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Author(s)	Horita, Mituru; Chittenden, Anthony R.; Sato, Yukie; Saito, Yutaka
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Mituru Horita • Anthony R. Chittenden • Yukie Sato • Yutaka Saito

**Function of web box as an anti-predator barrier in the spider mite,
*Schizotetranychus recki***

Mituru Horita¹•Anthony R. Chittenden•Yukie Sato• Yutaka Saito (✉)

Laboratory of Animal Ecology, Graduate School of Agriculture, Hokkaido University,
Kita-ku Sapporo 060-8589, Japan.

Tel. 011-706-3893, Fax. 011-757-5595, e-mail: yutsat@res.agr.hokudai.ac.jp,

URL:<http://www.agr.hokudai.ac.jp/ecosys/depes.html>

Present address

Meiji Dairies Corporation, 2-10 Shinsuna 1-Chome, Koto-ku Tokyo 136-8908, Japan

Abstract

Spider mites inhabiting *Sasa* bamboo show considerable variation in traits supposed to be the result of coevolution between predator and prey. In *Schizotetranychus recki* Ehara inhabiting the hairy leaves of a dwarf bamboo, *Sasa senanensis*, all quiescent stages including eggs, appear within web boxes in the leaf hairs of their host plant, and this habit is thought to be a trait involved in predator avoidance. To test this hypothesis, the survival rates of *S. recki* eggs inside a web box and those freed of a web box were assessed in relation to 6 predator species that co-occur with the spider mite in the field. The results clearly showed that the webbing behavior (web box) of *S. recki* has a function in avoiding 5 predator species. However, one predator species *Agistemus summersi* Ehara, preyed more on eggs protected by a web box. This suggests that this predator species has a special trait to overcome the nest barriers.

Key words

Acari, Tetranychidae, Phytoseiidae, Stigmaeidae, coevolution, Predator-prey interaction, *Sasa* bamboo

Introduction

Predation is an important process deciding the evolution of defense in prey organisms (Schmidt 1990). The universal distribution and astonishing diversity of defense mechanisms are testament to the enormous selection pressures imposed on victims by their enemies. This diversity is particularly evident in spider mites, small phytophagous creatures that inhabit plants. *Sasa senanensis* (Franch. et Sav.) (Gramineae) is a dwarf bamboo species widespread in Hokkaido, the northernmost island of Japan. Because leaves live for a long period, *Sasa* communities are temporally and spatially very stable and support a rich mite fauna (Saito and Ueno, 1979). At least 7 spider mite species and 8 predatory mite species are known to syntopically inhabit the undersurface of *S. senanensis* leaves (Saito, 1990a), which can vary considerably from hairless to very hairy. The tetranychid species show distinct habitat partitioning along this leaf hair continuum, and species richness increases with leaf hairiness (Chittenden 2002). It is known that populations of polyphagous enemies sustained by alternative prey species can cause competition between prey species for enemy free space (see Holt, 1977, 1984, Jeffries & Lawton 1984), and it is hypothesized that the diversity of life types seen in the spider mites on *Sasa* is a direct result of this competition and of predator-prey interactions (Saito, 1990b).

Previous studies have shown that many of the prey species present on *Sasa* have specific natural enemies and unique anti-predation behavior. The nest-weaving behavior of *Schizotetranychus celarius* (Banks) is known to have an important role in preventing nest intrusion by predatory mites (Saito, 1986; Mori et al., 1999; Mori, 2000). Also, the oviposition behavior of *Yezonychus sapporensis* Ehara on the tips of leaf hairs has been shown to have a predator avoidance function (Yanagida et al. 2001).

Like *Y. sapporensis*, *S. recki* requires quite hairy leaves for oviposition. This spider mite has a WN-r life type (Saito, 1983). It utilizes silk to weave leaf hairs into small box-like nests inside which it oviposits single eggs. Similar, but less dense boxes are produced by immature stages just prior to their molting (Saito, 1985). As the web boxes are not used by mobile stages, it is hypothesized that they must have an important role in the protection of immobile stages such as eggs and quiescent individuals. This hypothesis was investigated experimentally in this study.

Materials and Methods

The predator species used in this study are all known to occur syntopically on *S. senanensis*. They were *Agistemus iburiensis* Ehara, *Agistemus summersi* Ehara (Acari: Stigmaeidae), *Amblyseius orientalis* Ehara, *Amblyseius womersleyi* Schicha, *Phytoseius tenuiformis* Ehara and *Typhlodromus bambusae* Ehara (Acari: Phytoseiidae). All except *A. iburiensis* were collected from *S. senanensis* within the campus of Hokkaido University. *A. iburiensis* was collected from *S. senanensis* in Shizunai Village in Hidaka District, Hokkaido. All mites were collected between June and July 2001.

Stock cultures of *S. recki* were reared on leaf discs prepared from the undersurface of detached *S. senanensis* leaves (hairy variety) in the same manner as Yanagida *et al.* (2001).

No choice experiment

Initially, to assess the ability of all predator species to prey upon *S. recki* eggs, predators were supplied eggs of only one treatment (see below). Females were introduced onto the leaf discs, maintained there until approximately 20 eggs had been oviposited, then replaced back into the stock cultures. Two treatments were then prepared. The web boxes around 20 eggs on a leaf disc were left intact, or the web boxes around 20 eggs were removed using a fine needle. These became known as “box-intact” or “box-removed” eggs respectively. Any additional eggs and webbing were removed from the leaf. A single predator (adult female held under no-food conditions for 24 hours) was then introduced onto each leaf disc. After 24 hours the **female** was removed, and the number of eggs consumed on each leaf disc was counted. Trials were replicated at least 18 times per predator species with different individuals used each time.

For analysis, the unpaired Students *t*-test was adopted (using JMP[®], SAS Institute).

Choice experiment

Female spider mites were introduced onto the leaf discs, maintained there until approximately 40 eggs had been deposited, then replaced back into the stock cultures. The web boxes around 20 eggs (chosen arbitrarily) were removed using a fine needle. These were known as “box-removed” eggs. The web boxes around 20 other eggs were left intact. These were known as “box-intact” eggs. Any additional eggs and webbing were removed from the leaf. A single adult female predator (held under no-food conditions for 24 hours) was then introduced onto each leaf disc. After 24 hours the

female was removed, and the number of eggs consumed per treatment was counted. Trials were replicated at least 15 times per predator species with different individual spider mites and predatory mites used each time.

All stock cultures and experimental trials were maintained at $25^{\circ}\text{C} \pm 2^{\circ}\text{C}$, 15L-9D, and 60-80% RH conditions.

For analysis, the paired Students *t*-test was adopted (using JMP[®], SAS Institute).

Results

From the no choice experiment (Table 1), it is apparent that all predator species can prey upon either egg treatment albeit to varying degrees. With the exception of *A. summersi*, predator species preyed on higher numbers of "box-removed" eggs, although *P. tenuiformis* preyed on almost equal numbers of both treatments ($P=0.98$). *A. iburiensis*, *A. womersleyi*, *T. bambusae* and *A. orientalis* preyed on significantly more "box-removed" than "box-intact" eggs (all at $P<0.01$). Only *A. summersi* preyed on more "box-intact" eggs ($P=0.046$).

The results of the choice experiment (Table 2) also showed that all predator species ate the eggs of both treatments. However, 5 out of the 6 predator species preyed upon significantly more "box-removed" eggs than "box-intact" eggs ($P<0.0001$). Again, only *A. summersi* consumed more "box-intact" eggs than "box-removed" eggs and the difference was highly significant ($P=0.0007$).

Discussion

These results suggest that the web-boxes *S. recki* mothers make around each egg hinder most predator species that prey on the eggs. When faced with no other choice, predators can and will eat the web-protected eggs, but this is presumably a costly activity as all the predator species except for *A. summersi* show clear preferences for unprotected eggs if available. Phytoseiid and stigmatid mites are both non-visual hunters – relying on chemical and tactile cues (Sabelis & Dicke 1985, Sabelis & Van de Baan 1983, Walters & Proctor 1999), so it is expected that they should be readily able to locate the box nests, which can occur in quite high densities on the leaf surface. As such, it seems that many of the predator species on *Sasa* do not possess the ability to overcome the web barrier once they have encountered it. The results show that all predator species readily preyed upon the "box-removed" eggs, showing that the eggs are palatable to all species, but

only *A. summersi* consumed more “box-intact” than “box-removed” eggs. All other species ate more “box-removed” than “box-intact” eggs.

Why the “box-intact” eggs showed higher survival rates than “box-removed” eggs is an important question. Predator mites feed by grasping prey with their chelicerae and sucking out the contents (Chant 1985). In order to do this the mites must first get very close to their prey. For immobile prey such as eggs and quiescent individuals, this should not be difficult, but for some of the predator species at least, the presence of the web box seems to act as a barrier and effectively prevents this. This lends support to the hypothesis that the web boxes have an anti-predation function. *A. iburiensis*, *A. orientalis* and *T. bambusae* all demonstrated very low abilities to prey on the “box-intact” nests.

In the cases of *A. iburiensis* and *T. bambusae* this is not surprising and in agreement with previous reports, which stated that these 2 species are specific predators of 2 spider mite species making dense web-nests, i.e. *S. celarius* and *Schizotetranychus longus* Saito, respectively (Takahashi 1987; Saito 1990b; Chittenden and Saito 2001; Saito *et al.* unpublished).

In the case of *A. orientalis*, this is not an unexpected result either. Chittenden (2002) found *A. orientalis* to be a specific predator of *Aponychus corpuzae* Rimando, a spider mite species inhabiting *Sasa* with low leaf hair density.

By contrast, *A. womersleyi* fed mainly on “box-removed” eggs, but also consumed high numbers of “box-intact” eggs. This predator may have the ability to physically damage the webbing or intrude into it in order to get at the prey inside, but it cannot be considered a specific predator of *S. recki* due to its relative rarity on *Sasa*. In a survey mite fauna occurring on *Sasa* across the island of Hokkaido, *A. womersleyi* occurred only once in 132 sites (Chittenden 2002).

P. tenuiformis also preyed on significantly more “box-removed” than “box-intact” eggs, and it showed considerable ability to prey on “box-intact” eggs. Considering it is a specific predator of *Y. sapporensis* (Yanagida *et al.* 2001) that also occurs on very hairy leaves, *P. tenuiformis* should be expected to have evolved the ability to prey upon an alternate, co-occurring prey species when its preferred prey species is in short supply.

The most likely contender for specialized predator of *S. recki* is *A. summersi*, the only predator species to prey on more “box-intact” eggs than “web-removed” eggs. That it occurs so often with *S. recki* (Chittenden 2002) and was observed feeding on the egg

directly through the web on many occasions, suggests a coevolutionary relationship between these 2 species.

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Table 1. Number of *S. recki* eggs preyed upon under two different treatments presented separately to predator species on *S. senanensis*.

Predator Species	Eggs eaten				P-value
	"Box intact"		"Box removed"		
	N	Average \pm SD	N	Average \pm SD	
<i>Agistemus iburiensis</i>	18	1.17 \pm 1.51	17	4.65 \pm 2.03	<0.0001
<i>Agistemus summersi</i>	25	10.00 \pm 5.13	17	7.27 \pm 4.28	0.046
<i>Amblyseius orientalis</i>	23	2.52 \pm 2.06	20	5.40 \pm 3.02	0.0002
<i>Amblyseius womersleyi</i>	20	14.10 \pm 5.98	16	17.81 \pm 2.34	0.008
<i>Phytoseius tenuiformis</i>	21	8.48 \pm 2.99	18	8.50 \pm 2.89	0.98
<i>Typhlodromus bambusae</i>	20	3.55 \pm 2.50	17	5.41 \pm 1.94	0.005

Table 2. Number of *S. recki* eggs preyed upon under two different treatments presented simultaneously to predator species on *S. senanensis*.

Predator Species	Eggs eaten			P-value
	N	"Box intact"	"Box removed"	
		Average \pm SD	Average \pm SD	
<i>Agistemus iburiensis</i>	17	1.71 \pm 1.36	6.23 \pm 2.28	<0.0001
<i>Agistemus summersi</i>	16	7.56 \pm 1.41	4.81 \pm 2.40	0.0007
<i>Amblyseius orientalis</i>	19	1.63 \pm 1.21	7.37 \pm 2.36	<0.0001
<i>Amblyseius womersleyi</i>	15	9.20 \pm 4.02	13.07 \pm 3.47	<0.0001
<i>Phytoseius tenuiformis</i>	18	4.50 \pm 1.72	8.72 \pm 2.40	<0.0001
<i>Typhlodromus bambusae</i>	15	2.33 \pm 2.10	7.53 \pm 3.02	<0.0001