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The Role of Auditory Cues in Prey Location by the Spider *Pardosa Pseudoannulata*

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Abstract

The role of auditory cues in prey location by the spider *Pardosa pseudoannulata* was investigated. The effects of the distance from the sound source (4 cm, 6 cm, 8 cm, 10 cm, 12 cm, 14 cm, 16 cm) and sound pause interval (0 s, 1 s, 3 s, 5 s, 7 s, 9 s, 11 s) on prey location were measured. Morphology, quantity, and distribution of cuticular sensillae of *P. pseudoannulata* were analyzed by scanning electron microscopy. Spider speed (y) and sound source distance (x) were negatively correlated. Spider movements at 4 cm (5.12 ± 0.40 cm/min) and 6 cm (5.45 ± 0.31 cm/min) sound source distance were significantly faster ($P < 0.05$) than at other distances. Spider movement was slowest at 14 cm (2.95 ± 0.11 cm/min) and 16 cm (2.63 ± 0.11 cm/min) distances. At 6 cm distance, spider speed decreased with an increase in sound pause interval. When the sound pause intervals were 1 s and 3 s, spider speed peaked at 5.02 ± 0.31 cm/min and 5.15 ± 0.40 cm/min, respectively. As the sound pause interval increased, the spider speed decreased significantly ($P < 0.05$) and was 2.36 ± 0.15 cm/min when the sound pause interval was 11 s. Scanning electron microscopy (SEM) showed that *P. pseudoannulata* has many, widely distributed trichobothria on the pedipalps, first pair of legs, and the tibia of the fourth pair of legs. A few isolated slit sensillae were mainly distributed in the tarsus and tibia of the pedipalps. Lyriform organs were widely distributed and found on chelicerae, pedipalps and legs, and tibia segments. These results indicate that *P. pseudoannulata* is highly sensitive to sound and vibrations.

Keywords: *Pardosa pseudoannulata*, sound source distance, sound pause interval, predation speed, cuticular sensilla

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INTRODUCTION

Spiders are major predators and pest control agents in agroecosystems (Suenaga and Hamamura 2014). Spiders are voracious and consume a broad spectrum of pests. They have a long residence time in the field, have high reproductive rates, and are resistant to starvation. Spiders make significant contributions to the biological control of agricultural pests (Marc and Canard 1997, Xiao et al. 2006). Spider research has mainly focused on taxonomy (Zhang et al. 2009), phylogeny (Wang et al. 2008), predation (Xiao et al. 2007), hatching (Iida 2016), and foraging strategy (Jackson 1992, 1996). Fewer studies have examined prey search and localization mechanisms of spiders.

Spiders perceive external signals primarily through sensory organs. Some spiders have sophisticated courtship and mating behaviors using multiple communication methods such as visual, auditory, vibratory, olfactory and tactile (Huber 2005, Taylor et al. 2005). Spiders can also rely on visual, chemical and auditory signals to search for, and capture, prey. Studies on spider predation mechanisms have focused on visual and chemical cues. In some wandering spiders, the posterior eyes have a reflective pigment layer or a flexible iris. Each posterior eye has 10,000 photoreceptors, with 150° or wider field of view (Land 2009). In the anterior-median eyes of spiders, the ventral cells have rhabdoms with evenly distributed microvilli that can perceive polarized light. Wolf and funnel spiders can locate prey by polarized light (Dacke et al. 2003, Defrize et al. 2011).

Spider chemical communication can be intraspecific or interspecific (Jiao 2011, Roberts and Uetz 2005). Intraspecific chemical communication, like sex pheromones, can help the spider search and locate a mating partner, regulate courtship behavior, and evaluate mating partner quality (Chinta et al. 2010, Gaskett 2007, Jerhot et al. 2010, Roberts and Uetz 2004). Chemical signals play an important role in spider sexual communication (Xiao 2010, 2015). Spiders can also search and locate prey using chemical signals. For example, prey odor strongly attracts *Habrocestum pulex* (Clark et al. 2000).

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The role of auditory cues in spider prey location is unclear. We measured predation time and speed of *P. pseudoannulata* at different distances and sound pause intervals, and studied the morphology and distribution of selected cuticular sensilla (trichobothria and slit sensilla) by scanning electron microscopy. Our results indicate that auditory cues can play a role in prey location by *P. pseudoannulata*.

MATERIALS AND METHODS

P. pseudoannulata Pretreatment

Individual adult *P. pseudoannulata* were reared in 250 ml Erlenmeyer flasks containing wet cotton to maintain humidity. Rearing conditions were 23 ± 1°C with a 12:12 Light: Dark photoperiod. Spiders were fed with adult *Drosophila* to accustom them to fly wing vibrations. Food was withdrawn after 10 d to make spiders hungry. Spider behaviors were measured 7 d later.

Behavioral Experiments

Experimental device

An individual spider was placed in the end of the handle in a Y-shaped olfactometer tube (D=2.0 cm). Earphones were placed at equal correspondence position in each arm. Fly wing vibrations were played through the earphones in the experimental group, and no sound was played in the control group.

The effects of prey distance on spider predation behavior

The earplugs were placed 4, 6, 8, 10, 12, 14 cm away from the spider and spider behavior and the time to reach earplugs were recorded.

Measuring the effects of sound interval on spider predatory behavior

As in the 1.2.2 experiment, the earplugs were placed at the distance with fastest spider response. The prey wing vibrations were played continuously for 5 s. The effects of sound pause interval (0, 1, 3, 5, 7, 9, 11 s) on the prey localization and predatory behavior by spiders were measured, and the time for the spider to reach the earplug was recorded.

Data analysis

Data was represented as the mean ± standard deviation. Experimental data were analyzed by ANOVA using SPSS17.0 software (IBM) to test the relationship between independent variables and the dependent variables. The significance level was set at $\alpha = 0.05$.

Table 1. Time and speed for *P. pseudoannulata* to reach the sound source at different distances

	4 cm	**6 cm**	**8 cm**	**10 cm**	**12 cm**	**14 cm**	**16 cm**
Time (s)	47.1 ± 3.6	66.2 ± 3.8	112.0 ± 5.9	153.1 ± 7.3	226.2 ± 6.7	285.1 ± 10.4	365.1 ± 15.9
Speed (cm/min)	5.12 ± 0.40 [a]	5.45 ± 0.31 [a]	4.29 ± 0.22 [b]	3.92 ± 0.19 [b]	3.18 ± 0.09 [c]	2.95 ± 0.11 [cd]	2.63 ± 0.11 [d]

Data are mean ± standard deviation. Different letters to the right indicate significant difference (P < 0.05) between treatment groups

Scanning Electron Microscopy

Specimen preparation: Spiders were euthanized with ether, and washed extensively with a 0.65% NaCl solution. A total of 3 male and 3 female spiders were fixed in pre-chilled 2.5% glutaraldehyde at 4°C overnight. The spiders were washed with 0.1 mol/L pH 7.4 phosphate buffer for 15 min four times. Then spiders were dehydrated in an ethanol gradient series (30%, 50%, 70%, 80%, 90%, 100%), for 15 min twice in each concentration. The samples were dried by the critical point method, and sputter coated with gold in a vacuum. The samples were observed under a JSM-6360LV (JEOL) scanning electron microscope.

RESULTS

Behavior Results

The effects of distance from the sound source on spider predation

With different distances from the sound source, the time and speed for a spider to reach the earplugs are shown in **Table 1**. The time for spiders to reach the earplugs increased with increased distance, but the spider speed decreased. When the distances were 4 cm and 6 cm, the Spider speeds were fastest at 4 cm (5.12 ± 0.40 cm/mi and 6 cm (5.45 ± 0.31 cm/min), and these were significantly faster than other groups ($P < 0.05$). When the distances were 14 cm and 16 cm, Spider movement was the slowest at 14 cm (2.95 ± 0.11 cm/min) and 16 cm (2.63 ± 0.11 cm/min). Regression analysis showed that spider speed (y) and distance from the sound source (x) were negatively correlated, $y = -0.242x + 6.3561$, $R^2 = 0.932$.

The effects of sound pause interval on spider speed

In this experiment, the distance from the sound source was set at 6 cm where the spider speed was fastest, and the sound pause interval was varied to analyze its potential effect on prey localization and capture. With an increase of sound pause interval, the time for the spider to reach the earplugs increased, and the spider speed decreased (**Table 2**). When the sound intervals were 1 s and 3 s, Spider speed was fastest at sound intervals of 1 s (5.02 ± 0.31 cm/min) and 3 sec (5.15 ± 0.40 cm/min). The speed was slower (5.45 ± 0.31 cm/min, see section 2.1.1) when prey wing

Table 2. Time and speed for *P. pseudoannulata* to reach a sound source under different sound pause intervals. Different letters to the right indicate significant difference (P < 0.05) between different groups

	0 s	**1 s**	**3 s**	**5 s**	**7 s**	**9 s**	**11 s**
Time (s)	66.2 ± 3.8	71.9 ± 4.6	70.1 ± 5.3	78.9 ± 5.4	93.2 ± 6.0	108.4 ± 6.1	152.7 ± 9.6
Speed (cm/min)	5.45 ± 0.31^{a}	5.02 ± 0.31^{ab}	5.15 ± 0.40^{a}	4.58 ± 0.30^{b}	3.88 ± 0.26^{c}	3.33 ± 0.18^{d}	2.36 ± 0.15^{e}

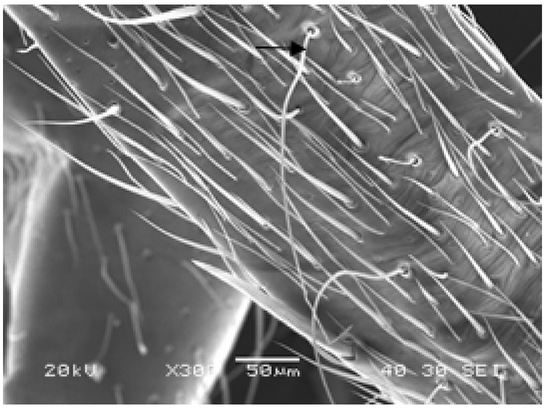

Fig. 1. Tibia on the right pedipalp of *P. pseudoannulata* (arrow indicates trichobothria)

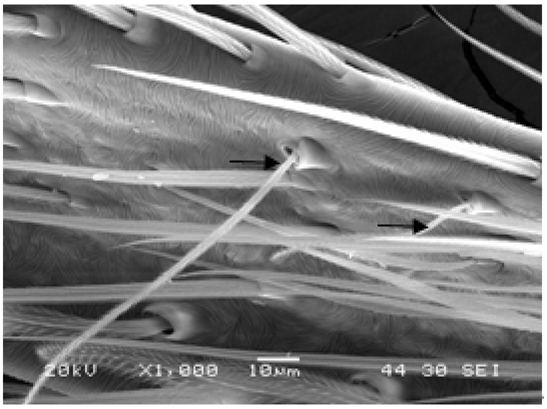

Fig. 2. Tibia on the left fourth leg of *P. pseudoannulata* (arrow indicates trichobothria)

vibrations was continuously played, but the difference was not significant (P > 0.05). With an increase in the sound pause interval, spider speed decreased significantly (P < 0.05). When the sound pause interval was 11 s, the spider speed was only 2.36 ± 0.15 cm/min. Regression analysis showed that spider speed (y) and sound pause interval (x) were negatively correlated, $y = -0.2639x + 5.6091$, $R^2 = 0.9376$.

SEM Results

Morphology and distribution of trichobothria

The trichobothria of *P. pseudoannulata* were distinct from other hairs (**Figs. 1** and **2**). They were slender and elongated with the shaft similar in diameter from the base to the tip. A bulge with a smooth surface was on

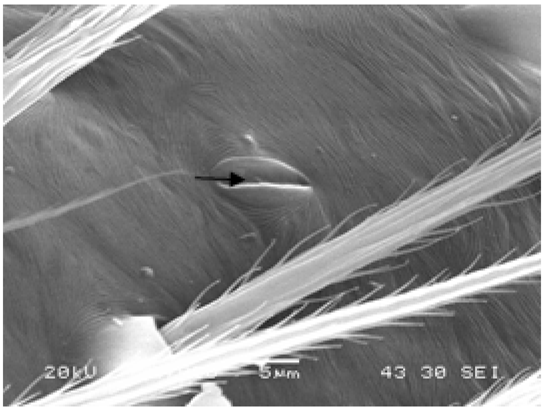

Fig. 3. Tarsus on the left pedipalp of *P. pseudoannulata* (arrow indicates slit sensillum)

the side of the base. The trichobothrium emerged from a deep cavity in the middle of the bulge, and there were gaps between the bulge and the trichobothrium. The trichobothria were mainly distributed on pedipalps and the tibia of the fourth pair of legs. Some were on the first pair of legs, and a few on the other legs. The morphology and length of trichobothria were similar at all locations.

Morphology and distribution of slit sensilla

There are two types of slit sensilla were observed in *P. pseudoannulata* using the SEM. These were isolated single slit sensillum and lyriform organs. The isolated single slit sensillum was approximately oval in shape and slightly larger than the pores (**Fig. 3**). The edge of the single slit sensillum was swollen and thick, with an obvious slit in the middle. Isolated single slit sensilla were mainly distributed on the tarsus and tibia of the pedipalps. There were very few single sensilla, with only one or two found on the entire pedipalp.

The lyriform organ was formed by multiple slit sensilla (**Fig. 4**). Each lyriform organ had multiple parallel folds, which were different in depth and length. Lyriform organs were widely distributed on chelicerae, pedipalps, legs, and many on tibia.

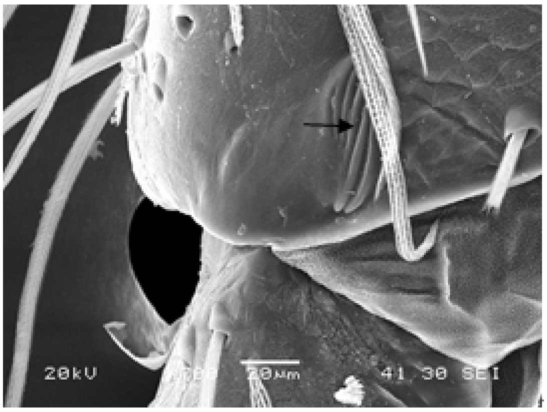

Fig. 4. Tibia on the left pedipalp of *P. pseudoannulata* (arrow indicates lyriform organ)

DISCUSSION

When the distances from the sound source were 4 cm and 6 cm, spider speed was significantly faster than other distances ($P < 0.05$). With an increase in distance between the earplugs and the spider, the time for the spider to reach the earplugs gradually increased and the spider speed decreased. Regression analysis showed that spider speed and distance from the sound source were negatively correlated. This indicated that with increasing distance, the sound level at the spider location decreased and the sound or air vibration signals weakened. Similarly, the sound pause interval also had a significant effect on the spider movement speed. At one distance (6 cm), an increase in the sound pause interval was associated with a gradual decrease in spider speed. When the sound pause intervals were 1 s and 3 s, spider speed was the fastest and not significantly different from continuously exposure to prey wing vibrations ($P > 0.05$). This suggests that during the pauses, spiders do not receive sound or air vibration signals, so more time is required to locate prey.

Both experiments demonstrated that spiders can perceive external auditory cues and also indicate that acoustic signals can play an important role in spider predation (Anton and Barth 1993). Trichobothria (Barth 2004) and slit sensilla (Patil 2006) are common sensory organs in spiders. Nearby air vibrations or distant sound waves can stimulate trichobothria responses (Witt and Rovner 1982). Barth (2000) found that trichobothria can be stimulated by air vibrations and sound waves, so the moving air or sound waves of nearby prey would help the spider to locate and capture that prey. SEM showed that *P. pseudoannulata* has many trichobothria which are widely distributed on the pedipalps, the first pair of legs, and the tibia of the fourth pair of legs. The above features can help spiders locate the position of sound sources.

Slit sensory organs capable of detecting mechanical vibrations include isolated the single slit sensillum and the lyriform organ formed by multiple slit sensilla. Hößl et al. (2009) suggest that the slit sensilla group and lyriform organ are 3.5 x more sensitive than an isolated single slit sensillum. In *P. pseudoannulata*, there are relatively few isolated single slit sensilla and these are mainly distributed on the tarsus and tibia of the pedipalps. Lyriform organs are widely distributed on chelicerae, pedipalps, and legs with many on the tibia. These findings suggest that *P. pseudoannulata* is highly sensitive to vibration signals.

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