies provided by the plant (Fiala et al., 1989; Itino et al., 2001). The low δ^{13}C values of *C. borneensis* indicate its dependence on the food bodies, which also exhibit low δ^{13}C values (average $\delta^{13}\text{C} = -33.7‰$, $n = 2$; F. Hyodo, unpubl. data). The depletion in ^{13}C of the food bodies indicates that this food source is rich in lipids (Heil et al., 1998), which are generally depleted in ^{13}C relative to bulk tissue (DeNiro and Epstein, 1977; Hobbie and Werner, 2004).

In contrast to *C. borneensis*, we observed a discrepancy between the previously known feeding habit of *C. gigas* and that inferred from the isotopic signatures. Pfeiffer and Linsenmair (2000) demonstrated that although *C. gigas* feeds on other arthropods and bird droppings, its diet consists mostly (90%) of nectar and honeydew on a by-weight basis. However, the δ^{13}C values of this ant species were more similar to the average values for invertebrate omnivores than to those for invertebrate herbivores. Note that *C. gigas* exhibited the relatively high δ^{13}C values, even though the ant sample used in this study included the abdomen, which is known to be depleted in ^{13}C compared to the rest of the body, likely due to the storage of nectar, honeydew and lipid (Tillberg et al., 2006; Feldhaar et al., 2010). It was also reported that the bullet ant *Paraponera clavata* exhibits δ^{13}C values more similar to those of prey than to those of nectar, even though nectar dominates its diet (Tillberg and Breed, 2004). Given our results and those of previous studies, the nectar and honeydew consumed by omnivorous ant species are likely used as energy sources, and the isotopic composition is not well retained in the body tissues. This is consistent with previous findings that the C isotopic composition of the body protein of omnivores reflects only the protein in its diet (Ambrose and Norr, 1993; Gannes et al., 1997). Therefore, the C isotopic signatures may underestimate the relative importance of carbohydrate sources, such as nectar, in omnivorous hymenopteran diets. Further feeding experiments are required to examine the fate of dietary carbohydrate sources in hymenopteran tissues.

The observed isotopic signatures provide insight into the feeding habits of several species. For example, the feeding habit of *Crematogaster difformis*, an arboreal ant that nests in myrmecophytic epiphytic ferns (Inui et al., 2009), likely differs from those of other arboreal ants. Arboreal ants tend to depend largely on extrafloral nectaries provided by plants and on honeydew excreted by homopterans (Blüthgen et al., 2003; Davidson et al., 2003). In contrast, our isotopic data suggest that *C. difformis* exhibits a more omnivorous feeding habit similar to that of the weaver ant *Oecophylla smaragdina*, which consumes honeydew and nectar sources as well as other arthropods and often dominates the ant community (Blüthgen and Fiedler, 2002). The unique feeding habit of *C. difformis* among arboreal ants may be consistent with the recent finding that this ant species dominates the canopy ant fauna and regulates the density of herbivores within the canopy layers (Tanaka et al., 2009). Moreover, the relatively high δ^{15}N of *C. difformis* can be explained by their consumption of the cockroach *Pseudoanaplectinia yumoto*, which also inhabits epiphytic ferns (Inui et al., 2009). The average δ^{15}N of the cockroach ($-1.0‰$, $n = 5$) was approximately 3‰ lower than that of *C. difformis*, whereas the δ^{13}C signatures of the two species were similar (δ^{13}C for *P. yumoto*: $-25.8‰$, $n = 5$).

The feeding habits of termites have been inferred using field observations of feeding substrates and sites as well as gut content analysis (Bignell and Eggleton, 2000). The feeding habits of *P. mirabilis*, which inhabits the soil surface rich in organic matter (Eggleton et al., 1999; Jones and Praestyo, 2002; Jones et al., 2010), and of *H. foraminifera*, which feeds on very decayed wood (Jeeva et al., 1999; Jones and Praestyo, 2002; Jones et al., 2010), remain unclear. Our results indicated that *P. mirabilis* does not differ from the soil-feeding termite *D. nemorosus* in terms of C and N isotopic composition, strongly suggesting that *P. mirabilis* can be classified as a soil feeder. Furthermore, *H. foraminifera* is unlikely to be a soil feeder but can instead be considered a wood feeder or a wood–soil interface feeder.

In general, predatory wasps consume arthropod prey or scavenge animal protein to develop brood while consuming carbohydrates, such as nectar and sap, as energy sources (Matsuura, 1991; Martin, 1995; Richter, 2000). The spider-hunting wasps Pompilidae sp. and *C. bengalense* and the homopteran-hunting wasp *Bembecinus* sp. were indeed enriched by about 3‰ in ^{15}N relative to invertebrate prey. This trophic enrichment in ^{15}N is consistent with previous results ($3.4 \pm 1.1‰$, mean ± SD) from food-web studies (Minagawa and Wada, 1984; Post, 2002). *Bembix* sp., which hunts flies (Bohart and Menke, 1976) and was frequently observed hunting scavenger flies at the study site, had high δ^{15}N values similar to the spider-hunting wasps Pompilidae sp. and *C. bengalense*. This result suggests that the prey flies may depend on dead body or faeces of consumers at higher trophic level or on soil organic matters, both of which could exhibit high values of δ^{15}N (Hyodo et al., 2010a).

Values of δ^{15}N of wasps varied greatly from $-0.1‰$ for the parasitoid wasp (Braconidae sp.) to 8.6‰ for the fly-hunting wasp (*Bembix* sp.). Parasitoid wasps oviposit on or in arthropod prey, which then become the food source for wasp larvae (Wäckers, 2004). The large difference in δ^{15}N between the two groups of parasitoid wasps (Ichneumonidae sp. and Braconidae sp.) may reflect the difference in their hosts. Likewise, the wasps *P. anomala* and *Ropalidia* spp. were more depleted in ^{15}N compared to the predatory wasp *Vespa affinis* and to the other general invertebrate predators at the study site. Based on their isotopic signatures, *P. anomala* and *Ropalidia* spp. probably use food sources similar to those of omnivorous ants such as *O.*

smaragdina and *C. gigas*. These results suggest that the feeding habits of the wasps range from omnivory and some degree of dependence on nectar and honeydew, which also contains some amino acids (Baker and Baker, 1986; Blüthgen et al., 2004), to predation and dependence mostly on animal prey, as has been shown for ants (Blüthgen et al., 2003; Davidson et al., 2003). Meanwhile, honeybees, stingless bees and other bees exhibited low δ^{15}N values, which were indicative of their use of plant materials. The significant differences in δ^{15}N and δ^{13}C between *Apis* spp. and *Trigona* spp. may indicate food resource partitioning (Roubik, 1989). The reasons for the relatively variable δ^{13}C in these species remain unclear. Future studies should examine the isotopic signatures of their food sources, i.e. nectar and pollen.

Overall, the present results provide insight into the feeding habits of tropical hymenopterans and isopterans. Note that similar isotopic signatures of consumers do not necessarily mean similar feeding habits, because the signatures do not provide information about whether the isotope ratios are brought about by feeding on single or several food items, and because the trophic enrichment in ^{13}C and ^{15}N can vary between different taxa (McCutchan et al., 2003; Vanderklift and Ponsard, 2003). This should be taken into account especially when the isotopic signatures of soil-feeding invertebrates are compared, because the soil organic matter on which they feed is a mixture of organic substrates, which can have different isotopic signatures (Pollierer et al., 2009). In particular, the soil-feeding termite, *D. nemorosus* exhibited values of δ^{15}N and δ^{13}C that were indistinguishable from those of the army ant *L. diminuta* and the fly-hunting wasp *Bembix* sp., despite clear differences in the feeding habits of these species. This result indicates that values of δ^{15}N and δ^{13}C can increase not only from trophic enrichment, but also from the humification of feeding substrates in terrestrial food webs (Hyodo et al., 2008). Therefore, this study highlights that stable isotope techniques should be coupled with knowledge of the natural history and physiology of focal organisms to achieve a more precise interpretation of the isotopic signatures.

Acknowledgments We thank Josef Kendawang (Forest Department, Sarawak) and Lucy Chong (Sarawak Forestry Corporation) for permission for research in Sarawak. We also thank Tohru Nakashizuka (Tohoku University) and Het Kaliang (Sarawak Forestry Corporation) for kind arrangement to conduct the field sampling, Seiki Yamane (Kagoshima University) for identification of ants and sphecid wasps and helpful discussion, Shuichi Ikudome (Kagoshima Women's Junior College) for identification of bees and two anonymous reviewers and the Associate Editor for constructive comments on an earlier draft of this manuscript. This study was supported by Research Institute for Humanity and Nature, Japan (P3-1 and P3-5), by Grant-in-Aids (no. 17405006 to T.I., and no. 16405009 to Y.T.) and partly by Special Coordination funds for Promoting Sciences and Technology from the Japanese Ministry of Education, Science, and Culture. F.H. and T.M. were supported by the Research Fellowships of the Japan Society for the Promotion of Science (JSPS) for Young Scientists.

Appendix

δ^{15}N and δ^{13}C values of Hymenoptera and Isoptera examined in this study.

No.	Taxa	*n*	δ^{15}N (‰)				δ^{13}C (‰)			
			Mean (SE)			Range (min–max)	Mean (SE)			Range (min–max)
	Hymenoptera									
	Ants									
	Formicidae									
1	*Crematogaster borneensis*	5	−1.2 (0.6)	D	hi	−2.3 to 0.8	−33.9 (0.7)	C	g	−35.7 to −31.7
2	*Crematogaster difformis*	5	2.6 (0.5)	B	de	1.0 to 3.7	−26.4 (0.2)	A	ab	−27.0 to −25.9
3	*Camponotus gigas*	9	1.8 (0.4)	B	def	0.5 to 4.3	−26.9 (0.2)	A	ab	−27.7 to −26.2
4	*Leptogenys diminuta*	3	6.3 (0.6)	A	ab	5.0 to 7.0	−26.6 (0.2)	A	abc	−26.9 to −26.3
5	*Tetraponera attenuata*	16	0.3 (0.1)	C	gh	−1.1 to 1.3	−28.4 (0.2)	B	cdef	−29.8 to −26.3
6	*Oecophylla smaragdina*	4	3.1 (0.2)	B	d	2.6 to 3.5	−26.5 (0.2)	A	ab	−27.1 to −26.0
	Bees									
	Apidae									
7	*Apis* spp.	3	−2.0 (0.1)	B	ij	−2.2 to −1.7	−25.4 (0.3)	A	a	−25.8 to −24.7
8	*Trigona* spp.	10	−0.6 (0.1)	A	ghi	−1.5 to 0.0	−27.2 (0.3)	B	abcd	−28.2 to −25.8
	Anthophoridae									
9	*Amegilla* sp.	1	−0.7				−28.9			
	Halictidae									

No.	Taxa	n	δ^{15}N (‰)				δ^{13}C (‰)			
			Mean (SE)			Range (min–max)	Mean (SE)			Range (min–max)
10	*Nomia* sp.	1	1.0				−31.0			
11	Megachilidae sp.	1	1.8				−23.2			
	Wasps									
12	Braconidae sp.	2	−0.1			−0.9 to 0.7	−26.2			−26.8 to −25.5
13	Ichneumonidae sp.	4	5.9 (0.9)	AB	bc	4.0 to 8.0	−26.9 (0.7)	A	abcd	−28.6 to −24.9
	Nyssonidae									
14	*Bembix* sp.	3	8.3 (0.9)	A	a	6.7 to 9.9	−25.4 (0.0)	A	a	−25.5 to −25.3
15	*Bembecinus* sp.	3	3.6 (0.7)	BC	cd	2.2 to 4.6	−26.5 (0.0)	A	ab	−26.6 to −26.5
16	Pompilidae sp.	2	7.4			5.4 to 9.4	−25.3			−26.1 to −24.5
17	Scoliidae sp.	1	2.8				−27.3			
	Sphecidae									
18	*Chalybion bengalense*	1	8.3				−28.4			
	Vespidae									
19	*Polybioides pescas*	2	2.0			1.8 to 2.2	−26.2			−26.4 to −26.0
20	*Provespa anomala*	6	2.3 (0.3)	C	def	1.3 to 3.3	−26.8 (0.1)	A	ab	−27.3 to −26.0
21	*Ropalidia* spp.	3	1.1 (0.3)	C	defg	0.5 to 1.5	−27.3 (0.4)	A	abcdef	−28.0 to −26.7
22	*Vespa affinis*	2	6.1			5.5 to 6.7	−26.5			−26.9 to −26.2
	Termites									
	Isoptera									
	Termitidae									
23	*Hospitalitermes hospitalis*	4	−3.4 (0.3)	E	j	−4.0 to −2.6	−28.9 (0.4)	B	def	−29.7 to −27.9
24	*Macrotermes malaccensis*	5	−1.6 (0.2)	D	ij	−2.2 to −1.1	−27.0 (0.4)	A	abcd	−28.4 to −26.1
25	*Odontotermes sarawakensis*	1	0.3				−25.4			
26	*Odontotermes denticulatus*	1	2.1				−25.9			
27	*Microcerotermes sabahensis*	4	−0.4 (0.3)	CD	ghi	−0.9 to 0.6	−29.2 (0.3)	B	e	−30.0 to −28.2
28	*Longipeditermes longipes*	3	0.5 (0.2)	BC	efghi	0.1 to 0.9	−29.3 (0.2)	B	ef	−29.6 to −29.0
29	*Homallotermes foraminifer*	9	0.7 (0.4)	B	fg	−1.0 to 2.6	−27.6 (0.4)	A	bcdef	−29.6 to -25.9
30	*Prohamitermes mirabilis*	9	5.9 (0.2)	A	b	5.1 to 6.6	−27.5 (0.2)	A	bcdf	−28.1 to −26.7
31	*Termes rostratus*	2	5.6			4.9 to 6.4	−25.3			−25.4 to −25.2
32	*Dicuspiditermes nemorosus*	4	6.7 (0.2)	A	ab	6.3 to 7.2	−26.7 (0.2)	A	ab	−27.1 to −26.2

Mean values with the same letter do not differ according to Tukey–Kramer HSD post hoc tests following ANOVA at $P = 0.05$. Uppercase and lowercase letters indicate the post hoc results for within-group tests (*t* test results for bees) and for tests among all species, respectively

n = Number of colonies or individuals examined in this study

References

Abe T. 1979. Studies on the distribution and ecological role of termites in a lowland rain forest of West Malaysia (2) Food and feeding habits of termites in Pasoh Forest Reserve. *Jap. J. Ecol.* **29:** 121-135

Abe T., Bignell D.E. and Higashi M. 2000. *Termites: Evolution, Sociality, Symbiosis, Ecology*. Kluwer Academic Publishers, Dordrecht. 488 pp

Ambrose S.H. and Norr L. 1993. Carbon isotopic evidence for routing of dietary protein to bone collagen, and whole diet to bone apatite carbonate: purified diet growth experiments. In: *Molecular Archaeology of Prehistoric Human Bone* (Lambert J. and Grupe G., Eds). Springer-Verlag, Berlin, Germany. pp 1-37

Baker H. and Baker I. 1986. The occurrence and significance of amino acids in floral nectar. *Plant Syst. Evol.* **151:** 175-186

Bignell D.E. and Eggleton P. 2000. Termites in ecosystems. In: *Termites: Evolution, Sociality, Symbiosis, Ecology* (Abe T., Bignell D.E. and Higashi M., Eds). Kluwer Academic Publishers, Dordrecht. pp 363-387

Blüthgen N. and Fiedler K. 2002. Interactions between weaver ants *Oecophylla smaragdina*, homopterans, trees and lianas in an Australian rain forest canopy. *J. Anim. Ecol.* **71:** 793-801

Blüthgen N., Gebauer G. and Fiedler K. 2003. Disentangling a rainforest food web using stable isotopes: dietary diversity in a species-rich ant community. *Oecologia* **137:** 426-435

Blüthgen N., Gottsberger G. and Fiedler K. 2004. Sugar and amino acid composition of ant-attended nectar and honeydew sources from an Australian rainforest. *Austral Ecol.* **29:** 418-429

Bohart R.M. and Menke A.S. 1976. *Sphecid Wasps of the World.* University of California Press, Berkeley. 600 pp

Bourguignon T., Šobotník J., Lepoint G., Martin J.M. and Roisin Y. 2009. Niche differentiation among neotropical soldierless soil-feeding termites revealed by stable isotope ratios. *Soil Biol. Biochem.* **41:** 2038-2043

Breznak J.A. and Brune A. 1994. Role of microorganisms in the digestion of lignocellulose by termites. *Annu. Rev. Entomol.* **39:** 453-487

Brian M.V. 1978. *Production Ecology of Ants and Termites*. Cambridge University Press, Cambridge. 409 pp

Buschinger A., Klein R.W. and Maschwitz U. 1994. Colony structure of a bamboo-dwelling *Tetraponera* sp. (Hymenoptera: Formicidae: Pseudomyrmecinae) from Malaysia. *Insect. Soc.* **41:** 29-41

Davidson D.W., Cook S.C., Snelling R.R. and Chua T.H. 2003. Explaining the abundance of ants in lowland tropical rainforest canopies. *Science* **300:** 969-972

DeNiro M.J. and Epstein S. 1977. Mechanism of carbon isotope fractionation associated with lipid-synthesis. *Science* **197:** 261-263

DeNiro M.J. and Epstein S. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochim. Cosmochim. Acta* **42:** 495-506

Eggleton P., Homathevi R., Jones D.T., MacDonald J.A., Jeeva D., Bignell D.E., Davies R.G. and Maryati M. 1999. Termite assemblages, forest disturbance and greenhouse gas fluxes in Sabah, East Malaysia. *Phil. Trans. R. Soc. B* **354:** 1791-1802

Feldhaar H., Gebauer G. and Blüthgen N. 2010. Stable isotopes: past and future in exposing secrets of ant nutrition (Hymenoptera: Formicidae). *Myrmecol. News* **13:** 3-13

Fiala B., Maschwitz U., Tho Y.P. and Helbig A.J. 1989. Studies of a South East Asian ant-plant association - protection of *Macaranga* trees by *Crematogaster borneensis*. *Oecologia* **79:** 463-470

Fittkau E.J. and Klinge H. 1973. On biomass and trophic structure of the central Amazonian rain forest ecosystem. *Biotropica* **5:** 2-14

Fry B. 2006. *Stable Isotope Ecology*. Springer, New York. 308 pp

Gadagkar R. 1991. *Belonogaster*, *Mischocyttarus*, *Parapolybia*, and independent-founding *Ropalidia*. In: *The Social Biology of Wasps* (Ross K.G. and Matthews R.W., Eds). Cornell University Press, Ithaca and London. pp 149-190

Gannes L.Z., O'Brien D.M. and Martínez del Rio C. 1997. Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments. *Ecology* **78:** 1271-1276

Grimaldi D. and Engel M.S. 2005. *Evolution of the Insects*. Cambridge University Press, Cambridge, U.K. 755 pp

Heil M., Fiala B., Kaiser W. and Linsenmair K.E. 1998. Chemical contents of *Macaranga* food bodies: adaptations to their role in ant attraction and nutrition. *Funct. Ecol.* **12:** 117-122

Higashi M. and Abe T. 1996. Global diversification of termites driven by the evolution of symbiosis and sociality. In: *Biodiversity: An Ecological Perspective* (Abe T., Levin S.A. and Higashi M., Eds). Springer-Verlag, New York. pp 83-112

Hobbie E.A. and Werner R.A. 2004. Intramolecular, compound-specific, and bulk carbon isotope patterns in C_3 and C_4 plants: a review and synthesis. *New Phytol.* **161:** 371-385

Hölldobler B. and Wilson E.O. 1990. *The Ants*. Belknap Press of Harvard University Press, Cambridge. 732 pp

Hyodo F., Kohzu A. and Tayasu I. 2010a. Linking aboveground and belowground food webs through carbon and nitrogen stable isotope analyses. *Ecol. Res.* **25:** 745-756

Hyodo F., Matsumoto T., Takematsu Y., Kamoi T., Fukuda D., Nakagawa M. and Itioka T. 2010b. The structure of a food web in a tropical rain forest in Malaysia based on carbon and nitrogen stable isotope ratios. *J. Trop. Ecol.* **26:** 205-214

Hyodo F., Tayasu I., Inoue T., Azuma J.-I. and Kudo T. 2003. Differential role of symbiotic fungi in lignin degradation and food provision for fungus-growing termites (Macrotermitinae: Isoptera). *Funct. Ecol.* **17:** 186-193

Hyodo F., Tayasu I., Konate S., Tondoh J.E., Lavelle P. and Wada E. 2008. Gradual enrichment of ^{15}N with humification of diets in a below-ground food web: relationship between ^{15}N and diet age determined using ^{14}C. *Funct. Ecol.* **22:** 516-522

Inui Y., Tanaka H.O., Hyodo F. and Itioka T. 2009. Within-nest abundance of a tropical cockroach *Pseudoanaplectinia yumotoi* associated with *Crematogaster* ants inhabiting epiphytic fern domatia in a Bornean dipterocarp forest. *J. Nat. Hist.* **43:** 1139-1145

Itino T., Davies S.J., Tada H., Hieda O., Inoguchi M., Itioka T., Yamane S. and Inoue T. 2001. Cospeciation of ants and plants. *Ecol. Res.* **16:** 787-793

Jeeva D., Bignell D.E., Eggleton P. and Maryati M. 1999. Respiratory gas exchanges of termites from the Sabah (Borneo) assemblage. *Physiol. Entomol.* **24:** 11-17

Jones D.T. and Gathorne-Hardy F.J. 1995. Foraging activity of the processional termite *Hospitalitermes hospitalis* (Termitidae, Nasutitermitinae) in the rain-forest of Brunei, North-West Borneo. *Insect. Soc.* **42:** 359-369

Jones D.T. and Praestyo A.H. 2002. A survey of the termites (Insecta: Isoptera) of Tabalong District, south Kalimantan, Indonesia. *Raffles Bull. Zool.* **50:** 117-128

Jones D.T., Rahman H., Bignell D.E. and Prasetyo A.H. 2010. Forests on ultramafic-derived soils in Borneo have very depauperate termite assemblages. *J. Trop. Ecol.* **26:** 103-114

Klein A.M., Steffan-Dewenter I. and Tscharntke T. 2004. Foraging trip duration and density of megachilid bees, eumenid wasps and pompilid wasps in tropical agroforestry systems. *J. Anim. Ecol.* **73:** 517-525

Lindeman R.L. 1942. The trophic-dynamic aspect of ecology. *Ecology* **23:** 399-417

Martin S.J. 1995. Hornets (Hymenoptera: Vespinae) of Malaysia. *Malay. Nat. J.* **49:** 71-82

Maschwitz U. and Mühlenberg M. 1975. Strategy of predation in some oriental *Leptogenys* species (Formicidae-Ponerinae). *Oecologia* **20:** 65-83

Matsuura K. 1991. *Vespa* and *Provespa*. In: *The Social Biology of Wasps* (Ross K.G. and Matthews R.W., Eds). Cornell University Press, Ithaca. pp 232-262

McCutchan J.H., Lewis W.M., Kendall C. and McGrath C.C. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* **102:** 378-390

Michener C.D. 2000. *The Bees of the World*. The Johns Hopkins University Press, Baltimore, Md. 913 pp

Minagawa M. and Wada E. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between δ^{15}N and animal age. *Geochim. Cosmochim. Acta*. **48:** 1135-1140

Momose K., Yumoto T., Nagamitsu T., Kato M., Nagamasu H., Sakai S., Harrison R.D., Itioka T., Hamid A.A. and Inoue T. 1998. Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. I. Characteristics of the plant-pollinator community in a lowland dipterocarp forest. *Am. J. Bot.* **85:** 1477-1501

Nadelhoffer K. and Fry B. 1994. Nitrogen isotope studies in forest ecosystems. In: *Stable Isotopes in Ecology and Environmental Science* (Lajtha K. and Michener R.H., Eds). Blackwell Scientific Publications, Oxford. pp 22-44

O'Neil K.M. 2001. *Solitary Wasps: Behavior and Natural History*. Cornell University Press, Ithaca. 406 pp

Pfeiffer M. and Linsenmair K.E. 2000. Contributions to the life history of the Malaysian giant ant *Camponotus gigas* (Hymenoptera, Formicidae). *Insect. Soc.* **47:** 123-132

Pollierer M.M., Langel R., Scheu S. and Maraun M. 2009. Compartmentalization of the soil animal food web as indicated by dual analysis of stable isotope ratios (^{15}N/^{14}N and ^{13}C/^{12}C). *Soil Biol. Biochem.* **41:** 1221-1226

Post D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* **83:** 703-718

Richter M.R. 2000. Social wasp (Hymenoptera: Vespidae) foraging behavior. *Annu. Rev. Entomol.* **45:** 121-150

Roubik D.W. 1989. *Ecology and Natural History of Tropical Bees*. Cambridge University Press, New York. 514 pp

Tanaka H.O., Inui Y. and Itioka T. 2009. Anti-herbivore effects of an ant species, *Crematogaster difformis*, inhabiting myrmecophytic epiphytes in the canopy of a tropical lowland rainforest in Borneo. *Ecol. Res.* **24:** 1393-1397

Tayasu I. 1998. Use of carbon and nitrogen isotope ratios in termite research. *Ecol. Res.* **13:** 377-387

Tayasu I., Abe T., Eggleton P. and Bignell D.E. 1997. Nitrogen and carbon isotope ratios in termites: an indicator of trophic habit along the gradient from wood-feeding to soil-feeding. *Ecol. Entomol.* **22:** 343-351

Tayasu I., Hyodo F., Takematsu Y., Sugimoto A., Inoue T., Kirtibutr N. and Abe T. 2000. Stable isotope ratios and uric acid preservation in termites belonging to three feeding habits in Thailand. *Isotopes Environ. Health Stud*. **36:** 259-272

Tillberg C.V. and Breed M.D. 2004. Placing an omnivore in a complex food web: Dietary contributions to adult biomass of an ant. *Biotropica* **36:** 266-272

Tillberg C.V., McCarthy D.P., Dolezal A.G. and Suarez A.V. 2006. Measuring the trophic ecology of ants using stable isotopes. *Insect. Soc.* **53:** 65-69

Tilman D. 1982. *Resource Competition and Community Structure*. Princeton University Press, Princeton, N.J. 296 pp

Van Mele P. and Cuc N.T.T. 2000. Evolution and status of *Oecophylla smaragdina* (Fabricius) as a pest control agent in citrus in the Mekong Delta, Vietnam. *Int. J. Pest Manage.* **46:** 295-301

Vanderklift M.A. and Ponsard S. 2003. Sources of variation in consumer-diet δ^{15}N enrichment: a meta-analysis. *Oecologia* **136:** 169-182

Wäckers F.L. 2004. Assessing the suitability of flowering herbs as parasitoid food sources: flower attractiveness and nectar accessibility. *Biol. Cont.* **29:** 307-314

Watanabe H. and Tokuda G. 2010. Cellulolytic systems in insects. *Annu. Rev. Entomol.* **55:** 609-632

Wilson E.O. 1958. The beginnings of nomadic and group-predatory behavior in the Ponerine ants. *Evolution* **12:** 24-31

Yumoto T. and Nakashizuka T. 2005. The canopy biology program in Sarawak: Scope, methods, and merit. In: *Pollination Ecology and the Rain Forest* (Roubik D.W., Sakai S. and Hamid A.A., Eds). Springer, New York. pp 13-21