

Research Article

Nonintegrated Host Association of *Myrmecophilus tetramorii*, a Specialist Myrmecophilous Ant Cricket (Orthoptera: Myrmecophilidae)

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Myrmecophilus ant crickets (Orthoptera: Myrmecophilidae) are typical ant guests. In Japan, about 10 species are recognized on the basis of morphological and molecular phylogenetic frameworks. Some of these species have restricted host ranges and behave intimately toward their host ant species (i.e., they are host specialist). We focused on one species, *M. tetramorii*, which uses the myrmicine ant *Tetramorium tsushimae* as its main host. All but one *M. tetramorii* individuals were collected specifically from nests of *T. tsushimae* in the field. However, behavioral observation showed that all individuals used in the experiment received hostile reactions from the host ants. There were no signs of intimate behaviors such as grooming of hosts or receipt of mouth-to-mouth feeding from hosts, which are seen in some host-specialist *Myrmecophilus* species among obligate host-ant species. Therefore, it may be that *M. tetramorii* is the species that is specialized to exploit the host by means other than chemical integration.

1. Introduction

Myrmecophilus (Orthoptera: Myrmecophilidae) is the only genus of orthopteran myrmecophilous insect [1]. About 60 species are described, and all of them are myrmecophilous species. These inquiline crickets live in ant nests and exploit food resources in diverse ways (i.e., eating ant eggs, larvae, and nest debris; licking the surfaces of the ants' bodies; disrupting ant trophallaxis; or feeding via direct mouth-to-mouth transfer) [2–8]. Some *Myrmecophilus* species mimic the ant colony's chemicals by acquiring cuticular hydrocarbons from the ants via physical contact to establish a “chemical mimicry” [5–7].

In Japan, at least 10 species of *Myrmecophilus* are recognized on the basis of differences in the surface structure of the body and are collected from the nests of specific ant species [9]. By using molecular phylogenetic methods, we previously found [10] that Japanese *Myrmecophilus* crickets

can be grouped into at least two types on the basis of their host specificity: one is commensally associated with a few ant species (specialist) and the other with many ant species or genera (generalist). This interesting differentiation of host specificities among congeneric species raises the question of whether behavioral differentiation also occurs.

The host ranges of some parasitic organisms are associated with the organisms' degree of behavioral specialization in relation to exploitation of food resources [11–14]. We observed the parasitic behaviors of two types of *Myrmecophilus* species, one of which used only a few ant species, the other, several ant species [8, 15]. From these observations, we hypothesized that all specialist *Myrmecophilus* species always show intimate behavior toward their host ant species.

The Japanese species *Myrmecophilus tetramorii* Ichikawa, which is distributed on the Japanese mainland islands of Honshu, Shikoku, and Kyushu, uses a few ant species as hosts [16]. The main host species is the myrmicine ant *Tetramorium*

tsushimae [16], but the details of the cricket's interaction with its host ant are unknown. If *M. tetramorii* is a specialist of *T. tsushimae*, like other specialist *Myrmecophilus* species [8, 15], it may show some intimate behaviors toward this ant.

We conducted exhaustive sampling across Japan to count the individuals of *M. tetramorii* collected from *T. tsushimae* nests. In addition, we observed the crickets' feeding behaviors and their interaction with ants in the laboratory.

2. Materials and Methods

2.1. Field Survey. Sampling was conducted from 2004 to 2008 in or around hardwood tree stands ranging from Honshu to Kyushu (total 88 sites), Japan. This sampling was conducted as part of our work about molecular phylogeny of Japanese *Myrmecophilus* crickets. 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 m × 5 m per randomly selected unit area (30 m × 30 m). Once a nest was located, we collected as many crickets as possible by excavating the nest if it was subterranean or spraying an insect repellent (to keep mosquitoes out) into the nest if it was arboreal. Most of ant species tend to avoid insect repellent (Komatsu and Maruyama's personal observations). So when repellent was sprayed into the entrance of ant nest, a lot of ant workers cause panic and escape out of nest, together with some individuals of myrmecophilous insects that contain *Myrmecophilus* crickets. The crickets were immediately preserved in 100% ethanol. We sorted individuals of *M. tetramorii* from all of the samples to count them and determine their host ant species. Generally, identification of *Myrmecophilus* by eye is difficult. However, *M. tetramorii* is easily distinguished from other species because of the specific shape of its body hair [9].

We also collected live *M. tetramorii* ($n = 20$) and a colony of *T. tsushimae* (about 200 workers and some dozens of larvae) to use them in experiments. All cricket individuals were collected from the same colony. Prior to the observation on cricket-ant interactions, ants and crickets were reared together for at least 3 days in a small plastic container (10 cm × 10 cm × 10 cm).

2.2. Cricket-Ant Interactions. Behavioral observations were performed by the same method we used previously [8, 15]. Four crickets and 20 to 30 *T. tsushimae* ant workers were released into a small plastic container (10 cm × 10 cm × 10 cm); they were supplied only with water and left undisturbed for 24 h. The next day, we placed 5 ant larvae from collected colony of *T. tsushimae* into the container, as well as a dead mealworm and 50% sugar water; these items closely approximated the foods of ant crickets and ants in the wild [1]. 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 on a 1 cm high 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 (a) was attacked by ants (i.e., the ants opened their mandibles and pursued or bit the cricket) and immediately escaped from the ant; (b) fed directly on the items provided; (c) groomed

TABLE 1: Host ant species investigated and numbers of *Myrmecophilus* spp. and *M. tetramorii* crickets collected.

Host subfamily	Host genus	Host species	Total no. of crickets	No. of <i>M. tetramorii</i>	
Formicinae	<i>Camponotus</i>	<i>japonicus</i>	8	0	
		<i>obscuripes</i>	1	0	
	<i>Formica</i>	<i>hayashi</i>	4	0	
		<i>japonica</i>	17	1	
		<i>sanguinea</i>	1	0	
		<i>yessensis</i>	1	0	
		<i>Lasius</i>	<i>capitatus</i>	1	0
	<i>Lasius</i>	<i>flavus</i>	5	0	
		<i>fuji</i>	3	0	
		<i>japonicus</i>	40	0	
		<i>nipponensis</i>	7	0	
		<i>sakagamii</i>	2	0	
		<i>spathepus</i>	5	0	
		<i>orientalis</i>	2	0	
		<i>umbratus</i>	1	0	
		<i>Polyrhachis</i>	<i>lamellidens</i>	1	0
		<i>Polyergus</i>	<i>samurai</i>	2	0
Myrmicinae	<i>Aphaenogaster</i>	<i>japonica</i>	1	0	
	<i>Myrmica</i>	<i>jessensis</i>	1	0	
		<i>kotokui</i>	1	0	
	<i>Pristomyrmex</i>	<i>punctatus</i>	1	0	
Termites	<i>Tetramorium</i>	<i>tsushimae</i>	79	33	
		<i>speratus</i>	1	0	
Outside ant nest			2	0	
Total			187	34	

an ant body; (d) disrupted trophallaxis between ants; and (e) fed via direct mouth-to-mouth transfer from the ants. Each cricket individual was distinguishable by subtle disparity of body size or body color. We repeated these observations 5 times with different sets of crickets and ants. These results were compared with those from our previous study of one clade within *M. kubotai* [10, 15] that lives sympatrically with *M. tetramorii* and also uses *T. tsushimae* frequently as a main host.

2.3. Statistical Analyses. Behavioral differences between the two cricket species in the host colony were compared by using Wilcoxon's rank-sum test based on the averages for 20 individuals of each species. Statistical analysis was performed with the R software package [17].

3. Results

3.1. Field Survey. We collected a total of 200 *Myrmecophilus* ant crickets from the nests of 22 ant species. In addition, one cricket was collected from a termite nest and two from

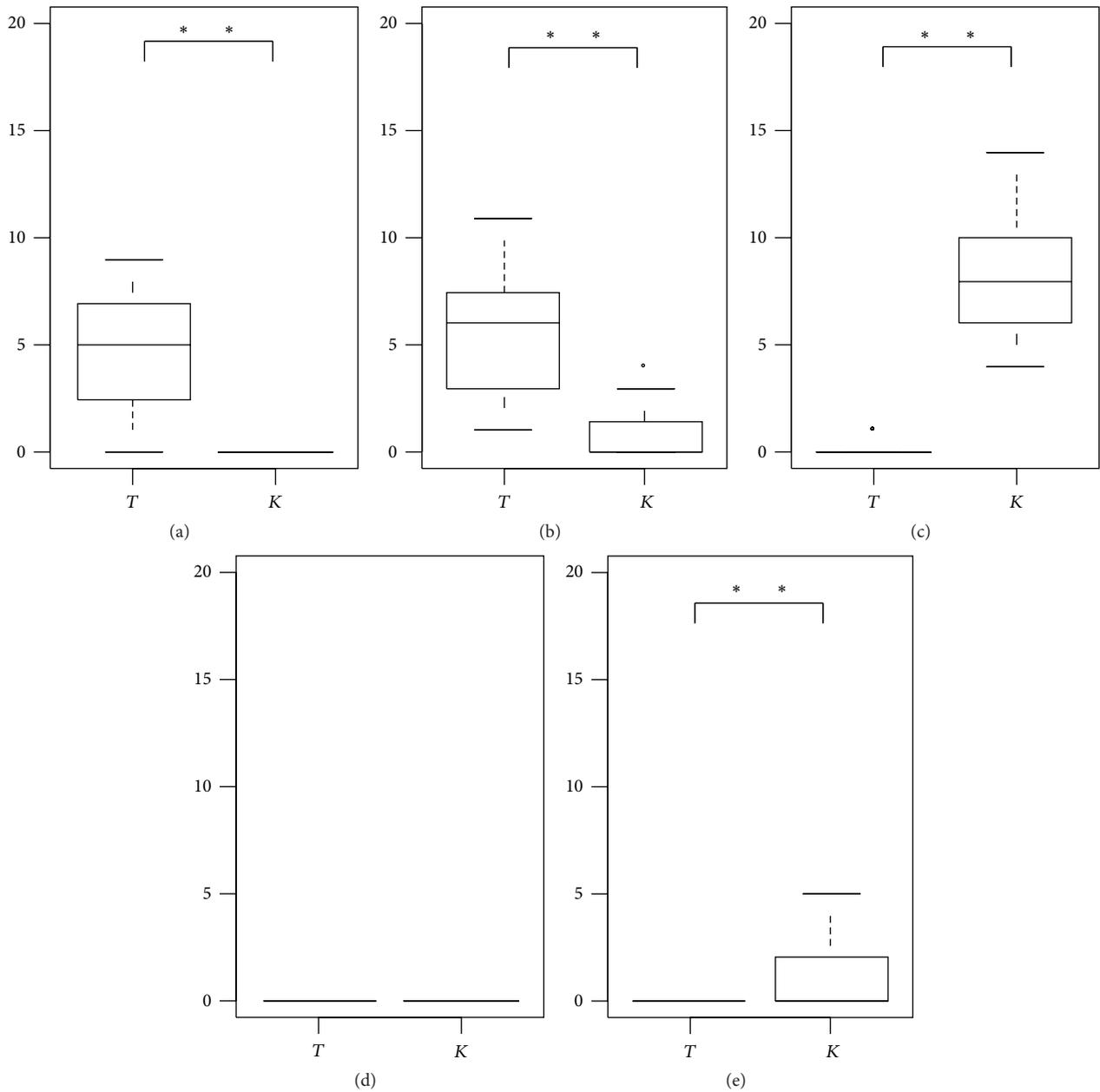


FIGURE 1: Behavior recognized in *M. tetramorii* (T) and in *M. kubotai* (K) in colonies of *T. tsushimae*. (a) Being attacked by ants and escaped from them immediately, (b) feed foods for themselves, (c) groom ant body, (d) muscle in trophallaxis between ants, (e) be done a feeding by direct mouth-to-mouth transfer by ants. Results of each behavior were based on averages of all individuals of each species ($N = 20$) observed. The box plot represents 25th, 50th, and 75th percentiles. The top and bottom whiskers represent largest and smallest nonoutlier observations, respectively. Dots represent outliers that are any value greater than 1.5 times the spread outside the closest hinge. * $P < 0.05$, ** $P < 0.01$ by Wilcoxon rank-sum test.

outside an ant nest (Table 1). Thirty-four of the crickets were *M. tetramorii*; 33 came from *Tetramorium tsushimae* nests and 1 from a *Formica japonica* nest. All individuals of *M. tetramorii* were collected from Honshu to the west.

3.2. Cricket-Ant Interactions. Aggressive reactions by the ants to *M. tetramorii* crickets were significantly higher than those to *M. kubotai* (*M. tetramorii* versus *M. kubotai*, mean \pm SD:

5.2 ± 2.8 versus 0 events/h, $P < 0.001$) (Figure 1). Both species of crickets fed directly on the items available, but feeding by *M. tetramorii* was significantly more frequent (6.1 ± 2.9 versus 0.8 ± 1.2 events/h, $P < 0.001$). *Myrmecophilus tetramorii* always ate the solid foods (ant larvae and dead insects). *Myrmecophilus kubotai* licked the surface of the ants' bodies significantly more frequently (0.2 ± 0.4 versus 8.4 ± 2.6 events/h, $P < 0.001$). Disruption of trophallaxis between

ants was not observed in either cricket species (0 versus 0 events/h). *Myrmecophilus tetramorii* showed no begging behavior toward its hosts, whereas *M. kubotai* did, especially just after fresh foods had been introduced; the cricket was fed by the ant via direct mouth-to-mouth transfer (0 versus 0.9 ± 1.5 events/h, $P < 0.001$).

4. Discussion

All but one individual of *M. tetramorii* were collected from nests of *T. tsushimae* in several regions of Japan. Therefore, this species should be classified as a specialist in terms of its host species range. Nevertheless, it ate only solid foods while it did not show any intimate behaviors toward *T. tsushimae*, like eating liquid food via direct mouth-to-mouth transfer. This means that our hypothesis that all specialist *Myrmecophilus* species always show intimate behaviors is not valid. In Japan, two other specialist species, *M. albicinctus* and one clade within *M. kubotai* [10, 15], have been collected from the nests of specific ant species and have comparatively specialized parasitic behaviors [8, 15]. They train or habituate clusters of ants and groom the bodies of the ants insistently; they even receive direct feeding. By contrast, *M. tetramorii* did not show any obvious integrated behaviors toward its host ants. Its series of behaviors, such as eating only solid foods and receiving hostile reactions from ants, resembled those of *M. formosanus*, a generalist species that can use several ant subfamilies as hosts [8]. Previous studies by using several parasite taxa suggested that parasitic behaviors of specialist species are more adapted to exploit specific host. However, at least for *Myrmecophilus*, the tendency is not always applicable.

It is unclear why *M. tetramorii* did not behave intimately toward the host ants. However, competition for food resources among *Myrmecophilus* species could be one reason. In mainland Japan, some *Myrmecophilus* species show a distinct preference for either a shaded or an open habitat [10]. In addition, some species that share the same habitat tend to differentiate host ant taxa [10]. However, *M. tetramorii* and one clade within *M. kubotai* occur exceptionally in the same open habitat and share the same ant species as their main host [10, 15]. It is possible that the trend we found here reflects the differentiation of food resources and feeding habits between two cricket species to avoid interspecific competition related to microhabitat.

Various degrees of host range or specificity, or both, are recognized in *Myrmecophilus* crickets. We showed that specialization does not necessarily correlate with intimate behavior of the ants in this genus. Nevertheless *M. tetramorii* is obviously adapted to *T. tsushimae* without sophisticated integration cues. This is surprising because congeneric species (e.g., *M. kubotai*) show such a high grade of integration. Moreover, within the genus, there are specialists and generalists and *M. tetramorii* is a specialist that is not as much integrated as a generalist. In laboratory observation, *M. tetramorii* quickly robbed food resources, such as ant larvae and dead insects, from ants. Several species of *Tetramorium* are known as the slow-moving ants [18, 19], and so is *T. tsushimae* [10]. One can argue that *M. tetramorii* is specialist

species that did not develop behavioral intimacy toward host ants but that developed foraging behavior without physical contact with ants.

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