# 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

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**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

This work was carried out in the Key Laboratory of Forest Protection, State Forestry Administration of China. Result of this paper has already instructed the biologic control of several longhorned beetle species by using different populations of *D. helophoroides* in China, and exciting results has been got in field.

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J.-R. Wei ((\subseteq)) · 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 **Keywords** Population differences · *Anoplophora* glabripennis · *Monochamus alternatus* · *Massicus* raddei · Wood borer · Tritrophic interactions

different species of longhorned beetle.

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

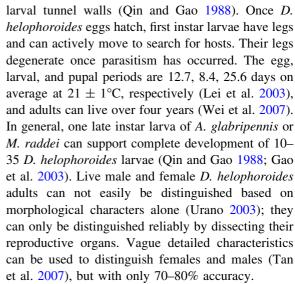
# Introduction

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



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<sup>-1</sup>. 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  $-20^{\circ}$ 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  $\times$  40 cm  $\times$  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  $(14 \pm 2^{\circ}C)$  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.  $\times$  *P. simonii* Carr.) (length 28 cm; diameter  $23 \pm 2$  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  $25 \pm 2^{\circ}\text{C}$  and  $60 \pm 10\%$  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,

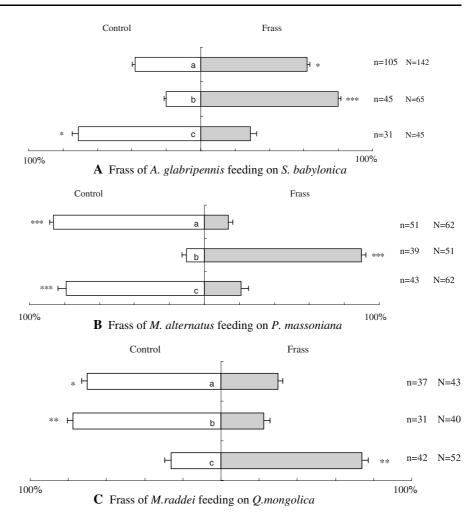
adults of type c *D. helophoroides* were significantly repelled by it (type c, Z=-2.155, P=0.031). Frass of *M. alternatus* larvae significantly attracted adults of type b *D. helophoroides* (type b, Z=-4.804, P<0.001), but significantly repelled adults of both type a and type c *D. helophoroides* (type 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), butthere 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



# Discussion

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

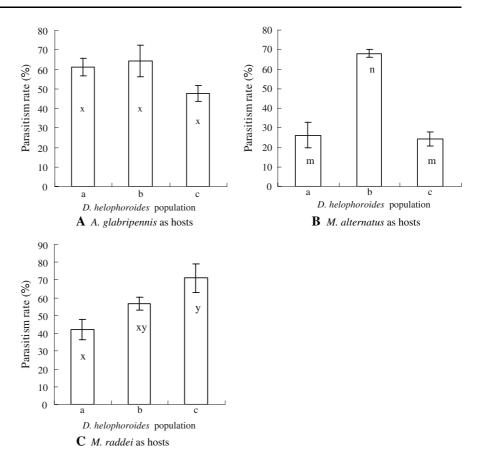
Our studies showed that different populations of *D. helophoroides* had different olfactory responses to different host frass, and were significantly attracted to the odor of frass from their original hosts (Fig. 1). However, type b *D. helophoroides* also showed a significant attraction to *A. glabripennis* 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 allelochemicals 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 parasitism 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. helophoroides (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  $\pm$ 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)



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. helo-phoroides* 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 nonoriginal 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 nonoriginal 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 long-horned beetles in order to better understand geographic or host-related differences and to optimize their use for biological control programs.

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# **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.

