

Differences in Host Specificity and Behavior of Two Ant Cricket Species (Orthoptera: Myrmecophilidae) in Honshu, Japan¹

Takashi Komatsu,² Munetoshi Maruyama³ and Takao Itino⁴

Interdisciplinary Graduate School of Science and Technology, Shinshu University, 3-1-1 Asahi, Matsumoto, Nagano 390-8621, Japan

J. Entomol. Sci. 45(3): 227-238 (July 2010)

Abstract The ant-loving crickets (Orthoptera: Myrmecophilidae) are obligate inquilines within ant colonies that obtain nourishment from ants in their nests. Recently, new morphological and genetic approaches have revealed more ant cricket species than had previously been recognized and have provided insights into their host specificity. In this study, we compare the degree of host specificity and behavior between 2 cryptic lineages of the ant cricket *Myrmecophilus kubotai* Maruyama that distinctly differ in their mtDNA sequences but are morphologically indistinguishable. In the field, crickets of lineage I (specialists) were found in nests of *Tetramorium tsushimae* Emery (Myrmicinae) at a high frequency (89%); whereas, crickets of lineage II (generalists) were found in nests of up to 12 ant species belonging to Formicinae and Myrmicinae. Behavioral observations in ant nests revealed that lineage I suffers few ant attacks and showed frequent intimate behavior with ants, i.e., grooming. In contrast, lineage II often suffers ant attacks and showed less frequent host grooming. In Japan's Nansei Islands, a "super-specialist" species of ant cricket that lives commensally with a single ant species has been reported to depend on mouth-to-mouth feeding from the worker ants; whereas, another "super-generalist" species that lives commensally with a variety of ant taxa feeds itself. Compared with these, the 2 lineages in the present study exhibited intermediate host specificity and behavioral specialization. These results suggest that there are various stages of specialization of commensalism in this genus.

Key Words inquilines, commensalism, ant-loving crickets, cryptic species, myrmecophile, *Myrmecophilus kubotai*

Myrmecophilus (Orthoptera: Myrmecophilidae) is the only genus of orthopteran myrmecophiles (Kistner 1982) and has a worldwide distribution (Maruyama 2004). Starting with the first record by Savis (1819), a number of observations are reported on the behavior of these obligate inquiline crickets (i.e., eating ant eggs, licking the surface of an ant body, disruption of ant trophallaxis, feeding via direct mouth-to-mouth transfer) (Wasmann 1901, Schimmer 1909, Hölldobler 1947, Wheeler 1900, Henderson and Akle 1986, Sakai and Terayama 1995, Akino et al. 1996). Ants generally use the composition of cuticular hydrocarbons that cover the body surface of other ants as a means to recognize members of the same colony (e.g., Smith and Breed 1995, Thomas et al. 1999, Wagner et al. 2000). Surprisingly, some *Myrmecophilus* species can mimic

¹Received 21 September 2009; accepted for publication 03 November 2009.

²Address inquiries (email: s07t405@shinshu-u.ac.jp).

³The Kyushu University Museum, Hakozaki 6-10-1, Fukuoka 812-8581, Japan.

⁴Department of Biology, Faculty of Science, Shinshu University, 3-1-1 Asahi, Matsumoto, Nagano 390-8621, Japan.

the colony chemistry by acquiring these cuticular hydrocarbons via physical contact to establish a “chemical mimicry” (Schimmer 1909, Henderson and Akle 1986, Sakai and Terayama 1995, Akino et al. 1996).

The taxonomy of *Myrmecophilus* crickets has been ambiguous because of the scarcity of morphological characteristics that can be used to distinguish among species. This has delayed the clarification of their ecological and ethological diversity. In Japan, 4 morphospecies were tentatively recognized based on unstable characteristics (e.g., body color, body size, size of leg spurs), and one of the morphospecies was thought to show random associations with >30 ant species (Sakai and Terayama 1995, Akino et al. 1996). The absence of host specificity in *Myrmecophilus* has often been reported for non-Japanese species (Schimmer 1909, Wheeler 1900, Bernard 1968), and ant crickets were thought to shift among host ant species in the course of their growth stages (Hölldobler 1947, Baccetti 1967, Sakai and Terayama 1995). Recently, however, Maruyama (2004) classified Japanese *Myrmecophilus* crickets into at least 10 species based on the structure of the body surface and noted that particular species of ant crickets tended to be collected from nests of specific ant species. Further, Komatsu et al. (2008) reported that Japanese ant crickets can be grouped into at least 2 types based on their host specificity: one that is commensally associated with a few ant species (a specialist) and another that is commensally associated with many ant species or genera (a generalist). Moreover, Komatsu et al. (2009) reported that the degree of host dependence and the frequency and type of inquiline–host interactions differed between a “super-specialist” ant cricket (*Myrmecophilus albicinctus* Chopard) and a “super-generalist” ant cricket (*Myrmecophilus formosanus* Shiraki). The super-specialist exhibited behavior and physiology adapted to a single host ant species; whereas, the supergeneralist adopted avoidance behavior such as quick movements to form commensalistic associations with as many as 9 ant species belonging to 3 subfamilies. This suggests that trade-offs occur between specialization for specific host species and the retention of generalization to exploit multiple host species (Komatsu et al. 2009).

It is unclear whether this extreme specialist–generalist dichotomy is applicable to every ant cricket species. For example, in the specialist *M. kubotai* Maruyama, one mtDNA lineage (lineage I) appears to be commensalistic primarily with *Tetramorium tsushimae* Emery (Formicidae: Myrmicinae), although a few individuals have been collected from colonies of other ant species (Komatsu et al. 2008); whereas, the super-specialist *M. albicinctus* Chopard was found in the nests of only 1 ant species, *Anoplolepis gracilipes* Fr. Smith (Komatsu et al. 2009). On the other hand, another cryptic lineage of the generalist *M. kubotai* (lineage II) that was recognized based on its mtDNA sequence seems to restrict itself to several ant species that belong to the subfamily Formicinae (Komatsu et al. 2008); whereas, the supergeneralist *M. formosanus* is commensalistic with many ant species from 3 subfamilies (Komatsu et al. 2009). These observations suggest that continuous variation exists among species in their behavioral specialization and host specificity.

The recent improvement of ant cricket species (lineage) identification based on a morphological and molecular taxonomic framework (Maruyama 2004, Komatsu et al. 2008) has enabled us to detect ecological and ethological differences among cricket taxa. In the present paper, we describe the host specificity and behavior of a specialist lineage (I) and a generalist lineage (II) of *M. kubotai* and compare them with those of the super-specialist *M. albicinctus* and the supergeneralist *M. formosanus*. Based on the results of this comparison, we discuss the diversity of specialization in ant crickets.

Materials and Methods

Host specificity. Sampling was conducted from 2004 - 2008 at 5 sites in or around hardwood tree stands ranging from Honshu to Kyushu, Japan (Table 1). Adult or nymph crickets were collected from host ant nests. At each sampling site, we located all ant nests within 20 study plots, each 2 × 5 m per randomly selected unit area (30 × 30m). Once an ant nest was located, we collected as many *M. kubotai* crickets as possible by excavating the nest if it was subterranean or by spraying insect rejectant (repellent to keep mosquitoes out) into the nest if it was arboreal. The collected cricket samples were immediately preserved in 100% ethanol. Many colleagues helped us collect samples in this way. Once in the laboratory, we macerated the ant crickets in DNA extraction buffer and conducted PCR with mtDNA primer pairs (cytb, 434bp) to generate mtDNA profiles for each of the ant crickets using the methods described by Komatsu et al. (2008). The mtDNA sequences were aligned using Clustal X (Thompson et al. 1997), then we performed Bayesian analysis using MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). MrModeltest (Nylander 2004) was used for hierarchical likelihood ratio tests for significant differences among increasingly complex substitution models. The GTR+G model was selected by the Akaike information criterion. The matrix was analyzed over 5,000,000 generations using the selected parameters. *M. tetramorii* (Komatsu et al. 2008, Genbank accession No. AB443897) and *M. formosanus* (Komatsu et al. 2008, Genbank accession No. AB443926) were used as outgroups.

Cricket-ant interactions. In June 2009, we established 2 laboratory ant colonies—one of *T. tsushimae* with crickets from lineage I, and the other of *Formica japonica* Motschulsky (Formicinae) with crickets from lineage II. Both colonies were obtained near Nagano, Japan. The composition of both was kept the same (50 workers, 30 ant larvae, 20 crickets), and each was maintained in a plastic container (20 × 10 × 15 cm, w×d×h) filled with gypsum to a depth of 7 cm. The ants and crickets were fed 50% sugar water and a dead mealworm for 2 wk after collection. These meals were replaced everyday.

After 2 wk, behavioral observations were performed on the 2 cricket lineages in a smaller plastic container (10 × 10 × 10 cm). Four crickets from lineage I and 20 - 30 *T. tsushimae* ant workers were released into 1 container, and 4 crickets of lineage II and 20 - 30 *F. japonica* ant workers were released into another container. The insects were supplied only with water and were left undisturbed for 24 h. The next day, we placed 5 ant larvae into the container, as well as a dead mealworm and 50% sugar water (w/v), which closely approximates the foods of ant crickets and ants in the wild (Kistner 1982). The ant larvae and the dead mealworm were placed on the floor of the container, and the sugar water was absorbed into a ball of cotton and placed in a 1-cm-tall stand that only the ants could climb and the crickets could not feed upon directly. We then recorded the number of times in 1 h that each cricket: (1) was attacked by ants (i.e., the ants opened their mandibles and pursued or bit the cricket) and immediately escaped from the ant, (2) fed itself, (3) groomed an ant body, (4) disrupted trophallaxis between ants, and (5) fed via direct mouth-to-mouth transfer from the ants. For each cricket species, we repeated these observations 5 times with different sets of individuals.

It is difficult to visually distinguish between the two lineages of *M. kubotai*. Therefore, we initially assumed that crickets collected from the *T. tsushimae* colony were specialists and the ones collected from the *F. japonica* colony were generalists. After our observations, we identified these samples as belonging to lineage I or II based upon their mtDNA sequences.

Table 1. Overview of the sampled specimens, mtDNA lineages (see Fig.1), locality, and their cytb Genebank accession numbers.

mtDNA lineage	Sample No.	Locality	Genebank accession No.
I	1.1	Nishiyahata, Kai, Yamanashi	AB566211
I	1.2	Nishiyahata, Kai, Yamanashi	AB566191
I	1.3	Nishiyahata, Kai, Yamanashi	AB566183
I	1.4	Suminoe, Osaka, Osaka	AB566214
I	1.5	Suminoe, Osaka, Osaka	AB566212
I	1.6	Suminoe, Osaka, Osaka	AB566187
I	1.7	Suminoe, Osaka, Osaka	AB566184
I	1.8	Suminoe, Osaka, Osaka	AB566186
I	1.9	Yayoi, Saeki, Oita	AB566182
I	1.10	Uzue, Tahara, Aichi	AB566188
I	1.11	Sakai, Sakai, Osaka	AB566190
I	1.12	Matsugasaki, Sakyo, Kyoto	AB566189
I	1.13	Chiya, Niimi, Okayama	AB566225
I	1.14	Matsugasaki, Sakyo, Kyoto	AB566227
I	1.15	Shiroyama-machi, Matsuyama, Ehime	AB566226
I	1.16	Ono, Ichikawa, Chiba	AB566223
I	1.17	Ono, Ichikawa, Chiba	AB566224
I	1.18	Shiroyama-machi, Matsuyama, Ehime	AB566228
I	1.19	Hakozaki, Fukuoka, Fukuoka	AB566192
I	1.20	Kokura, Kitakyushu, Fukuoka	AB566194
I	1.21	Shiroyama-machi, Matsuyama, Ehime	AB566217
I	1.22	Chuo, Kobe, Hyogo	AB566185
I	1.23	Makino-cho, Takashima, Shiga	AB566221
I	1.24	Tanushimaru-machi, Kurume, Fukuoka	AB566222
I	1.25	Bunkyo, Mito, Ibaraki	AB566220
I	1.26	Chuo, Kobe, Hyogo	AB566202
I	1.27	Uchiura, Numazu, Shizuoka	AB566216
I	1.28	Yasaka-machi, Hikone, Shiga	AB566208
I	1.29	Megi-cho, Takamatsu, Kagawa	AB566200
I	1.30	Shiroyama-machi, Matsuyama, Ehime	AB566196
I	1.31	Uchiura, Numazu, Shizuoka	AB566193

Table 1. Continued

mtDNA lineage	Sample No.	Locality	Genebank accession No.
I	1.32	Megi-cho, Takamatsu, Kagawa	AB566195
I	1.33	Uchiura, Numazu, Shizuoka	AB566207
I	1.34	Makino-cho, Takashima, Shiga	AB566201
I	1.35	Uchiura, Numazu, Shizuoka	AB566197
I	1.36	Makino-cho, Takashima, Shiga	AB566199
I	1.37	Shiroyama-machi, Matsuyama, Ehime	AB566213
I	1.38	Machikaneyama-cho, Toyonaka, Osaka	AB566215
I	1.39	Makino-cho, Takashima, Shiga	AB566218
I	1.40	Uchiura, Numazu, Shizuoka	AB566219
I	1.41	Makino-cho, Takashima, Shiga	AB566203
I	1.42	Izuhara, Tsushima, Nagasaki	AB566206
I	1.43	Izuhara, Tsushima, Nagasaki	AB566198
I	1.44	Uchiura, Numazu, Shizuoka	AB566210
I	1.45	Izuhara, Tsushima, Nagasaki	AB566205
I	1.46	Machikaneyama-cho, Toyonaka, Osaka	AB566204
I	1.47	Naka, Ibaraki	AB566209
II	2.1	Suminoe, Osaka, Osaka	AB566161
II	2.2	Uchiura, Numazu, Shizuoka	AB566163
II	2.3	Aido, Jinzeki, Hiroshima	AB566162
II	2.4	Uchiura, Numazu, Shizuoka	AB566166
II	2.5	Tessei, Niimi, Okayama	AB566165
II	2.6	Inokashira, Fujiyoshida, Yamanashi	AB566164
II	2.7	Hisayo, Tojyo, Hiroshima	AB566175
II	2.8	Chuo, Kobe, Hyogo	AB566178
II	2.9	Suminoe, Osaka, Osaka	AB566177
II	2.10	Akahone-shima, Kamijima, Ehime	AB566176
II	2.11	Akashikoen, Akashi, Hyogo	AB566181
II	2.12	Hisayo, Tojyo, Hiroshima	AB566140
II	2.13	Machikaneyama-cho, Toyonaka, Osaka	AB566160
II	2.14	Satoyamabe, Matsumoto, Nagano	AB566159
II	2.15	Satoyamabe, Matsumoto, Nagano	AB566169
II	2.16	Kouzushima, Tokyo	AB566180

Table 1. Continued

mtDNA lineage	Sample No.	Locality	Genebank accession No.
II	2.17	Chuo, Kobe, Hyogo	AB566174
II	2.18	Hikari, Azumino, Nagano	AB566167
II	2.19	Satoyamabe, Matsumoto, Nagano	AB566170
II	2.20	Chuo, Kobe, Hyogo	AB566168
II	2.21	Satoyamabe, Matsumoto, Nagano	AB566151
II	2.22	Asakawa, Nagano, Nagano	AB566150
II	2.23	Satoyamabe, Matsumoto, Nagano	AB566149
II	2.24	Satoyamabe, Matsumoto, Nagano	AB566148
II	2.25	Hikari, Azumino, Nagano	AB566147
II	2.26	Asahi, Matsumoto, Nagano	AB566171
II	2.27	Ishioka, Ibaraki	AB566141
II	2.28	Asahi, Matsumoto, Nagano	AB566146
II	2.29	Asahi, Matsumoto, Nagano	AB566145
II	2.30	Asahi, Matsumoto, Nagano	AB566144
II	2.31	Nakabusa, Azumino, Nagano	AB566143
II	2.32	Nakabusa, Azumino, Nagano	AB566142
II	2.33	Yata, Mishima, Shizuoka	AB566139
II	2.34	Satoyamabe, Matsumoto, Nagano	AB566152
II	2.35	Ueno, Taitou, Tokyo	AB566153
II	2.36	Asakawa, Nagano, Nagano	AB566154
II	2.37	Satoyamabe, Matsumoto, Nagano	AB566155
II	2.38	Soga, Shiojiri, Nagano	AB566156
II	2.39	Hikari, Azumino, Nagano	AB566157
II	2.40	Satoyamabe, Matsumoto, Nagano	AB566158
II	2.41	Yata, Mishima, Shizuoka	AB566134
II	2.42	Satoyamabe, Matsumoto, Nagano	AB566129
II	2.43	Inokashira, Fujinomiya, Shizuokai	AB566136
II	2.44	Kamioshidari, Higashimatsuyama, Saitama	AB566132
II	2.45	Uchiura, Numazu, Shizuoka	AB566138
II	2.46	Uchiura, Numazu, Shizuoka	AB566130

Table 1. Continued

mtDNA lineage	Sample No.	Locality	Genebank accession No.
II	2.47	Uchiura, Numazu, Shizuoka	AB566128
II	2.48	Uchiura, Numazu, Shizuoka	AB566135
II	2.49	Uchiura, Numazu, Shizuoka	AB566131
II	2.50	Uchiura, Numazu, Shizuoka	AB566137
II	2.51	Yata, Mishima, Shizuoka	AB566133
II	2.52	Yata, Mishima, Shizuoka	AB566172

Statistical analyses. Behavioral differences between the 2 cricket species in the host colony were compared using the Wilcoxon rank-sum test based on the averages for 20 individuals per species. Statistical analysis was performed using the R software package (ver. 2.3.1, R Development Core Team 2005).

Results

Host specificity. We surveyed 495 ant colonies representing 63 species. We collected 47 crickets of lineage I (2.14 individuals/colony) and 52 of lineage II (1.63 individuals/colony) from the ant colonies. The numbers of ant species and colonies for each ant subfamily were: Formicinae (27 species, 195 colonies); Dolichoderinae (2 species, 18 colonies); Myrmicinae (24 species, 225 colonies); Ponerinae (6 species, 51 colonies); Proceratiinae (3 species, 4 colonies), and; Amblyoponinae (1 species, 2 colonies). Most crickets of lineage I (89%) were commensals with *T. tsushimae* (Table 2). In contrast, lineage II individuals were commensals with 7 Formicine and 5 Myrmicine species (Table 2).

Phylogenetic analysis. The cricket phylogeny revealed two *M. kubotai* lineages (Fig. 1). All 99 in-group specimens were identified unambiguously as lineage I or II. The monophyly of each lineage were well supported with high Bayesian posterior probability although several genetic variations were recognized within each lineage.

Cricket-ant interactions. Aggressive behavior exhibited by the ants against specialist crickets of lineage I were significantly less frequent than those against generalist crickets of lineage II (lineage I versus lineage II, mean $\pm$ SD; 0 versus 2.8 ± 0.4 events/h, $P < 0.001$). Lineage II crickets were threatened or attacked when the ants touched them with their antennae or when the crickets passed in front of the ants; however, none were injured because they were able to escape quickly.

Crickets from both lineages fed themselves; the frequency of feeding was not significantly different between them (0.8 ± 0.3 versus 1.2 ± 0.3 events/h, $P = 0.312$). The specialists did not eat ant larvae but ate dead mealworms; whereas, the generalists consumed both.

Grooming of the ant body surface was exhibited by both the specialists and the generalists, but the frequency was significantly higher in lineage I (8.4 ± 0.6 versus 2.4 ± 0.5

events/h, $P < 0.001$). Lineage I individuals walked into clusters of ants and frequently groomed both themselves and the ants. Few were attacked by the ants when they touched or groomed the bodies of their hosts. When ants were groomed by a cricket, they usually accepted this attention by contracting their legs and antennae in the same way as when they were groomed by a nestmate ant. Similar grooming also was observed in lineage II, but these crickets often received an aggressive response from the ants.

Disruption of trophallaxis between ants was rarely observed with either lineage (0 versus 0.3 ± 0.2 events/h, $P = 0.163$). Direct feeding from host ants was observed in both lineages, with no significant differences between lineages (0.9 ± 0.3 versus 0.8 ± 0.2 events/h, $P = 0.696$). This behavior was primarily seen immediately after fresh food was supplied to the containers; both cricket lineages groomed the ants from the body toward the head. When crickets groomed around an ant's mandibles, the ant regurgitated liquid food and the cricket consumed it. *Myrmecophilus albicinctus* (the superspecialist) is known to show peculiar "begging" behavior toward ants, such as beating the ant's mouthparts with its forelegs or maxillary palps (Komatsu et al. 2009), but this behavior was not seen in either lineage of *M. kubotai*.

Discussion

The two lineages of *M. kubotai* exhibited different degrees of host specificity and different behaviors toward their host ants. Lineage I crickets showed strong specificity to *T. tsushimae*; whereas, lineage II crickets were commensals with up to 12 Formicine and Myrmicine species. The primary host species with which lineage II was associated (e.g., *Lasius japonicus* Santschi, *F. japonica*, and *Camponotus japonicus* Mayr) are the predominant ant species in Japan and form huge colonies (e.g., 16,000 in a colony for *F. japonica*) (Myrmecological Society of Japan 1991, Yamaguchi 2004). Therefore, the crickets often encounter these ant species in the wild and may easily use them as hosts.

Lineage I crickets (specialists) received significantly fewer aggressive reactions from the ants and groomed the host ants significantly more frequently than was the case for lineage II crickets. These behaviors resemble those of *M. albicinctus*, the superspecialist ant cricket found in Japan's Nansei Islands. *Myrmecophilus albicinctus* even shows "begging" behavior to induce trophallaxis from ants when they meet (Komatsu et al. 2009). Lineage I crickets did not show mouth-to-mouth feeding immediately after meeting its host and did not demonstrate the begging behavior during trophallaxis. This indicates that lineage I crickets exhibit less efficient exploitation of its host due to a lower level of specialization, even though it uses *T. tsushimae* as its primary host (89% of the colonies).

Myrmecophilus formosanus, the supergeneralist species from the Nansei Islands, does not show any begging behavior and avoids physical contact with host ants (Komatsu et al. 2009). This species shows a low dependency on any one ant species and is entirely a predator and scavenger that eats ant larvae or dead insects. These feeding habits may increase survival by enabling the species to live in nests of many ant species (Komatsu et al. 2009). In contrast, lineage II crickets of *M. kubotai* exhibited intimate behaviors, such as grooming and trophallaxis with the ants, although at a relatively low frequency. Therefore, if *M. formosanus* is defined as a supergeneralist, lineage II crickets appear to be a moderate generalist. The former species exhibits a wide host range that is somewhat independent of the ant subfamilies; whereas, lineage II crickets are mainly restricted to the Formicinae (Table 2). This limitation of its host range at the subfamily level may enable lineage II crickets to exploit the Formicinae

Table 2. Host ant species composition of lineage I and II of *M. kubota*. Host ant taxon codes; Cj: *Camponotus japonicus*, Fj: *Formica japonica*, Lc: *Lasius capitatus*, Lf: *L. fuji*, Lj: *L. japonicus*, Ln: *L. nipponensis*, Ls: *L. sakagamii*, Mj: *Myrmica jessensis*, Mk: *M. kotokui*, Ps: *Polyergus samurai*, Tt: *Tetramorium tsushimae*, Rs: *Reticulitermes speratus* (a termite species), ON: outside of ant nests (freely walking). See text for other ant species that were surveyed but neither ants were detected.

Host ant Subfamily	Species	No. of ant nests surveyed	Nests with Lineage I (n = 47)		Nests with Lineage II (n = 52)	
			No. of nests	No. of crickets	No. of nests	No. of crickets
Formicinae	Cj	13	0	0	3	5
	Fj	28	2	3	5	9
	Lc	1	0	0	1	1
	Lf	4	0	0	1	2
	Lj	40	1	1	14	24
	Ln	5	0	0	1	3
	Ls	2	0	0	1	2
	Ps	2	1	1	0	0
	Mj	1	0	0	1	1
	Mk	4	0	0	1	1
Myrmicinae	Tt	94	18	42	2	2
	Rs	1	0	0	1	1
	ON			0		1

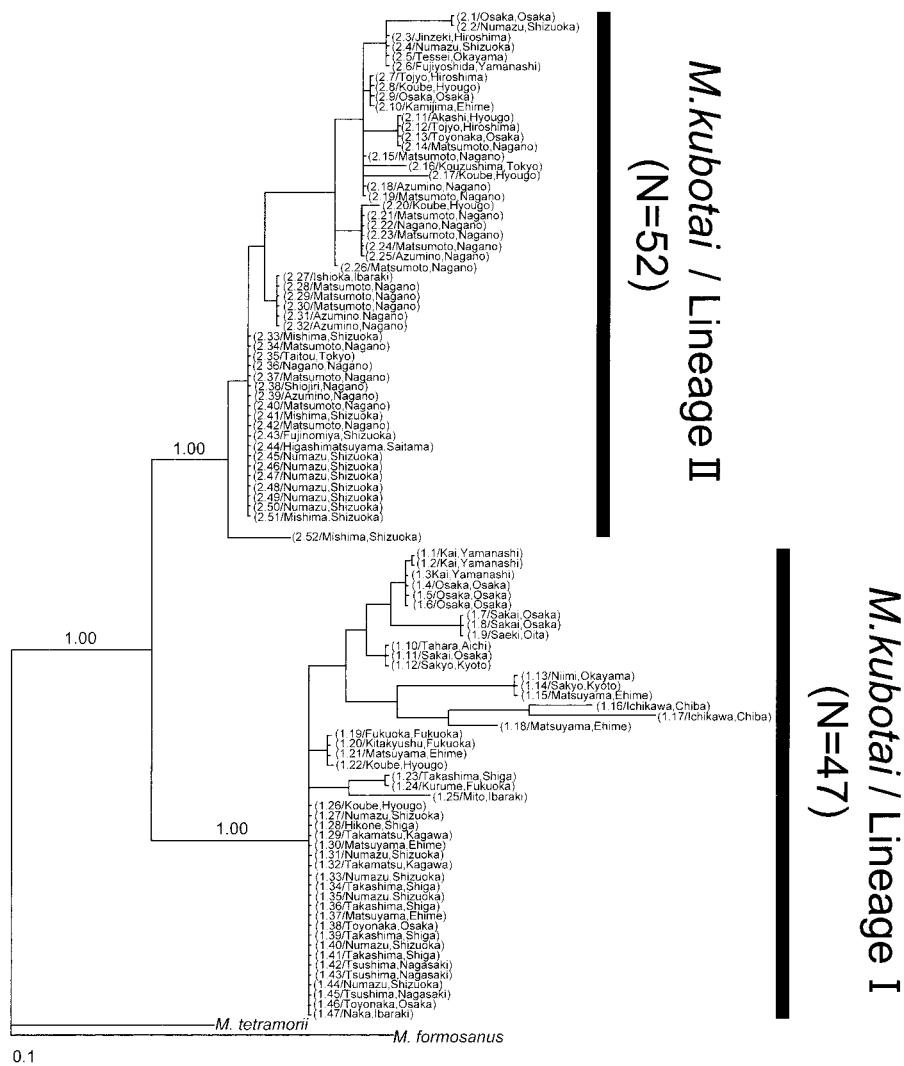


Fig. 1. Bayesian tree of the two lineage of *Myrmecophilus kubotai*, as estimated from cytb sequences (434bp). *M. tetramorii* and *M. formosanus* were used as outgroups. Posterior probability (1.00) that are analyzed over 5,000,000 generations are shown above branches. Branches are drawn to scale, with the bar representing 0.1 substitutions / site. Sample No. and the collection localities are shown in the parenthesis.

more efficiently. To elucidate this relationship, it will be necessary to compare the survival rate for this species in colonies of other species in the Formicinae or in different subfamilies and to assess the frequency of intimate behavior with these hosts.

In conclusion, *Myrmecophilus* ant crickets were previously thought to be generalists. However, recent ethological investigations combined with taxonomic reviews have revealed a remarkable diversification of their host specificities and the types of dietary resources and how they are used among species in this genus. One superspecialist species is reported to be associated with a single ant host species; whereas, a super-generalist species is associated with at least 9 ant species representing 3 subfamilies. In the present study, we demonstrated the existence of ant cricket species with intermediate degrees of host specificity and behavioral specialization. Predaceous (generalist) and cuckoo (specialist) species in the lepidopteran genus *Maculinea* are a typical example of intrageneric polarization in behavior among myrmecophilous insects (e.g., Thomas and Wardlaw 1992, Thomas and Elmes 1998, Als et al. 2004). In *Myrmecophilus*, however, species with an intermediate level of specialization, exhibiting characteristics of both specialists and generalists, are now known to exist. Caution is necessary when we compare behaviors among cricket species, because ant cricket species that have been used in the present study and in previous research (Komatsu et al. 2009) differed in the host species that are available to them. However, the fact that a gradual change in the extent of specialization has been detected within a single genus nonetheless provides insights into the evolutionary diversification of these parasitic organisms. Future phylogenetic analysis of *Myrmecophilus* will elucidate further intrageneric evolution of host specificity.

Acknowledgments

The authors thank S. Shimamoto for assistance in sampling and A. Ichikawa, Y. Hagiwara, K. Harukawa, T. Kurihara, K. Maruyama, Y. Mori, S. Takaishi, T. Takagi, and Y. Tsuneoka for providing cricket samples and W. A. Gardner for accepting our paper. This work was supported by a Grant-in-Aid for JSPS Fellows to TK (No. 19-6495).

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