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RESEARCH ARTICLE

Behavioral differences between two ant cricket species in Nansei Islands: host-specialist versus host-generalist

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Abstract Ant crickets (Orthoptera, Myrmecophilidae) are typical ant guests that obtain nourishment from the ants in their nests. Some ant crickets are host-specific, whereas other species are host-generalists. We investigated the behavioral polarization between the specialist cricket *Myrmecophilus albicinctus* and generalist *Myrmecophilus formosanus*. In the field, *M. albicinctus* was found exclusively in nests of *Anoplolepis gracilipes* (185/185), whereas 62 *M. formosanus* were found in nests of 9 ant species from 3 subfamilies. Behavioral observations revealed that *M. albicinctus* could not survive in the absence of *A. gracilipes* and was killed when it was introduced into colonies of non-host ant species. In addition, *M. albicinctus* showed intimate behavior, such as trophallaxis, with its host. In contrast, *M. formosanus* swiftly avoided frequent attacks by host ants, independently took food, and survived well in the absence of ants. Overall, the specialist adapted its behavior and physiology to those of a specific ant host, whereas the generalist adopted versatile parasitic behaviors, such as quick movements. Our findings revealed interspecific polarization in the degree of host dependence and inquiline–host interaction, and they indicate that trade-offs occur between specialization to specific hosts and retention of generalization in order to exploit alternative hosts.

Keywords Ant guests · Host specificity · Myrmecophiles · *Myrmecophilus* · Symbiosis

Introduction

Ant guests that live within ant nests comprise up to 100,000 species across many invertebrate taxa (Elmes, 1996). Generally, ants show aggressive and exclusive reactions to non-nestmates (Yamaoka, 1990). Thus, ant guests have evolved various ways to break their host's communication or recognition cues, allowing them to be accepted (Wheeler, 1908; Akino et al., 1996, 1999; Thomas and Elmes, 1998). Several species of inquilines have extreme intimacy with their ant hosts, having the ability to biosynthesize the chemical cues of certain ant species (*Maculinea*, Lycaenidae: Akino et al., 1999), and even no longer executing simple daily skills, such as movement or feeding, without assistance from the ants (*Aribates*, Oribatidae: Ito and Takaku, 1994; Ito and Aoki, 2003).

Myrmecophilus ant crickets (Orthoptera, Myrmecophilidae) are the only orthopteran ant guests within ant nests, with up to 60 species distributed from temperate to tropical regions across the world (Kistner, 1982; Maruyama, 2004). *Myrmecophilus* crickets feed on ant eggs, lick the body surfaces of ants, disrupt the trophallaxis between ants, or are fed liquid food from ants by direct mouth-to-mouth contact (Wheeler, 1900; Hölldobler, 1947; Henderson and Akle, 1986; Sakai and Terayama, 1995; Akino et al., 1996). Given the ants' aggressive behavior toward nest invaders, such intimate contacts are surprising. Generally, ants use the composition of cuticular hydrocarbons (CHCs) that

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cover the body surface for nestmate identification (Smith and Breed, 1995; Thomas et al., 1999; Wagner et al., 2000). However, some *Myrmecophilus* species can coexist with their hosts by acquiring the ants' CHCs and coating their own bodies with them (Akino et al., 1996). Komatsu et al. (2008) observed six species of ant crickets in host nests in the field and reported two general types: those avoiding ant attacks by quick movement, and those having intimate contact with their hosts. It remains unclear, however, what kind of host–inquiline interactions and dependence underlies these types of behavior among *Myrmecophilus* species.

The taxonomy of Japanese *Myrmecophilus* crickets is ambiguous because of the scarcity of morphological characters useful for distinguishing among species. Historically, four morphospecies were recognized and were thought to show random associations with various ant species (Sakai and Terayama, 1995; Akino et al., 1996). Recently, however, Maruyama (2004) classified Japanese *Myrmecophilus* crickets into at least ten species on the basis of the structure of the body surface, and he noted that particular species of ant crickets tended to be collected from nests of specific ant species. Komatsu et al. (2008) reported that two types of species existed; one tended to be collected from the nests of single ant species (specialist) and the other from nests of several ant species or genera (generalist).

In studies of the evolution of host–parasite interactions, phytophagous and parasitoid insects have been used extensively as models (Futuyma et al., 1995; Kelley and Farrell, 1998; Stireman, 2005). These insects are good models, because they have experienced trade-offs between specialization to overcome host defenses and retention of generalization in order to exploit alternative hosts (Rausher, 1984; Jaenike, 1990; Joshi and Thompson, 1995; Kraaijeveld et al., 2001). This holds true for myrmecophilous insects, because they face trade-offs between the ability to overcome a specific host's nestmate recognition system and the capacity to exploit alternative host species (Kistner, 1979; Davies and Bourke, 1989; Brandt et al., 2005). As seen in *Myrmecophilus*, the fact that there are many cryptic species with different degrees of host specificity (Komatsu et al., 2008) indicates that the members of this genus should be good models for the use in investigating the evolution of host–parasite interactions and trade-offs in survival. We therefore investigated the differences in the degree of behavioral specialization to host, and survival between specialist and generalist *Myrmecophilus* species.

Till date, no studies have examined the array of behaviors of ant crickets within their hosts' nests and how host interactions differ between specialist and generalist ant crickets. Previous studies in behavior of ant crickets

have been confined to fragmentary observations (e.g., Hölldobler, 1947; Sakai and Terayama, 1995; Akino et al., 1996), and some of these studies have been conducted on individuals with ambiguous species identification (e.g., Akino et al., 1996), making it impossible to draw conclusions about the behavior of particular species. Likewise, the difficulties with visual identification have continued to be a problem in making interspecific comparisons of behavior among *Myrmecophilus* species. Maruyama's (2004) taxonomic information, however, allows us to make behavioral comparisons between easily distinguishable specialist and generalist species living in a sympatric environment and sharing the same host species.

Two species of *Myrmecophilus* cricket are recognized in the Nansei Islands of Okinawa Prefecture in Japan (Maruyama, 2006; Terayama and Maruyama, 2007). *Myrmecophilus albicinctus* Chopard is blackish overall, with a white line on the thorax. The species is distributed broadly from the Nansei Islands to Southeast Asia and is usually collected only in yellow crazy ant nests, *Anoplolepis gracilipes* Smith (Formicinae) (Terayama and Maruyama, 2007). *Myrmecophilus formosanus* Shiraki is also blackish over the whole body, but it lacks the white thorax line. This species is distributed from the Nansei Islands to Taiwan and is collected from the nests of *Diacamma* sp. (Ponerinae), some species of *Pheidole* (Myrmicinae), *A. gracilipes*, and two species of *Paratrechina* (Formicinae) (Maruyama, 2006; Terayama and Maruyama, 2007; see Table 1). These two sympatric *Myrmecophilus* species are suitable for specialist-versus-generalist behavioral comparison, because they can be easily distinguished by eye and share a host, namely *A. gracilipes*.

We compared feeding habits, behavior used to avoid ant attack, and survival rate in these two species in the absence and presence of host/non-host ants, in order to highlight behavioral and survival polarization between specialist and generalist parasites.

Materials and methods

Field survey

Field work was conducted on several Nansei Islands (Okinawa, Tarama, Miyako, Ishigaki, Iriomote, and Yonaguni Islands) from 1996 to 2008. We surveyed the frequencies of occurrence of the two species of cricket in primary and secondary forests, agricultural fields, and urban lands. We searched for ant nests by locating nest entrances, turning over stones, or breaking down decayed wood. When an ant nest was found, we dug a circle (radius 30 cm) around the nest and 10-cm deep, excavating the soil. During

Table 1 Frequency occurrence of the two ant crickets in ant nests in Nansei islands

Host ant		Nests with *M. albicinctus*			Nests with *M. formosanus*	
Subfamily	Species	No. of ant nests surveyed	No. of nests	No. of crickets	No. of nests	No. of crickets
Formicinae	*Anoplolepis gracilipes*	59	28	185	14	26
	Paratrechina amia	5	0	0	1	1
	Paratrechina longicornis	31	0	0	1	1
	Camponotus kaguya	1	0	0	1	1
Myrmicinae	*Pheidole megacephala*	42	0	0	4	13
	Pheidole noda	15	0	0	3	3
	Pheidole parva	3	0	0	1	1
	Pheidole sp.	1	0	0	1	1
Ponerinae	*Diacamma* sp.	9	0	0	3	12

See text for other ant species that were surveyed but in which neither ant cricket was detected

the excavation, ant crickets in the nest were collected, and the number and species were recorded. After the nest census, the ants and soil were dropped back, and the crickets were collected in 100% ethanol for molecular research.

Behavior toward host ants

Before the behavioral observations were conducted, *A. gracilipes* (the host ant common to both crickets) and the two species of cricket (*M. albicinctus* and *M. formosanus*) were collected over a week in August 2008 from a single *A. gracilipes* colony in Yona Field at the Subtropical Field Science Center, University of the Ryukyus, Okinawa (queens: $N = 7$, workers $N = 90$–100, ant larvae: $N = 50$–60, *M. albicinctus*: $N = 40$, *M. formosanus*: $N = 40$). Additionally, workers of *Diacamma* sp. ($N = 10$, Ponerinae) and *Pheidole megacephala* Fabricius ($N = 40$, Myrmicinae) were collected from the same site. Collected insects were placed in plastic containers with wet filter paper and brought back to the laboratory. Both the ants and the two species of cricket were kept in the plastic containers ($20 \times 10 \times 15$ cm/width × depth × length), which were filled with gypsum to a depth of 7 cm. They were fed with sugared water and mealworms until they were used in the experiments 2 weeks after the collection.

Behavioral observations were performed on the two cricket species and the *A. gracilipes* ants. Four crickets of one species and 20–30 ant workers were released into a small plastic container ($10 \times 10 \times 10$ cm). They were given only water and left undisturbed for 24 h. The next day, we placed five ant larvae into the container, as well as a dead insect (a mealworm) and 50% sugared water, which closely approximated the foods of ant crickets in the wild (Kistner, 1982). *A. gracilipes* likes homopteran honeydew (Reimer et al., 1990; Lach, 2003), which is mostly composed of sugar (Mittler, 1958; Völkl et al., 1999). Given the

fact that the ant crickets can disrupt trophallaxis between ants (Sakai and Terayama, 1995; Akino et al., 1996), it was likely that there would be abundant opportunities for them to take in sugar-rich liquid as food. For these reasons, we used sugared water for the experiment. The ant larvae and the dead insect were placed on the floor of the container, and the sugared water was soaked into absorbent cotton and placed in a stand 1-cm high that only the ants could climb; the crickets could not feed on it 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 escaped from them immediately; (b) fed itself; (c) groomed an ant body; (d) disrupted trophallaxis between ants; and (e) fed via direct mouth-to-mouth transfer by ants. For each cricket species, these observations were repeated five times with different sets of individuals.

Survival rate in absence of host ants

We investigated the survival rates of *M. albicinctus* and *M. formosanus* in the absence of ant hosts to determine their degree of dependence on the host. Twenty crickets from one species were released into a small plastic container ($10 \times 10 \times 10$ cm) with five ant larvae, one dead mealworm, and sugared water soaked into absorbent cotton, as described above. These meals were replenished once everyday. The crickets were left in the container for 2 weeks. Each day, the number of dead crickets was recorded, the dead individuals were removed, and the food items were replaced with fresh ones.

Introduction to colonies of alternative hosts

Akino et al. (1996) reported that the ant-derived components on the body surface of *Myrmecophilus* crickets in Honshu

volatilized within about 1 week in the absence of additional physical contact with ants. In addition, *Myrmecophilus* crickets introduced to another, conspecific, colony tend to receive attacks from the ants in the colony immediately after introduction, although these attacks later decrease in frequency. This may occur because the crickets are carrying residual CHCs from the first colony (Akino et al., 1996). Therefore, before this experiment, we isolated the crickets in a container and fed them only sugared water for 1 week in order to reduce any effects of chemicals derived from previous hosts. *M. albicinctus* and *M. formosanus* crickets collected from the *A. gracilipes* (Formicinae) nests were introduced into containers with an alternative host ant, *Diacamma* sp. (Ponerinae) or *P. megacephala* (Myrmicinae). These ant species are potential hosts of *M. formosanus* in the wild (Terayama and Maruyama, 2007; Table 1). Ten to 40 workers of *Diacamma* sp. or *P. megacephala* and ten crickets of one species were placed in a small plastic container (10 × 10 × 10 cm), with one dead mealworm and the sugared water in cotton, as above. For 1 h immediately after introduction, for each cricket individual, we recorded the numbers of the five behavior events noted above. Each day, the number of dead crickets was recorded; the experiment ended after 1 week or when all the crickets had died.

Statistical analyses

Behavioral differences between the two cricket species in the host colony were compared by Wilcoxon rank-sum test based on the averages for 20 individuals of each species, or of 10 individuals in the case of the alternative host colonies. Statistical analysis was performed with the R software package (ver. 2.3.1; R Development Core Team, 2005).

Results

Field survey

We surveyed a total of 260 ant nests belonging to 35 different ant species. We collected a total of 247 juvenile and adult ant crickets (185 *M. albicinctus*, 62 *M. formosanus*) from the ant nests. We found all *M. albicinctus* in *A. gracilipes* nests. In contrast, we found *M. formosanus* in the nests of nine ant species in three subfamilies: *A. gracilipes*, *Paratrechina amia* Forel, *P. longicornis* Latreille, *Camponotus kaguya* Terayama, *Pheidole megacephala*, *P. noda* Smith, *P. parve* Mayr, *Pheidole* sp., and *Diacamma* sp. (Table 1). We also found three *M. formosanus* outside ant nests.

We found no ant crickets in nests of the other 26 ant species (number of nests excavated in parentheses): *Amblyopone silvestrii* Wheeler (1), *Cerapachys biroi* Forel (2),

Tapinoma melanocephalum Fabricius (16), *Technomyrmex brunneus* Forel (7), *Paratrechina otome* Terayama (1), *P. ryukyuensis* Terayama (7), *P. yaeyamensis* Terayama (2), *Aphaenogaster concolor* Watanabe and Yamane (1), *Carebara hannya* Terayama (1), *Monomorium chinense* Santschi (3), *M. latinode* Mayr (2), *Pheidole pieli* Santschi (3), *Pristomyrmex punctatus* Smith (1), *Strumigenys* sp. (2), *Tetramorium bicarinatum* Nylander (6), *T. lanuginosum* Mayr (3), *Tetramorium* sp. (2), *Anochetus shohki* Terayama (2), *Cryptopone tengu* Terayama (1), *Odontomachus kuroiwae* Matsumura (9), *Pachycondyla chinensis* Emery (5), *P. javana* Mayr (5), *P. luteipes* Mayr (3), *P. sakishimensis* Terayama (2), *Ponera* sp. (3), *Proceratium japonicum* Santschi (1).

Behavior toward host ants

Aggressive reactions by the ants to *M. albicinctus* crickets were significantly less frequent than those to *M. formosanus* (*M. albicinctus* vs. *M. formosanus*, mean ± SD; 0.1 ± 0.5 vs. 4.8 ± 2.2 events/h, $P < 0.001$), and two of the *M. albicinctus* individuals that received slight attacks showed remarkable behavior not seen in *M. formosanus*. The cricket stopped, became stiff (while staying on its feet), rounded its back, stretched itself, and tucked its antennae to the side of its body. The ant that caught up with the cricket stopped, sat on it, rounded its back a little, became stiff, and tucked its antennae also. The ant also showed other behaviors, such as rubbing the dorsal line of the cricket with its antennae and licking the cricket's cerci. After a few seconds, the cricket escaped by quickly weaving its way through the legs of the ant or jumping. The ant paused a little and ran after the cricket, but was not able to catch it in either case. No cricket of either species was harmed or killed during the 1-h observation. In contrast, all individuals of *M. formosanus* spent their time with minimal contact with the ants and escaped quickly when the ants approached. The ants appeared to be aware of *M. formosanus* and tried to catch the crickets when the ants' antennae touched them or when a cricket passed in front of them, but *M. formosanus* always escaped by a quick movement.

Myrmecophilus albicinctus individuals did not feed themselves, whereas *M. formosanus* frequently did (0 vs. 3.9 ± 2.1 events/h, $P < 0.001$). *M. formosanus* ate solid foods (ant larvae and dead insects). When they were approached by ants during feeding they escaped, leaving behind the larger food pieces but putting smaller pieces in their mouths.

Licking of the surface of an ant's body was observed only in *M. albicinctus* and never in *M. formosanus* (4.8 ± 1.6 vs. 0 events/h, $P < 0.001$). *M. albicinctus* individuals worked their way into an ant cluster and frequently showed behaviors such as grooming themselves or

ants. Few were attacked by ants when they touched or licked the host's bodies. When ants were groomed by the crickets, the ants usually accepted it by drawing in their legs and antennae in the same way as when groomed by a nestmate.

Disruption of trophallaxis between ants was rarely observed in either cricket species, although it was significantly more frequent in *M. albicinctus* (0.2 ± 0.4 vs. 0 events/h, $P < 0.05$). Whereas, *M. formosanus* never showed begging behavior toward its hosts, *M. albicinctus* frequently did so, especially just after fresh food had been introduced; the cricket was fed by the ant via direct mouth-to-mouth transfer (4.1 ± 2.7 vs. 0 events/h, $P < 0.001$). *M. albicinctus* stood over the ant, beating the ant's mouthparts with its forelegs or maxillary palps and receiving food from the ant through trophallaxis.

Survival rate in the absence of host ants

In the absence of a host ant, all *M. albicinctus* died off by day 10, but all *M. formosanus* survived the 2-week observation period.

Introduction to colonies of alternative hosts

In the colony of *Diacamma* sp., both cricket species—especially *M. albicinctus*—were frequently attacked by ants (14.8 ± 12.8 vs. 1.7 ± 3.06 events/h, $P < 0.05$). When the ants quickly chased the crickets moving in front of them, *M. formosanus* escaped by running or jumping, as in the experiments with *A. gracilipes*. *M. albicinctus* also escaped in a similar manner, but most were caught by the ants because of their slow movement relative to that of *M. formosanus*. In addition, the stiffening behavior that several of them showed toward *A. gracilipes* was not observed. Individuals of both cricket species were always killed by biting or stinging when they were caught by the ants. *M. albicinctus* was not observed to feed itself, whereas *M. formosanus* did (0 vs. 0.3 ± 0.4 events/h, $P < 0.05$).

Similar reactions of the two crickets were seen in the colony of *P. megacephala* (7.3 ± 3.0 vs. 1.8 ± 1.3 events/h, $P < 0.001$). However, these ants tried to catch the crickets only when the ant's antennae touched them. *M. albicinctus* individuals were not observed to feed themselves, whereas *M. formosanus* did, although the difference between the species was not significant (0 vs. 0.4 ± 0.7 events/h, $P = 0.08$). Physical contacts (behaviors c to e, see "Materials and methods") were not observed between *Diacamma* sp. or *P. megacephala* and individuals of either cricket species.

In the colony of *Diacamma* sp., all *M. albicinctus* were killed within 2 days, whereas *M. formosanus* survived

longer, but all were killed within 5 days. In the *P. megacephala* colony, all *M. albicinctus* were killed by day 1, whereas all but three *M. formosanus* individuals survived for the 1-week observation period.

Discussion

This study revealed clear differences in the degree of dependence on host ants between a specialist and a generalist *Myrmecophilus* species. *M. albicinctus* was highly specialized to live with *A. gracilipes*. Indeed, it was not collected from other ants' nests in the wild (Table 1). In addition, *M. albicinctus* could not survive in the absence of its host ant *A. gracilipes* and showed host-intimate behavior such as being fed mouth-to-mouth by *A. gracilipes*. Although some researchers have hypothesized that ant crickets migrate from nest to nest as they grow—from a small ant species to a large ant species (Hölldobler, 1947; Baccetti, 1967; Sakai and Terayama, 1995), this does not apply to *M. albicinctus*, because individuals at various stages of growth were collected only from *A. gracilipes* nests.

Adaptations of the specialist

Anoplolepis gracilipes, the obligate host of *M. albicinctus*, is distributed widely over the tropical and subtropical regions of the world. It has been designated as one of world's worst invasive alien species, and this is due to the ant's aggressiveness to other organisms, high fecundity, and the difficulty in its extirpation (Abbott, 2005). Also, *A. gracilipes* is one of the tramp ant species that have expanded their distribution accompanying human activity (Abbott, 2005). These characteristics, together with its huge colony size may contribute to the survival and dispersal of the ant crickets that specialize on this ant species with a wide distribution and huge colonies.

We found that two *M. albicinctus* showed apparent defensive behavior when they were attacked by a host ant. When a cornered cricket rounded its back suddenly and stopped moving, the ant that caught up with it from behind became stiff, allowing the cricket to escape. These behaviors were not seen in *M. formosanus* and have not been reported in other *Myrmecophilus* species. Although some *Myrmecophilus* obtain host ant chemicals (e.g., CHCs) that permit them to coexist with the ants (Akino, 2002), it is very probable that *M. albicinctus* may be able to biosynthesize and secrete chemicals specifically mimic to *A. gracilipes* given their strong dependence on this host. However, *M. albicinctus* may also have opportunities to take CHCs from the ants' bodies during their frequent episodes of physical contact. Detailed analysis of the CHCs

of ant crickets in the presence or absence of ants may reveal whether these chemicals are derived from the crickets or the ants.

Myrmecophilus albicinctus beat the ant's mouthparts with its forelegs or maxillary palps to stimulate trophallaxis. Similar behavior is seen in several other myrmecophilous insects that are fed by trophallaxis (*Hetaerius*, Histeridae: Wheeler, 1908; *Amphotis*, Nitidulidae: Hölldobler, 1968; *Atemeles*, Staphylinidae: Hölldobler, 1971). However, this is the first report of a cricket species depending exclusively on mouth-to-mouth feeding by its hosts. All of these mouth-to-mouth feeding insects are known to have high host specificity, and this behavior is an adaptation of a specialist. In addition, those myrmecophilous insects that use both behavioral and chemical strategies can be fed more efficiently than those that use only behavioral strategies (Kistner, 1979). Our observations suggest that *M. albicinctus* uses both types of strategy to integrate into colonies of *A. gracilipes*.

Adaptation of generalist

Most of the *M. formosanus* individuals were collected from nests of *A. gracilipes*, although they were collected from nests of several ant species across three subfamilies (Table 1). This indicates that *M. formosanus* is a host-generalist. In addition, our observations showed that they had less dependence on ants than did *M. albicinctus*; *M. formosanus* consistently avoided physical contact with the ants and was able to live in the absence of ants. In fact, we collected several individuals of this species from under stones where no ant colonies existed. Tropical and subtropical ant species tend to be migratory and frequently move their colonies (Schneirla, 1957; Wilson, 1958a, 1958b; Hölldobler and Traniello, 1980; Maschwitz et al., 1989). Thus, *M. formosanus* individuals found away from ant nests may have failed to migrate with the ants when the colony moved. The consistently aggressive reactions that we observed in the ants suggest that *M. formosanus* has a poor, or absent, chemical mimicry ability. Our observations also suggest that this species cannot obtain CHCs from ants, because individuals hardly made physical contact with the ant's body surface. This lack of chemical cues would allow this generalist species to inhabit the nests of numerous ant species across subfamilies.

Several ant species showed little or no association with *M. formosanus*, despite the cricket being a sympatric host-generalist. Ant species that have huge colonies are potentially used as hosts by numerous myrmecophilous insects (Akino, 2002). Nevertheless, *M. formosanus* was not found in colonies of *P. longicornis*, *T. brunneus*, or *T. melanocephalum*, all of which form large colonies (ranging from dozens to many millions of ants) and often are the dominant

species in habitats of the Nansei Islands (Myrmecological Society of Japan, 1989, 1991). It is notable, however, that *M. formosanus* was collected from the nests of *Diacamma* sp., which has small colonies (around 20–400 ants) and has a restricted distribution pattern on these islands (Myrmecological Society of Japan, 1989). Many factors other than colony size, such as the level of ant aggressiveness, are likely related to host ant selection by crickets. All of the ant crickets that we placed within the colony of *Diacamma*. sp. were killed. However, this may have occurred because the proportion of ants to crickets in the container was too large, because several *M. formosanus* individuals were collected from *Diacamma*. sp. nests in the field (Table 1). Altogether, our observations strongly suggest that the generalist *M. formosanus* has poor, or no, ability to chemically mimic its ant hosts.

Trade-offs

The bipolarization of host specificity and the degree of behavioral specialization among congeneric inquiline species shed light on specialist–generalist trade-offs. Each strategy—to specialize in a particular host species or to utilize various host species—has advantages and disadvantages. Trade-offs are necessary in the adaptation of an organism to a specialist or generalist lifestyle (Self et al., 1964; Duffey, 1980; Bernays and Minkenberg, 1997; Wheeler et al., 1998). The frequencies of occurrence of these two species of ant cricket in the wild (Table 1), as well as their survival patterns in the experimental ant nests, suggest the existence of such trade-offs. First, more individuals of *M. albicinctus* were found than *M. formosanus* in nests of *A. gracilipes* (Table 1), suggesting higher survival and/or fecundity of *M. albicinctus* in their target host nests. Second, the higher survival rates of the generalist *M. formosanus* than of the specialist *M. albicinctus* in alternative host ant colonies indicate the advantage of being general in host use (although it is possible that all the *M. albicinctus* individuals that we used in the experiment were weakened by the 1-week quarantine from their hosts). This specialization within the genus is also interesting from the viewpoint of whether it is completely bipolarized or whether there are graded stages of specialization. To elucidate this, broad behavioral comparisons across more *Myrmecophilus* species are necessary.

Conclusion

We found different behavioral adaptations in a *Myrmecophilus* host-specialist and a host-generalist. The specialist was able to avoid recognition by the host through behavioral, and perhaps chemical, cues, allowing it to be fed

directly by the ant. The generalist was not able to avoid recognition by the hosts but escaped quickly, allowing it to feed on items available in the ant nest. *M. albicinctus* and *M. formosanus* should serve as good models for investigating the evolution of behavioral and physiological adaptation of specialists and generalists in host–parasite interactions. The phylogenetic relationship between *M. albicinctus* and *M. formosanus* in this genus remains unknown (Komatsu et al., 2008). More exhaustive sampling and phylogenetic analysis will be needed to reveal the intrageneric evolution of host specificity in *Myrmecophilus*.

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