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Can praying mantises escape from spider webs?

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Orb-weaving spiders may encounter predacious insects in their own webs, leading to the question of how they may prey on them. To address this question, the French entomologist Jean-Henri Fabre (1905) observed how the orb-weaving spider *Argiope bruennichi* (Araneae: Araneidae) responded to a praying mantis, *Mantis religiosa* (Mantodea: Mantidae), that was placed experimentally on the spider's orb web. Interestingly, the spider immobilized the mantis by wrapping the mantis' body with silk threads spun from the spider's abdominal spinnerets, and successfully preyed upon it. However, Fabre (1905) asserted that he had never observed orb-weaving spiders attacking praying mantises under field conditions. Because mantises frequently fly (e.g., Yager and Svenson 2008), they run the risk of becoming trapped in spider webs (Nentwig 1982). What factors have reduced the chances of observing predation by orb-weaving spiders on mantises under field conditions? Although mantises may potentially be trapped by spider webs, this question has remained unexplored.

On September 28, 2018, we observed and photographed a praying mantis, *Hierodula patellifera* (Mantidae), trapped in an orb web constructed by a female *A. bruennichi* in a grassland at Miki-shi, Hyogo, central Japan (Fig. 1A). The mantis was alive and attempting to escape from the web, although its body had been partially wrapped by the spider's sticky silk (Fig. 1A). We observed that the mantis was able to escape from the spider web in the end. On the basis of the photograph and observation, we hypothesized that praying mantises may remove spider silk from their bodies to escape spider webs. To test this hypothesis, like Fabre (1905), we experimentally placed praying mantises on webs that had been constructed by female *A. bruennichi* under field conditions.

For the field experiments, we placed adult mantises of four species into randomly selected webs in southeast Hyogo, central Japan (Table 1; Fig. 1B). We used a total of 26 orb webs that had been constructed by *A. bruennichi* females (body length [mean ± SE] 23.3 mm ± 0.5 mm; $n = 26$). We experimentally placed a single mantis on each web. To investigate whether the mantises were eaten by the spiders or escaped from the webs, we observed the behaviors of both the mantises and the spiders for 15 min and checked the presence/absence of the mantises at 30 min, 1 h, and 24 h after their placement on the webs. We scored any mantises that died on the webs as successful predation by spiders. We considered the absence of a mantis on a spider web as a successful escape by the mantis. These experiments were conducted during the daytime (i.e., 12:00–17:00) on sunny days in October 2018. Individual mantises and spiders were used only once.

Of the 26 spiders, seven attacked the mantises by enveloping them in silk (Table 1). These spiders used a pair of their hind legs to cast the silk threads spun from their abdominal spinnerets over the mantises (Appendix S1, Videos S1, S2). Although the mantises attempted to launch a counterattack on the spiders using their forelegs, the spiders evaded these attacks with swift movements (Appendix S1, Videos S1, S2), and no spider was injured by the mantises. Four spiders successfully wrapped the mantises' raptorial forelegs to immobilize them (Table 1; Appendix S1, Video S1). Having encased the mantises' entire bodies, the spiders bit the mantises' abdomens; two *Statilia maculata* and two *H. patellifera* were ultimately eaten by the spiders (Fig. 1C; Appendix S1, Video S1). The body lengths of the mantises eaten by spiders were < 56 mm. Three spiders failed in their attempts to prey upon the mantises; two *Tenodera angustipennis* and one *Tenodera sinensis* eventually eluded the spiders' attacks (Table 1). Surprisingly, two of the three mantises were able to remove the spider silk from their forelegs using their mouths, and they escaped (Fig. 1D; Appendix S1, Video S2).

Nineteen of the spiders did not attack the mantises (Table 1), although some were observed to swing their webs violently (i.e., bobbing behavior; Eisner 2003). This rejection was likely not due to satiation, as the same individual spiders accepted grasshoppers (*Oxya yezoensis*; body length 25.1–28.0 mm). The mantises grasped

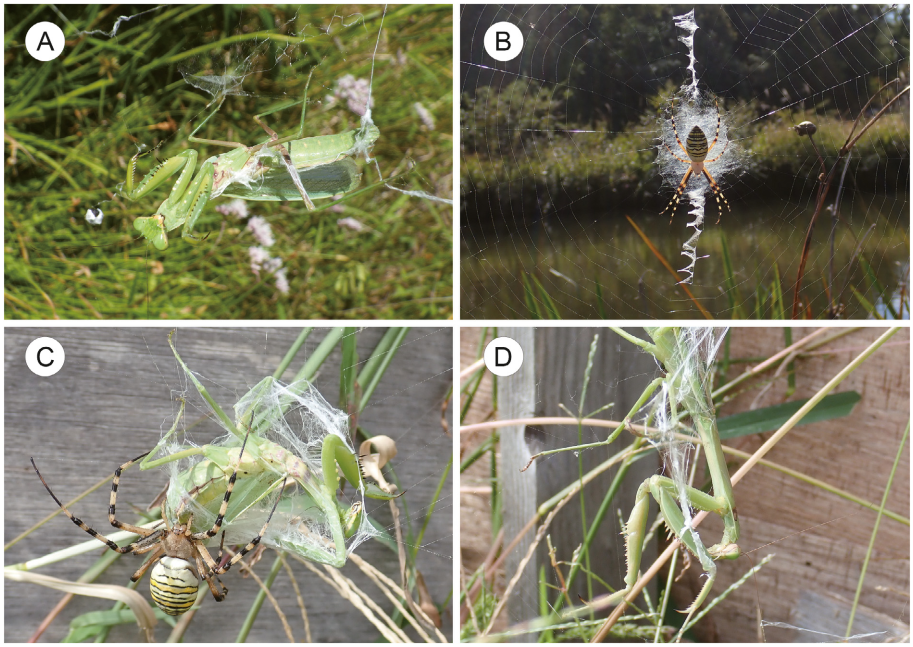

FIG. 1. Praying mantises on orb webs constructed by *Argiope bruennichi*. (A) An *Hierodula patellifera* mantis trapped in an orb web. (B) An orb web constructed by *A. bruennichi*. (C) An *H. patellifera* mantis wrapped and bitten by *A. bruennichi* in a field experiment. (D) A *Tenodera angustipennis* mantis using its mouth to remove spider silk from its foreleg in a field experiment. Photo credits: (A) Kota Sakagami, (B–D) Shinji Sugiura.

TABLE 1. Results of praying mantises experimentally placed on orb webs constructed by female *Argiope bruennichi* spiders.

Mantis species	Body length (mm)†	*n*	Attacked by spiders		Eaten by spiders		Escape from spider webs	
			%	*n*	%	*n*	%	*n*
Statilia maculata	48.0 ± 1.2 (46.8–49.1)	2	100	2	100	2	0.0	0
Hierodula patellifera	57.1 ± 0.8 (55.1–59.0)	5	40.0	2	40.0	2	60.0	3
Tenodera angustipennis	73.0 ± 3.1 (61.8–81.3)	6	33.3	2	0.0	0	83.3	5
Tenodera sinensis	83.7 ± 1.6 (74.6–92.6)	13	7.7	1	0.0	0	100.0	13
		26	26.9	7	15.4	4	80.8	21

†Values are mean ± SE with range in brackets.

plant leaves and other objects using their forelegs in their attempts to escape from the spiders' webs. A total of 21 mantises succeeded in escaping (Table 1); 15 of these left the webs within 15 min. The frequent escape of the mantises from the spider webs indicates that the chances of observing predation by orb-weaving spiders upon mantises under field conditions are limited.

Spiders attacked small mantis species more frequently than they attacked large mantis species, and the large species succeeded in escaping more frequently (Table 1). The *M. religiosa* that Fabre (1905) observed being eaten by the spider *A. bruennichi* was similar in terms of body size to the small species *S. maculata* and *H. patellifera*. Here, we used generalized linear mixed models (GLMMs; see the Appendix S1 for details) to determine the role of mantis body size in a spider's decision and the mantis's escape. The GLMM analysis revealed that large mantises were attacked by spiders less frequently than small mantises (Appendix S1: Table S1), and, therefore, large mantises succeeded in escaping from the spider webs more frequently (Appendix S1: Table S2). Larger prey trapped in webs may launch a counterattack on the web owners, and/or obligate them to expend large amounts of silk to immobilize their prey. Thus, risk and cost may induce *A. bruennichi* to refrain from attacking larger mantises.

Praying mantises may frequently be trapped by *A. bruennichi* webs under natural conditions because both animals are commonly found in the same habitats. Therefore, mantises may provide selective pressure on spider behavior, and vice versa. The aciniform silk that

Argiope spiders use to wrap their prey is among the toughest known biological materials (Hayashi et al. 2004, Addison et al. 2018). The "wrapping" attacks with aciniform silk are an important behavior aimed at immobilizing dangerous prey (Fabre 1905, Eisner 2003), suggesting that praying mantises are not the only selective pressure on the evolution of wrapping attacks. Although aciniform silk is extremely tough, some mantises were able to remove the silk from their bodies using their mouths in their attempts to escape (Fig. 1D). The powerful mouthparts of mantises are used to devour tough prey (Reitze and Nentwig 1991) and to clean their own body parts (Zack 1978). Therefore, we do not consider the relationship between spider attack (tough silk) and mantis escape (powerful mouthparts) to be part of a coevolutionary arms race. Escape from spider webs may be observed in other insects with powerful mouthparts (e.g., hornets). Further observations and experiments are required to test this hypothesis.

Acknowledgments

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