Parasitism and olfactory responses of *Dastarcus helophoroides* (Coleoptera: Bothrideridae) to different Cerambycid hosts

Jian-Rong Wei · Zhong-Qi Yang · Therese M. Poland · Jia-Wei Du

Abstract *Dastarcus helophoroides* (Fairmaire) (Coleoptera: Bothrideridae) is an important natural enemy of longhorned beetles (Coleoptera: Cerambycidae). It is distributed throughout most Provinces in China. We investigated whether there were differences among *D. helophoroides* populations collected from different hosts in different geographic locations. Results showed that different *D. helophoroides* populations displayed different olfactory responses to larval frass from different longhorned beetle species. All populations were significantly attracted to the frass of their original hosts. Parasitism rates of different populations also varied when supplied with host larvae of the same longhorned beetle species. These results indicate that the three *D. helophoroides* populations tested differed in host-related behaviors. Therefore, the population of *D. helophoroides* must be taken into consideration when implementing biological control programs for different species of longhorned beetle.

Keywords Population differences · *Anoplophora glabripennis* · *Monochamus alternatus* · *Massicus raddei* · Wood borer · Tritrophic interactions

J.-R. Wei (✉) · Z.-Q. Yang
The Key Laboratory of Forest Protection, State Forestry Administration of China, Research Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry, 100091 Beijing, China
e-mail: weijr@caf.ac.cn; jrwei9@126.com

T. M. Poland
USDA Forest Service, Northern Research Station, East Lansing, MI 48823, USA

J.-W. Du
Institute of Plant Physiology and Ecology, Shanghai Institute of Biological Sciences, Chinese Academy of Science, 200032 Shanghai, China

Introduction

Longhorned beetles (Coleoptera: Cerambycidae) are considered major pests of forest and shade trees, shrubs, and raw wood products. For example, *Anoplophora glabripennis* (Motsch.) (Asian Longhorned Beetle, ALB) is a wood-boring beetle with an unusually broad host range (Gao and Li 2001). It was discovered in the United States in the late 1990s and has the potential to destroy many landscape trees within urban landscapes (Haack et al. 1997; Nowak

et al. 2001). Following the discovery of *A. glabripennis* in the USA, many countries have become concerned about its establishment as a serious threat to their national forests (MacLeod et al. 2002). In addition to *A. glabripennis*, several other longhorned beetles have also caused serious damage to forests, including *Massicus raddei* (Blessig) and *Batocera horsfieldi* (Hope), which have experienced outbreaks in China in recent years and caused heavy economic losses to *Quercus mongolicus* Fisch. ex. Turcz. and poplar trees (*Populus* spp.), respectively. Some longhorned beetles also act as vectors of tree diseases in some countries. *Monochamus alternatus* Hope, which is a primary vector of the pine wood nematode [*Bursaphelenchus lignicolus* Mamiya and Kiyohara] (Mamiya and Enda 1972), causes serious damage to several pine species both in China and Japan. Methods to effectively control these longhorned beetles present a major challenge to scientists and natural resource managers worldwide.

Considerable interest in *Dastarcus helophoroides* (Fairmaire) (Coleoptera: Bothrideridae; synonym: *Dastarcus longulus* Sharp) has developed in recent years because of its status as an important natural enemy of longhorned beetles. This parasitic beetle is distributed in China and Japan (Qin and Gao 1988; Miura et al. 2003; Urano 2003). *D. helophoroides* larvae are ecto-parasitoids of late instar larvae, pupae, and young adults of several longhorned beetle species such as *A. glabripennis*, *M. raddei*, *M. alternatus*, *Apriona germari* (Hope), *Apriona swainsoni* (Hope), as well as *Batocera horsfieldi* (Hope) (Coleoptera: Cerambycidae) (Gao et al. 2003; Qin and Gao 1988; Pal and Lawrance 1986; Piel 1938; Wang et al. 1996; Zhou et al. 1985). It is the most predominant and efficacious natural enemy of these longhorned beetles and hence is a potential biological control agent for pest management (Urano 2003; Wang et al. 1996; Qin and Gao 1988; Li et al. 2007; Zhang and Yang 2006; Wei et al. 2007, 2009). Studies have been conducted investigating its biology (Lei et al. 2003; Qin and Gao 1988; Zhou et al. 1985), techniques for mass-rearing (Ogura et al. 1999; Wang et al. 1999), as well as its efficacy in control of *A. glabripennis* (Li et al. 2007; Qin and Gao 1988) and *M. alternatus* (Miura et al. 2003; Urano 2003). Results showed that *D. helophoroides* adults can lay eggs twice per year (Lei et al. 2003; Qin and Gao 1988). Eggs are laid on the outer surface of the bark near the host entrance hole, frass-extrusion hole or around the host larval tunnel walls (Qin and Gao 1988). Once *D. helophoroides* eggs hatch, first instar larvae have legs and can actively move to search for hosts. Their legs degenerate once parasitism has occurred. The egg, larval, and pupal periods are 12.7, 8.4, 25.6 days on average at $21 \pm 1°C$, respectively (Lei et al. 2003), and adults can live over four years (Wei et al. 2007). In general, one late instar larva of *A. glabripennis* or *M. raddei* can support complete development of 10–35 *D. helophoroides* larvae (Qin and Gao 1988; Gao et al. 2003). Live male and female *D. helophoroides* adults can not easily be distinguished based on morphological characters alone (Urano 2003); they can only be distinguished reliably by dissecting their reproductive organs. Vague detailed characteristics can be used to distinguish females and males (Tan et al. 2007), but with only 70–80% accuracy.

In order to optimize the use of natural enemies in biological control programs, surveys of longhorned beetle parasitism were conducted in different locations throughout China. *D. helophoroides* was found to be distributed in most areas of China. However, parasitism by *D. helophoroides* varied in different locations (Qin and Gao 1988). This phenomenon leads to the question of whether *D. helophoroides* populations from different locations and different hosts have similar behavior. If so, *D. helophoroides* could be mass-reared and released to control any host species, regardless of its original host. Since *A. glabripennis* is an invasive pest in some countries, introducing natural enemies from its original habitat might provide biological control and reduce its damage. However, if there are differences among *D. helophoroides* populations, it would be necessary to consider which population would be the most effective biological control agent. Therefore, studies were conducted to investigate whether *D. helophoroides* has different populations in China.

Semiochemicals are necessary signals used by natural enemies in long distance location of the host's or prey's habitat and in short range location of hosts or prey in their micro-habitat (De Moraes et al. 1998; Vinson 1998; Tinzaara et al. 2005). Many parasitoids and predators orient towards plant odors, including specific chemical signals released following feeding and oviposition by herbivores (Turlings et al. 1998; Hilker and Meiners 2006), or excretions by their hosts (Sullivan et al. 2000; Pettersson 2001), such as feces, silk, or exuviae. These informational chemical

cues might be either specific for certain host/prey complexes or they might be generally present in various complexes (Vinson 1976), and the reaction to the cues may be either innate or may be associatively learned after a host/prey encounter in their presence (Turlings et al. 1993; Vet et al. 1995). Variation in responses to the herbivore-plant complex may lead to different foraging decisions among different populations, thereby affecting their olfactory responses. Based on tritrophic studies among *D. helophoroides*, *M. raddei* and *Q. mongolicus*, host frass is significantly more attractive to the parasitoid than host larvae, wood with larval tunnels, or bark with larval tunnels, from the complex of the host and host tree (Wei et al. 2008). Therefore, bioassays were conducted to investigate the behavioral response of adults of different *D. helophoroides* populations toward frass odors from different longhorned beetle species feeding on different trees in order to determine if they have similar olfactory responses to different host species.

Parasitism rate is an important index for predicting or evaluating biological control potential of a parasitoid. We also tested the hypothesis that different *D. helophoroides* populations would have similar parasitism rates when supplied with the same host and host tree.

Materials and methods

Insect

Three populations of *D. helophoroides* were provided by the Research Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry (CAF), Beijing, China. The ancestor of the first laboratory colony (type a) parasitized larvae and pupae of *A. glabripennis* in the trunks of *Salix babylonica* Linn., which were collected in 2002 in Xian City (Latitude 34°15′N, longitude 108°50′E and altitude 450 m), Shaanxi Province, China. The ancestor of the second colony (type b) parasitized larvae and pupae of *M. alternatus* in the trunks or branches of *Pinus massoniana* Lamb., which were collected in 2003 in Guangzhou City (Latitude 23°80′N, longitude 113°17′E and altitude 120 m), Guangdong Province, China. The ancestor of the

third colony (type c) originated from *D. helophoroides* which parasitized larvae and pupae of *M. raddei* in the trunks of *Quercus mongolicus*, which were collected in 2002 in Meihekou City (Latitude 42°10′N, longitude 125°30′E and altitude 500 m), Jilin Province, China. Until 2008, no other host species were found to be parasitized by *D. helophoroides* in the three different locations. There were no differences in morphological characteristics between the three populations. All tested adults of the three populations were from the third generation reared on the same substitute host (*Thyestilla gebleri* (Fald.)) in the same environment in the laboratory (rearing methods are patent pending). The duration of development from egg to adult eclosion is less than two months, and after about two months of adult sexual maturation, newly emerged adults can lay eggs and produce offspring in the same year or the following year. Therefore, we obtained third generation *D. helophoroides* after three years of rearing in our laboratory.

Orientation responses of *D. helophoroides* adults to frass odor of longhorned beetles

Results showed that wood with *M. raddei* larval tunnels could significantly attract both sexes of *D. helophoroides* adults that were collected in Jilin Province parasitizing *M. raddei*. Furthermore, adults of *D. helophoroides* preferred the odor of *M. raddei* larval frass over that of wood with larval tunnels in a dual choice test (Wei et al. 2008). Therefore, we did not use Tan et al.'s method (2007) to distinguish sex, and both sexes were used in bioassay experiments. Before being selected as test adults, adults of different populations used in behavioral bioassays had already lived for 3–12 months after emergence. They had been mass-reared on artificial diet. Test adults were starved individually in glass tubes at 25°C, 60% RH, and 20–30 Lux (10:14 h L:D) for 30–35 days after feeding (Wei et al. 2009).

Bioassay procedures

Bioassays were conducted in a Y-tube olfactometer (Wei et al. 2008), that was a modified version of the one developed by Takabayashi and Dicke (1992) in which the angle between the two arms was 75°. A

constant supply of air filtered by activated charcoal and silica gel, flowed into each arm at 0.3 l min^{-1}. Since adults generally take 10–30 min to respond to stimuli in the Y-tube, we added a funnel at the end of each arm into which adults dropped. Adults were individually introduced into the release chamber. Observation of an individual beetle ended when the beetle had walked to the midpoint of one of the olfactometer arms or dropped into the funnel, with maximum observation duration of 30 min per beetle. Then the beetle was removed from the Y-tube. Every tested beetle was used only once. Beetles that did not make any choice within this time period allowed were excluded from the statistical analyses. Detailed bioassay settings and procedures were the same as described in Wei et al. (2008) for experiments testing the kairomone of type c *D. helophoroides*.

Host frass

We collected frass from fourth or fifth instar larvae in May or September when *M. raddei*, *M. alternatus*, and *A. glabripennis* were actively feeding in wood since *D. helophoroides* parasitizes older longhorned beetle larvae in the wood (Qin and Gao 1988). We collected fresh frass directly from larval tunnels by splitting the trunks or branches of at least ten host trees in the forest to obtain an adequate quantity (more than 30 g per host species). Frass of *A. glabripennis* was collected from its host tree *S. babylonica* in Xian City, in 2005; frass of *M. alternatus* was collected from its host tree *P. massoniana* in Guangzhou City in 2005; and frass of *M. raddei* was collected from its host tree *Q. mongolica* in Meihekou City in 2006. We did not collect from the large proportion of frass on the ground extruded by larvae because it may have been contaminated by other insects and external factors.

All frass was kept in separate clean glass bottles in a laboratory freezer at −20°C after being collected in the field. Test frass was kept in the freezer at night since each experiment lasted for over three days. In the Y-tube bioassay, 5 g of frass was used as an odor cue. Frass was used only once. For single choice experiments, frass was placed in a jar at one arm of the olfactometer, and an empty jar was placed at the other arm. Behavioral bioassays were conducted in May 2006 and 2007.

Parasitism of different hosts by different *D. helophoroides* populations collected from different places

Three healthy *Q. mongolicus* trees were felled and cut into bolts (length 28 cm; diameter 18–22 cm) in Meihekou City in June 2007. The two ends of each bolt were sealed with paraffin to prevent desiccation. Fifth instar or older larvae of *M. raddei* were also collected at the site by cutting more than 15 infested trees and splitting and dissecting them with an axe and a chisel in June 2007. The larvae were placed individually in glass tubes and held at 7–9°C to prevent development until they were used in the experiment. Experiments were conducted immediately after both logs and larvae were transported to the laboratory at the Chinese Academy of Forestry (CAF) in Beijing, China. Five separate holes were drilled (20 mm diameter and 55 mm in depth) in each log into which larvae were individually inserted. After introducing the larvae, each hole was covered tightly with its original bark. Each log was placed into a metal screen cage (40 cm × 40 cm × 60 cm); 18 logs and 18 cages were used for this experiment. Four *D. helophoroides* adults (type a) were introduced into each of six cages for the first treatment. Four adults of type b were introduced into each of six cages for the second treatment. Four adults of type c were introduced into each of six cages for the third treatment. In order to ensure that adult *D. helophoroides* (age: about 10–12 months) would lay eggs, they were kept at low temperature (14 ± 2°C) for over four months to prevent mating and egg-laying before being released into the cages. Previous studies have shown that once adults are provided suitable conditions, they readily mate and lay eggs. Detailed characteristics (Tan et al. 2007) were used to distinguish females and males to guarantee both sexes were released into cages. After one month, all logs were split to check how many longhorned beetle larvae were parasitized by *D. helophoroides*. During the one month experiment, all *D. helophoroides* were confined in cages and no food was supplied.

The experimental protocol and procedures were repeated to test parasitism of *A. glabripennis* and *M. alternatus* by different *D. helophoroides* populations in two additional experiments. For *A. glabripennis*, uninfested fresh logs of *Populus × gansuensis* C. Wang et H.L. Yang (*Populus nigra* L. var. *thevestina*

(Dode) Bean. × *P. simonii* Carr.) (length 28 cm; diameter 23 ± 2 cm) were collected in Linhe City in Inner Mongolia (Latitude 40°45′N, longitude 107°20′E and altitude 1,218 m) in June 2007, and older larvae of *A. glabripennis* were collected in the field near Xian City, Shaanxi Province in early May 2007. For *M. alternatus*, uninfested fresh logs of *P. massoniana* (length 28 cm; diameter 16–20 cm) and older larvae of *M. alternatus* were collected in the field near Guangzhou City, Guangdong Province in late September 2006. All materials were transported to CAF for experiments.

Different experiments and treatments were conducted in separate rooms in order to prevent any interactions or influence of odors from hosts and host plants, or from different populations of *D. helophoroides*. All experiments were conducted at 25 ± 2°C and 60 ± 10% RH, and there were three replications of each experiment.

Statistical analysis

A sign test was used to determine the significance of differences in *D. helophoroides* responses in the olfactometer experiments. To determine if parasitism by different *D. helophoroides* populations on the same host were similar, parasitism rates were compared among different *D. helophoroides* populations using the Tukey test (One-Way ANOVA) after arcsine transformation of the data. All statistical analyses were carried out using SPSS software.

Results

Orientation responses of different *D. helophoroides* population to frass odor of different longhorned beetle hosts

Results showed that different *D. helophoroides* populations had different behavioral response to the same host frass in the Y-tube olfactometer. For example, both adults of type a and type b *D. helophoroides* were significantly attracted to frass of *A. glabripennis* (type a, $Z = -2.342$, $P = 0.019$; type b, $Z = -3.876$, $P < 0.001$, sign test, two tailed) (Fig. 1A), however,

adults of type c *D. helophoroides* were significantly repelled by it (type c, $Z = -2.155$, $P = 0.031$). Frass of *M. alternatus* larvae significantly attracted adults of type b *D. helophoroides* (type b, $Z = -4.804$, $P < 0.001$), but significantly repelled adults of both type a and type c *D. helophoroides* (type a, $Z = -5.041$, $P < 0.001$; type c, $Z = -3.660$, $P < 0.001$, Fig. 1B). Adults of type c *D. helophoroides* were significantly attracted to frass of their original host *M. raddei* ($Z = -2.932$, $P = 0.003$), but type a and type b *D. helophoroides* were significantly repelled by it (type a: $Z = -2.302$, $P = 0.021$; type b $Z = -2.874$, $P = 0.004$, Fig. 1C).

Parasitism of different hosts by different *D. helophoroides* populations collected from different locations

Parasitism rates by the different *D. helophoroides* populations were compared for each host species (Fig. 2). For *A. glabripennis* larvae, the average parasitism rates by three *D. helophoroides* populations differed slightly, and type b appeared to have the highest parasitism, but differences among the three populations were not significant (Tukey multiple comparisons, $F = 2.259$, $df = 2, 6$; $P = 0.186$) (Fig. 2A). With *M. alternatus* as host, the average parasitism rate by type b *D. helophoroides* was significantly higher (68.09%) than for the other two types of *D. helophoroides* (26.09% and 24.21% for type a and type c *D. helophoroides*, respectively) ($F = 35.862$, $df = 2, 6$, $P < 0.001$; type b vs. type a, $F = 42.811$, $df = 1, 4$, $P = 0.003$; type b vs. type c, $F = 118.010$, $df = 1, 4$, $P < 0.001$) (Fig. 2B). With *M. raddei* as host, the average parasitism rate by type c *D. helophoroides* was 71.11%, whereas it was only 42.22% and 56.67% by type a and type b *D. helophoroides*, respectively. The average parasitism rates of *M. raddei* by the three types of *D. helophoroides* were not significantly different ($F = 4.833$, $df = 2, 6$, $P = 0.056$, Fig. 2C), but there was a larger difference between a and c. In all cases, once *D. helophoroides* had parasitized the host larvae, they could successfully complete development, no matter which population the host came from.
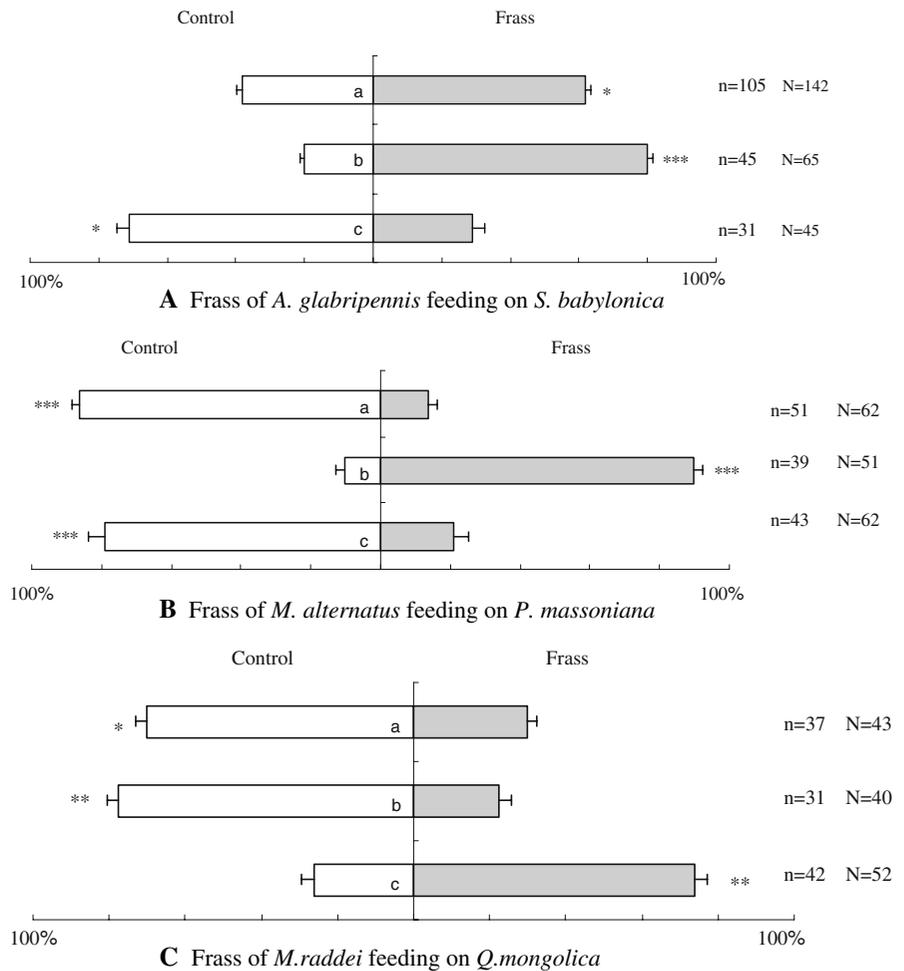
Fig. 1 Response of
D. helophoroides
(populations a, b, and c) to
frass of different host
species in Y-tube
olfactometer.
A *D. helophoroides* adults
collected in Shaanxi
Province parasitizing
A. glabripennis;
B *D. helophoroides* adults
collected in Guangdong
Province parasitizing
M. alternatus;
C *D. helophoroides* adults
collected in Jilin Province
parasitizing *M. raddei*; N
represents the number of
tested adults; n represents
the number of adults, that
made a choice; bars in the
graphs indicate the
percentages ±SE of n,
which choose frass or
control; * significantly
different at $P < 0.05$;
** significantly different at
$P < 0.01$; *** significantly
different at $P < 0.001$, sign
test

A Frass of *A. glabripennis* feeding on *S. babylonica*

B Frass of *M. alternatus* feeding on *P. massoniana*

C Frass of *M.raddei* feeding on *Q.mongolica*

Discussion

Comparison of olfactory response and parasitism of the three populations of *D. helophoroides*

Our studies showed that different populations of
D. helophoroides had different olfactory responses to
different host frass, and were significantly attracted to
the odor of frass from their original hosts (Fig. 1).
However, type b *D. helophoroides* also showed a
significant attraction to *A. glabripennis* frass. These
results indicate that the kairomonal activity of two
populations (type a and type c) is specific to their host
frass. The reason for this specific response might be
that under some conditions, populations of insect
parasitoids may adapt to specific plants, the allelo-
chemicals produced by host plants (Kester and
Barbosa 1991), or the host. Possible explanations
for the observation that type b *D. helophoroides*

populations showed stronger attraction to frass of
A. glabripennis compared to type a *D. helophoroides*
populations requires further investigation.

The results of parasitism experiments demonstrate
that all three *D. helophoroides* populations were able
to parasitize the different longhorned beetle species
tested when confined in cages. However, their para-
sitism rates differed (Fig. 2). In most cases, the
parasitism rate of each *D. helophoroides* population
was highest on its original host (Fig. 2B, C). However,
the response by type b *D. helophoroides* was an
exception. The parasitism rate by type b *D. helo-
phoroides* (64.49%) on *A. glabripennis* did not differ
from the parasitism rate by type a *D. helophoroides*
(61%) (Fig. 2A). The high parasitism rate of *A.
glabripennis* by the type b population was consistent
with its attraction to frass of *A. glabripennis* (Fig. 1A).
Although type b *D. helophoroides* was repelled by
frass of *M. raddei*, its parasitism rate reached 56.67%

Fig. 2 Parasitism rate (%) of different longhorned beetles by different *Dastarcus helophoroides* populations. **A** *D. helophoroides* collected in Shaanxi Province parasitizing *A. glabripennis*; **B** *D. helophoroides* collected in Guangdong Province parasitizing *M. alternatus*; **C** *D. helophoroides* collected in Jilin Province parasitizing *M. raddei*; Parasitism rates (%) are average ±SE; for each host species, bars marked with different letters are significantly different at $P < 0.05$ (x and y) or $P < 0.001$ (m and n) (Tukey, one-way ANOVA)

A *A. glabripennis* as hosts

B *M. alternatus* as hosts

C *M. raddei* as hosts
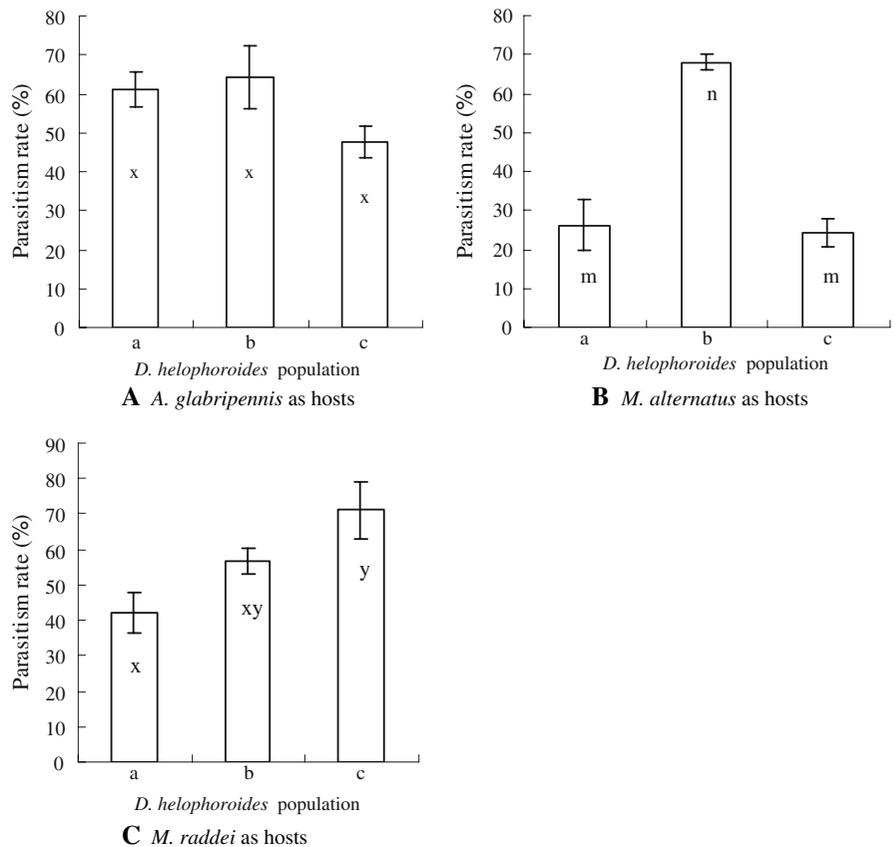
and was not significantly different from the parasitism rate of *M. raddei* by type c *D. helophoroides*. Therefore, results of the parasitism experiment could be a reference to differentiate populations of *D. helophoroides* but not an actual effective measure. On the other hand, the parasitism rates of the type a and c populations, that were from hardwood stands, were much lower than the parasitism rate of type b *D. helophoroides* on *M. alternatus* (Fig. 2B). This suggests that both type a and c *D. helophoroides* are adapted to hosts from hardwoods and may not be well suited to hosts in coniferous stands, whereas, type b *D. helophoroides* which originated from a coniferous host appeared to be less specific and may also be suited to hosts from hardwood stands.

Different biotypes of *D. helophoroides*?

Walsh (1864) was probably the first to seriously consider the status of insects that morphologically resemble one another so closely that they can only be distinguished on the basis of subtle biological traits

such as preference for or the ability to survive on different hosts. The term "biotype" was employed by applied biologists to distinguish populations of insects and other organisms whose differences were due to a very wide range of underlying causes. Diehl and Bush (1984) summarized and discussed the applicability of the terminology for "biotype". They classified biotype into the following five categories: (a) nongenetic polyphenisms, (b) polymorphic or polygenic variation within populations, (c) geographic races, (d) host races, and (e) species. Differences in olfactory responses and parasitism of hosts were observed among *D. helophoroides* populations in this study, so there might be different "biotypes" among populations of *D. helophoroides*. However, because the genetic basis and evolutionary status of the differences between different populations have yet to be ascertained, and "biotype" is such a vague term, it cannot be used to designate the different populations of *D. helophoroides* that parasitized different Cerambycidae host species in this study.

Generalist or specialist parasitoid?

Most specialist parasitoids are known to differentiate between volatiles emitted from host-infested plants and odors from plants damaged by non-hosts (De Moraes et al. 1998; Powell et al. 1998), but generalist parasitoids do not show restricted preferences for their hosts and the respective plants they feed upon for habitat location (Vet and Dicke 1992). Because *D. helophoroides* parasitizes many genera of Cerambycidae (Qin and Gao 1988), they should be called "generalist" or "polyphagous parasitoids". However, traditional definitions of specialists and generalists are not easily applied to coleopteran predators of bark beetles (Erbilgin and Raffa 2001). Considering that *D. helophoroides* is also a coleopteran insect and can parasitize many species of longhorned beetles, but its different populations prefer certain hosts, it is best considered a "habitat specialist" (Jermy 1988; Gaston 1990) or "host specialist".

In the cage experiments, populations of *D. helophoroides* were able to parasitize host species other than the original host. Differences in parasitism rates might be attributed to both adults and first instar larvae of *D. helophoroides*. Factors affecting host acceptance and host suitability of first instar larvae are unknown.

Biological control perspectives

Different *D. helophoroides* populations displayed different behavior when supplied with the same host species. Even though three generations of each population were reared on the same alternate host, the different populations still maintained their host selectivity. Whether these differences could be reduced through learning requires further investigation. Results of the parasitism experiment showed that *D. helophoroides* populations could accept new host larvae under certain conditions (i.e., no-choice caged experiments, Fig. 2). Therefore, it is possible that new relationships could be established between different *D. helophoroides* population types and non-original hosts. However, in our laboratory experiments *D. helophoroides* were given no-choice but to parasitize the non-original host species in cages. New parasitism relationships might be more difficult to establish in the field because different *D. helophoroides* populations might be repelled by frass of non-original hosts and fail to find host habitat, i.e. 'host location' would affect subsequent 'host acceptance' and 'host suitability'. Therefore, one population of *D. helophoroides* would not survive in the field if they have difficulty locating the new target species. Adults of population b appeared to be somewhat less host-specialized than the type a or type c populations, and they might be able to exploit a new target species since they were also attracted to *A. glabripennis* frass.

For traditional biological control, differences between populations of natural enemies sometimes arouse interest (Madeira et al. 2001; Schrey et al. 2005; de León et al. 2008). In our studies, the three populations of *D. helophoroides* showed differences in attraction to host-frass, which would help to select the type of *D. helophoroides* population to use for biocontrol of a certain longhorned beetle species. It is possible that biological control would be ineffective if one population of *D. helophoroides* were released against a longhorned beetle species other than its original host.

Our studies show that different populations of *D. helophoroides* parasitize different species of Cerambycidae hosts. However, parasitism of *A. glabripennis* caused by *D. helophoroides* also varied by location in field. Many factors affect *D. helophoroides* parasitism efficacy, including climatic effects on the host, host population density, duration of host infestation, and host tree suitability (Qin and Gao 1988). Therefore, whether there are different populations for type a *D. helophoroides* requires further investigation. Results will lead to a more effective biological control program against *A. glabripennis*.

In China, there are several other species of longhorned beetles in addition to *A. glabripennis*, *M. alternatus* and *M. raddei*, which have been found to be parasitized by *D. helophoroides* (Qin and Gao 1988). Therefore, additional research is needed on *D. helophoroides* populations parasitizing other longhorned beetles in order to better understand geographic or host-related differences and to optimize their use for biological control programs.

beetle species" (no. 30371162) funded by National Natural Science Foundation of China (NSFC).

References

De León JH, Logarzo GA, Triapitsyn SV (2008) Molecular characterization of *Gonatocerus tuberculifemur* (Hymenoptera: Mymaridae), a prospective *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae) biological control candidate agent from South America: divergent clades. Bull Entomol Res 98(1):97–108

De Moraes CM, Lewis WJ, Paré PW, Alborn HT, Tumlinson JH (1998) Herbivore-infested plants selectively attract parasitoids. Nature 393:570–573

Diehl SB, Bush GL (1984) An evolutionary and applied perspective of insect biotypes. Annu Rev Entomol 29:471–504

Erbilgin N, Raffa KF (2001) Kairomonal range of generalist predators in specialized habitats: responses to multiple phloeophagous species emitting pheromones vs. host odors. Entomol Exp Appl 99:205–210

Gao RT, Li GH (2001) Review and prospect of research on *Anoplophora glabripennis* in China. Entomol Knowl 38(4):252–258 (In Chinese with English summary)

Gao JC, Shang GM, Zhao HB, Wu XG, Gao LJ, Hou B, Cao YC (2003) *Dastarcus helophoroides* (Fairmaire), a natural enemy of *Massicus raddei* in Jilin Province. Jilin For Sci Tech 32(1):45 (In Chinese)

Gaston KJ (1990) Patterns in the geographical ranges of species. Biol Rev 65:105–129

Haack RA, Law KR, Mastro VC, Ossenbruggen HS, Raimo BJ (1997) New York's battle with the Asian long-horned beetle. J For 95(12):11–15

Hilker M, Meiners T (2006) Early herbivore alert: insect eggs induce plant defense. J Chem Ecol 32(7):1379–1397

Jermy T (1988) Can predation lead to narrow food specialization in phytophagous insects? Ecology 68:902–904

Kester KM, Barbosa P (1991) Behavioral and ecological constraints imposed by plants on insect parasitoids: implications for biological control. Biol Control 1(2):94–106

Lei Q, Li ML, Yang ZQ (2003) A study on biological feature of *Dastarcus longulus*. J Northwest Sci Tech Univ Agric For 31(2):62–66 (In Chinese with English summary)

Li ML, Wang PX, Ma F, Yang ZQ (2007) Study on the parasitic efficiency of *Dastarcus helophoroides* on *Anoplophora glabripennis*. J Northwest A & F Univ 35(6): 152–156, 162 (In Chinese with English summary)

Macleod A, Evans HF, Baker RHA (2002) An analysis of pest risk from an Asian longhorn beetle (*Anoplophora glabripennis*) to hardwood trees in the European community. Crop Prot 21:635–645

Madeira PT, Hale RE, Center TR, Buckingham GR, Wineriter SA, Purcell M (2001) Whether to release *Oxyops vitiosa* from a second Australian site onto Florida's melaleuca? A molecular approach. BioControl 46:511–528

Mamiya Y, Enda M (1972) Transmission of *Bursaphelenchus lignicolus* (Nematoda: Aphelenchoidae) by *Monochamus alternatus* (Coleoptera: Cerambycidae). Nematologica 18:159–162

Miura K, Abe T, Nakashima Y, Urano T (2003) Field release of parasitoid *Dastarcus helophoroides* (fairmaire) (Coleoptera: Bothrideridae) on pine logs infested with *Monochamus alternatus* Hope (Coleoptera: Cerambycidae) and their dispersal. J Jpn For Soc 85(1):12–17 (in Japanese)

Nowak DJ, Pasek JE, Sequeira RA, Crane DE, Mastro VC (2001) Potential effect of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) on urban trees in the United States. J Econ Entomol 94(1):116–122

Ogura N, Tabata K, Wang WD (1999) Rearing of the colydiid beetle predator, *Dastarcus helophoroides*, on artificial diet. BioControl 44:291–299

Pal TK, Lawrance JE (1986) A new genus and subfamily of *Mycophagous bothrideridae* (Coleoptera: Cucujoidae) from the Indo-Australian region, with notes on related families. J Aust Entomol Soc 25:185–210

Pettersson EM (2001) Volatile attractants for three Pteromalid parasitoids attacking concealed spruce bark beetles. Chemoecology 11:89–95

Piel SJ (1938) Note sur le parasitisme de *Dastarcus helophoroides* Fairmaire (Coleoptera: Colydiidae). Notes Entomol Mus Heude Chin 5(1):1–5

Powell W, Pennachio F, Poppy GM, Tremblay E (1998) Strategies involved in the location of hosts by the parasitoid *Aphidius ervi* Haliday (Hymenoptera: Braconidae: Aphidiinae). Biol Control 11:104–112

Qin XX, Gao RT (1988) Studies on bionomics and application of *Dastarcus longulus* Sharp. Entomol Knowl 25(2):109–112 (in Chinese)

Schrey NM, Reeve JD, Anderson FE (2005) Mitochondrial DNA analysis of the bark beetle predator *Thanasimus dubius* F. (Coleoptera: Cleridae) reveals regional genetic differentiation. Mol Ecol 14:3317–3324

Sullivan BT, Pettersson EM, Seltmann KC, Berisford CW (2000) Attraction of the bark beetle parasitoid *Roptrocus xylophagorum* (Hymenoptera: Pteromalidae) to host-associated olfactory cues. Environ Entomol 29(6):1136–1151

Takabayashi J, Dicke M (1992) Response of predatory mites with different rearing histories to volatiles of uninfested plants. Entomol Exp Appl 64:187–193

Tan H, Yang ZQ, Zhang YN, Li GW (2007) Technical research on distinguishing female and male alive adults of the main parasite of longhorn beetles, *Dastarcus helophoroides* (Coleoptera, Bothrideridae), without injuring. Acta Zootaxon Sin 32(3):649–654 (In Chinese with English summary)

Tinzaara W, Gold GS, Dicke M, van HA (2005) Olfactory responses of banana weevil predators to volatiles from banana pseudostem tissue and synthetic pheromone. J Chem Ecol 31(7):1537–1553

Turlings TCJ, Wäckers FL, Vet LEM, Lewis WJ, Tumlinson J (1993) Learning of host-finding cues by hymenopterous parasitoids. In: Papaj DR (ed) Insect Learning: Ecological and Evolutionary Perspectives. Kluwer Academic Publishers, Norwell, pp 51–78

Turlings TCJ, Bernasconi M, Bertossa R, Bigler F, Caloz G, Dorn S (1998) The induction of volatile emissions by three herbivore species with different feeding habits: possible consequences for their natural enemies. Biol Control 11:122–129

Urano T (2003) Preliminary release experiments in laboratory and outdoor cages of *Dastarcus helophoroides* (Fairmaire) (Coleoptera: Bothrideridae) for biological control of *Monochamus alternatus* Hope (Coleoptera: Cerambycidae). Bull For For Prod Res Inst 2(4):255–261

Vet LEM, Dicke M (1992) Ecology of infochemical use by natural enemies in a tritrophic context. Annu Rev Entomol 37:141–172

Vet LEM, Lewis WJ, Cardé RT (1995) Parasitoid foraging and learning. In: Cardé RT, Bell WJ (eds) Chemical Ecology of Insects 2. Chapman and Hall, New York, pp 65–104

Vinson SB (1976) Host selection by insect parasitoids. Annu Rev Entomol 21:109–133

Vinson SB (1998) The general host selection behavior of parasitoid Hymenoptera and a comparison of initial strategies utilized by larvaphagous and oophagous species. Biol Control 11:79–96

Walsh B (1864) On phytophagic varieties and phytophagic species. Proc Entomol Soc Phila 3:403–430

Wang XM, Ren GD, Ma F (1996) Classification position of *Dastarcus helophoroides* and its applied prospects. Acta Agri Boreali-occidentalis Sin 5(2):75–78 (In Chinese with English summary)

Wang WD, Zhao J, Ogura N (1999) Artificial fodder ingredient for *Dastarcus helophoroides* larvae. J Beijing For Univ 21(4):48–51 (In Chinese with English summary)

Wei JR, Yang ZQ, Ma JH, Tang H (2007) Progress on the research of *Dastarcus helophoroides*. For Pest Dis 26(3):23–25 (In Chinese with English summary)

Wei JR, Yang ZQ, Hao HL, Du JW (2008) (*R*)-(+)-Limonene, kairomone for *Dastarcus helophoroides* (Fairmaire), a natural enemy of longhorned beetles. Agric For Entomol 10:323–330

Wei JR, Yang ZQ, Niu YL, Zhao HB, Tang H (2009) Distribution and ecological biology of *Dastarcus helophoroides*. For Pest Dis 28(1):16–18 (In Chinese with English summary)

Zhang YN, Yang ZQ (2006) Studies on the natural enemies and biocontrol of *Monochamus alternatus* Hope (Coleoptera: Cerambycidae). Plant Prot 32(2):9–14 (In Chinese with English summary)

Zhou JX, Lu XZ, Lu YZ (1985) Reports on introducing *Dastarcus longulus* Sharp to control *Anoplophora nobilis* Ganglbauer. Entomol Knowl 2(22):84–86 (In Chinese)

Author Biographies

Jian-Rong Wei This research is part of a PhD project of the author and devoted to the analysis of the host specificity of *Dastarcus helophoroides* against several serious longhorned beetle species in China.

Zhong-Qi Yang is studying biological control of forest pests.

Therese M. Poland is involved in developing effective programmes to monitor and control invasive wood borers in USA.

Jia-Wei Du is an expert of chemical ecology.