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Nest size variation reflecting anti-predator strategies in social spider mites of *Stigmaeopsis* (Acari: Tetranychidae)

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Abstract

The social spider mites (Acari: Tetranychidae) of *Stigmaeopsis* weave dense nests on the underside of host leaves. Four species occur on the leaves of bamboo in Japan: *Stigmaeopsis longus*, *S. celarius*, *S. takahashii* and *S. saharai*. We initially reconfirmed the occurrence of distinct variation in nest size among the species. Based on the hypothesis that this variation plays a role in protecting the spider mites from predators, we looked at the behavior of the natural enemies that occur on the host plants along with members of *Stigmaeopsis*. We found considerable variation in the ability of nests to protect the spider mite eggs. The smallest nests protected the eggs against 3 predators, whereas the largest nests protected the eggs only against one predator species. In other words, decreases in nest size increased egg defense. Thus we concluded that nest size variation reflects a strategy for reducing predation.

Key words: spider mites, silken web nest, protective refuge, predator-prey interaction, *Stigmaeopsis*

Introduction

In animals other than those at the highest trophic level, defense mechanisms are one of the most important adaptations for survival, and extraordinary variation in the means of defense has been reported in arthropods (Evans and Schmidt 1990) as well as in other animals (Alcock 1989). In a review of lepidopteran insect defense, Lederhouse (1990) said: "Although many of the more spectacular adaptations have engendered "just-so" adaptive stories, experimental demonstrations of their efficacy are limited. Well-designed experimental studies and perceptive field observations are required if we hope to make substantial progress in understanding the role of diverse primary defense mechanisms in reducing predation."

Most social animals inhabit fully or semi-permanent nests (e.g. Seger 1991). Since the nest structure determines the social unit in which individuals will interact with each other, the forces molding nest morphology should influence social behavior and even social organization. In plant-parasitic arthropods, many aphids, thrips and mites form nest-like structures and include several social species (Saito 1986a; Crespi 1992; Foster and Northcott 1994; Crespi and Mound 1997; Saito 1997; Stern and Foster 1997). The nest (or gall) that is constructed by such animals is thought to have at least 2 important functions: feeding site and protective refuge (Dixon 1973; Saito 1985; Price et al. 1987; Crespi 1994; Foster and Northcott 1994). The diversity of nest (gall) forms in such animals is supposed to be maintained primarily through natural selection for such functions (Price et al. 1987). The functions of protective refuges are,

however, not always clear because it is usually difficult for nest-making animals to live normally under "non" nest conditions, i.e. it is often difficult to settle on appropriate controls for the study of nest function. In fact, several experiments, which could have revealed the functions of traits for protecting young, were limited to studies that used artificial "trait-removal" experiments (Kudo and Ishibashi 1996; Mori et al. 1999; Toyama 1999; Yanagida et al. 2001). If there is great variation in nest characteristics such as size and structure among very closely related and sympatric species, a comparison of the shared ecologies should make it possible to detect the function of the nest.

The nest-weaving spider mites of *Stigmaeopsis* (Saito et al. 2004) weave dense nests over depressions on the underside of host leaves (Fig. 1). This genus, which infests dwarf bamboo and bamboo plants, can be classified into 4 species: *Stigmaeopsis longus*, *S. celarius*, *S. takahashii* and *S. saharai* according to nest size (Saito and Takahashi 1980; Takahashi 1987). In addition, a molecular phylogeny study using partial sequences of ribosomal DNA (945 bps) demonstrated that these species are close sibling species in Tetranychidae (Sakagami 2002). Moreover, reciprocal cross experiments supported the results of phylogenetic analysis because reproductive isolation between *S. takahashii* and *S. saharai* was incomplete (Mori 2000). Therefore, we thought that a comparison of the effects of different nest sizes among these species could demonstrate the function of nests.

Saito (1986a, b) reported that there is biparental defense against the predatory mite, *Typhlodromus bambusae* in the social spider mite, *S. longus*, which has the largest nest size among these species. This counterattack behavior is known to be effective if many individuals cohabit in the same nest, thus the group living guaranteed by a large nest is supposed to be adaptive. Furthermore, Mori et al. (1999) demonstrated by a series of removal experiments in a natural forest that both the web and female attendance of *S. longus* improve the survival of young. In this context, we had doubts as to why the other 3 species, which make smaller nests, sometimes cohabit with *S. longus* on the same dwarf bamboo leaves, as it shows no counterattack behavior (Mori 2000). In order to answer this question, we attempted to determine how the nest size differences known in the 4 species are effective for protection against predatory intrusion under experimental conditions.

Methods

Biological remarks on the species

S. longus occurs on the leaves of the dwarf bamboo plants, *Sasa senanensis* and *Sasa kurilensis* in Hokkaido, Japan and makes very large nests (Saito and Takahashi 1980;

Saito 1986a). There are 3 other species: *S. celarius*, *S. takahashii* and *S. saharai*. *S. celarius* mainly occurs on Moso bamboo, *Phyllostachys pubescens* and Machiku bamboo, *Dendrocalamus latiflorus* in southern Japan, although it can develop and reproduce normally on *S. senanensis* and *S. kurilensis* (Mori 2000). *S. takahashii* usually occurs on *S. senanensis*. *S. saharai* mainly occurs on *S. senanensis* and *S. kurilensis* in Hokkaido, Japan and makes the smallest nests of *Stigmaeopsis*. The nest sizes of these species are in the order of *S. longus*>*S. celarius*>*S. takahashii*>*S. saharai* (cf. Fig. 2). The morphological characteristics and life histories of all species are very similar except for the lengths of certain dorsal setae (Saito and Takahashi 1982; Saito 1990; Mori 2000). The length of dorsal seta P2 shows 4 separate frequency distributions according to the species and this seta length is correlated with nest size (Saito and Takahashi 1980). Group size (i.e., number of individuals per nest) is basically proportional to nest size, and it can often become very large in *S. longus* and *S. celarius* through nest-extension (“united nest” in Fig. 1). *S. longus* or *S. celarius* individuals live gregariously inside web-nests throughout their lifetimes and show cooperative nest defense behavior against predators (reported in the former by Saito (1986a) and in the latter by Mori (2000)). On the other hand, because the nests of the *S. takahashii* and *S. saharai* are smaller than those of *S. longus* and *S. celarius*, *S. takahashii* and *S. saharai* females repeatedly disperse and found new nests during their lifetimes (Saito and Takahashi 1982). These facts indicate that the variation among species of *Stigmaeopsis* in the characters mentioned above can be accounted for by the selection pressures that cause a change in nest size.

The predatory mites used in this study all inhabit *S. senanensis* and they were often observed with the mites of *Stigmaeopsis*. At least 7 spider mite species and 7 predacious mite species (including 5 species used in this study) occur on *S. senanensis*.

Materials

All spider mite species used in this study were the progeny of those obtained from field populations as shown in Table 1. These mites were reared in the laboratory under conditions of 23±2°C, 40-80% R.H. and 15L-9D. The host plants for the cultures and experiments (*S. senanensis* and *S. kurilensis*) were cultivated in a green house.

The predatory mites used in the experiments were collected on *S. senanensis* and *P. pubescens* on which most of the spider mites used in this experiment sympatrically inhabited (Table 2). They were reared on the detached leaves of *S. senanensis* using the 4 species as well as another co-occurring species, *Yezonychus sapporensis*, for prey.

Evaluation of nest size

The prey populations of A, C, E, and F in Table 1 were used. The experiments were conducted under conditions of $25\pm 1^{\circ}\text{C}$, 50-70 % R.H. and 15L-9D. Adult females aged one day subsequent to mating (i.e., just after the final molt) were taken from stock cultures of each species and placed individually onto detached leaves (ca. 1.5 cm^2) of host plants (*S. senanensis* or *S. kurilensis*) placed on water-soaked cotton sheets which had been spread on polyurethane mats in petri dishes. In order to prevent water evaporation from lowering the temperature of the leaf surface (Saito and Suzuki 1987), the surfaces of the cotton and the polyurethane mats surrounding the detached leaves were covered with polyethylene film. After 48 h, we measured surface area (=maximum length x maximum width) of each nest with a divider, because the nest size of *S. longus* is known to be stable c.a. 24 h after commencement of nest building (Saito unpublished data; Mori unpublished data).

Protection efficiency of nest

The prey populations of A, C, D and F in Table 1 were used for this experiment. A detached leaf measuring 3 cm x 3 cm was prepared by surrounding it with water-soaked cotton. Seven to 10 females of each species were introduced from stock cultures onto experimental arenas and kept under conditions of $23\pm 1^{\circ}\text{C}$, 40-80% R.H. and 15L-9D for 3 to 4 days. After the females had constructed their nests and deposited a sufficient number of eggs within them, we removed the females from the leaves and prepared two treatments, i.e. the “web-removal” and “web-intact” treatments.

Gravid female predatory mites of each species (Table 2) were introduced individually onto each experimental arena. Forty-eight hours after predator introduction, we recorded the number of prey eggs eaten, the number of eggs laid by the predator and the location of the predator female and her eggs (inside or outside the web-nest in the “web-intact” treatments). These parameters are the criteria for predator intrusion. In particular, the number of eggs consumed indicates the intensity of predation of the respective spider mites.

Statistical analyses were carried out using the software, StatView[®] for Windows (Abacus Concepts, Inc., Berkeley, California).

Results

Nest size variation

The nest sizes constructed by females of each species are shown in Fig. 2. There was a significant difference in mean nest area (Fig. 2) among the 4 species (one-way ANOVA, $F_{3, 122}=144.84$ $P<0.0001$). Multiple-comparison tests (Scheffe's method)

detected significant differences between all combinations other than between *S. celarius* and *S. takahashii* (Fig. 2).

Effect of webs

When no web was present, the eggs of all 4 species were fed on by all predators (Fig. 3), indicating that each predator species can eat the eggs of each spider mite without difficulty. Namely, all the predatory species used in this study are potential natural enemies for all prey species. Several predator species showed preferences for certain prey species eggs: more *S. longus* eggs than those of *S. celarius* and *S. takahashii* eggs were eaten by *P. tenuiformis* (one-way ANOVA, $F_{3,60}=4.50$, $P=0.0065$; Scheffe's test, *S. longus* vs. *S. celarius*: $P=0.036$, *S. longus* vs. *S. takahashii*: $P=0.024$). More *S. longus* eggs than *S. celarius* and *S. saharai* eggs (one-way ANOVA, $F_{3,61}=6.39$, $P=0.0008$; Scheffe's test, *S. longus* vs. *S. celarius*: $P=0.005$; *S. longus* vs. *S. saharai*: $P=0.0374$), and more *S. takahashii* eggs than *S. celarius* eggs were more eaten by *A. summersi* (Scheffe's test, *S. takahashii* vs. *S. celarius*: $P=0.0373$). The other predators consumed the eggs of all prey species indiscriminately.

In the “web-intact” experiments, it was shown that the nest of each spider mite greatly affected predation efficiency (Fig. 4). In particular, *Amblyseius* sp. 1 which was the most serious predator for all species in the “web-removal” experiments could not consume any prey eggs. The other predator species could feed on the prey eggs inside nests. Then, we applied a two-way ANOVA to compare the number of eggs eaten during 48h by each predator between “web-removal” and “web-intact” treatments, and between prey species. *A. iburiensis* females consumed prey eggs regardless of web presence (“presence of web” effect: $F_{1,133}=3.43$, $P=0.066$). *T. bambusae* females also consumed prey eggs regardless of web presence (“presence of web” effect: $F_{1,128}=0.72$, $P=0.397$) while the interaction between the effects of “prey species” and “presence of web” was significant ($F_{3,128}=11.98$, $P<0.0001$). On the other hand, *P. tenuiformis* and *A. summersi* females were blocked by prey web-nests (“presence of web” effect for *P. tenuiformis*: $F_{1,115}=138.33$, $P<0.0001$; “presence of web” effect for *A. summersi*: $F_{1,122}=110.90$, $P<0.0001$), although the interaction between effects of “prey species” and “presence of web” for *A. summersi* was also significant ($F_{3,122}=2.97$, $P=0.034$).

In order to evaluate the overall effect of web size variation on the protection of eggs from predators during 48h, we applied a two-way ANOVA to the data of all predators in “web-intact” treatments except *Amblyseius* sp. 1 which never ate eggs in web-nests. There was a great difference in the effect of web types (“prey species” effect) on the number of eggs eaten (by two-way ANOVA, “prey species” effect: $F_{3,250}=7.97$, $P<0.0001$, “predator species” effect: $F_{3,250}=158.82$, $P<0.0001$, interaction

between “prey species” and “predator species”: $F_{9, 250}=24.21$, $P<0.0001$). Paired comparisons by the use of *post hoc* testing showed that there were significant differences in predation pressure between *S. lonus* and *S. celarius* (Scheffe's test, $P<0.0067$) and between *S. lonus* and *S. saharai* (Scheffe's test, $P<0.0206$). *S. longus* eggs were preyed upon by 4 predator species: (*T. bambusae*, *A. iburiensis*, *P. tenuiformis* and *A. summersi*), and those of *S. celarius* and *S. takahashii* by 2 predator species: (*T. bambusae* and *A. iburiensis*). On the other hand, the eggs of the *S. saharai* were preyed upon by 3 predator species: (*T. bambusae*, *A. iburiensis* and *A. summersi*), though a *A. summersi* female sometimes preyed on *S. saharai* eggs directly through the nest roof without intruding into *S. saharai* nest. These results could be summarized as that decreases in nest size increased egg defense.

The proportion of predator females and their eggs observed inside the nests 48h after their introduction in “web-intact” experiments corresponded well to the pattern of prey egg consumption (Table 3). Most *T. bambusae* and all *A. iburiensis* females and all their eggs were observed inside the nests regardless of prey species. In addition, many *P. tenuiformis* and *A. summersi* females (and their eggs) also remained in *S. longus* nests, although no females from either of these two predator species were observed in the web-nests of the other species.

Discussion

We have been able to show that the nest size variation of *Stigmaeopsis* had great differences in the effectiveness of predator avoidance. First we discuss why such variation has evolved in this mite group.

If the web-nest functions as a protective refuge against predator intrusion, then variation in its structure will change the actual predation pressure from which spider mites have usually suffered in a particular environment. As known previously, the fauna of phytophagous mites on *Sasa* plants is very complex (at least 7 spider mite species and several eriophid species) and varies strongly depending upon the leaf hair density of hosts (Chittenden 2002). The fauna of predacious mites also varies due to the change in prey composition. In such a situation, it is possible to hypothesize that the nest size variants were selected under various environments. For example, they may interact with different predators and/or phytophagous animals in different environments. In other words, the species making smaller nests were generated under stronger predation pressure from generalist predators. In this case, the species have differentiated allopatrically.

On the other hand, some populations of *S. longus* live with *S. takahashii* or *S. saharai* in the same natural forests (Takahashi 1987 and Table 1). This suggests that

there are alternative anti-predation strategies at work in such forests. As shown in the present study, the nests of *S. takahashii* or *S. saharai* are very effective as protective refuges against several predator species, such that these species have a great advantage over *S. longus* in habitats where these predators occur. In such environments, the predation pressure on *S. longus* must be very intense, such that it has needed to develop additional anti-predator adaptations. The counterattack behavior performed by adult males and females (biparental defense) of *S. longus* (Saito 1986a,b) is thus thought to be another strategy for improving the survival of this species. It should be noted here that the effect of such counterattack behavior increases with the increases in mite density within a nest and with the staying time of parents in a nest, conditions which are only realized in large nests (Saito 1986b; Mori 2000). Therefore, we could conclude that there are at least two extremes in strategies, i.e. “protection by smaller nests” in the *S. takahashii* and *S. saharai* and “defense by many individuals in larger nests” in *S. longus* and *S. celarius*.

In other words, this involves a very important view from the point of social evolution. Spatio-temporal aggregation and biparental defense are two sets of traits which characterize the sociality of *S. longus* (=L form, Saito 1997). On the other hand, small nests with a small number of eggs and short maternal attendance duration in *S. takahashii* and *S. saharai* mean that there is no highly developed sociality in these species, even though they are sub-social (Saito 1995). Therefore, the alternative anti-predatory adaptations are thought to be connected to what kinds of sociality have evolved in these mite species. Namely, the anti-predation adaptations are primarily responsible for the evolution of sociality in this mite group.

So far, we have discussed only the effectiveness of the self-constructing protective refuge and sociality of 4 species, but there seems to be additional point of view of anti-predator behavior in these 4 species, i.e. aggregation and dispersion. The function of aggregation has received considerable attention as anti-predator behavior (Hamilton 1971; Pulliam and Caraco 1984; Inman and Krebs 1987; Vulinec 1990) and two distinct mechanisms can be involved: “encounter effect” and “dilution effect”. These were combined and termed “attack abatement” by Turner and Pitcher (1986). (See also Wrona and Dixon 1991; Uetz and Hieber 1994). We have also studied the effect of egg depositing patterns in relation to nest size under experimental conditions, with the result that smaller nests distributed sparsely (i.e. ovipositing eggs in small clumps) effectively decrease the probability of predation (deluding effect, Saito et al. unpublished).

We thus believe that the effects of counterattack (Saito 1986a, b), making protective refuges (in this study) and egg depositing patterns are all anti-predatory

strategies and may thoroughly explain why there is variation in nest size in *Stigmaeopsis*.

Lastly, we have to discuss the mechanisms of how the smaller nests effectively prevent predator intrusion. The nest size variation referred to in this study involves several differences in the nest structure. For instance, the nest size may be closely related to nest entrance size. Furthermore, the density of the silken threads of the nest web may be higher in small nests, if the investment in nest construction is equal in all species. Although we have no quantitative data, we believe that the size of the nest entrance is primarily responsible for the effectiveness of anti predatory intrusion, because most predators usually tried to enter from the nest entrance.

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figure legends

Fig. 1

Nesting patterns of *Stigmaeopsis*.

Fig.2

Mean areas (\pm SE) per nest of *Stigmaeopsis*.

The results of post hoc tests (Scheffe's method) are shown. n= numbers of females analyzed.

Fig. 3

Mean numbers (+SE) of 4 species' eggs eaten by 5 predators in "web-removal" treatments. Numerals over columns are the numbers of replicates.

Fig. 4

Mean numbers (+SE) of 4 species' eggs eaten by 5 predators in "web-intact" treatments. Numerals over columns are the numbers of replicates.

Table 1 Collection and culture record of *Stigmaeopsis* used in this study

Culture ID	Species	Date	Locality (Prefecture)	Host plant	Plant for culture
A	<i>Stigmaeopsis longus</i>	May 10, 1997	Sapporo (Hokkaido)	<i>Sasa senanensis</i>	<i>Sasa senanensis</i>
B	<i>Stigmaeopsis celarius</i>	March 30, 1998	Toyonaka (Osaka)	<i>Phyllostachys pubescens</i>	<i>Sasa senanensis</i>
C	<i>Stigmaeopsis celarius</i>	March 30, 1998	Toyonaka (Osaka)	<i>Phyllostachys pubescens</i>	<i>Sasa kurilensis</i>
D	<i>Stigmaeopsis takahashii</i>	May 12, 1997	Sapporo (Hokkaido)	<i>Sasa senanensis</i>	<i>Sasa senanensis</i>
E	<i>Stigmaeopsis takahashii</i>	June 15, 1998	Sapporo (Hokkaido)	<i>Sasa senanensis</i>	<i>Sasa senanensis</i>
F	<i>Stigmaeopsis saharai</i>	June 9, 1998	Higashikawa (Hokkaido)	<i>Sasa senanensis</i>	<i>Sasa senanensis</i>

Table 2 Collection record of predatory mites used in this study

Species	Date	Locality (Prefecture)	Host plant
<i>Typhlodromus bambusae</i>	May 12, 1997	Sapporo (Hokkaido)	<i>Sasa senanensis</i>
<i>Typhlodromus bambusae</i>	March 30, 1998	Toyonaka (Osaka)	<i>Phyllostachys pubescens</i>
<i>Agistemus iburiensis</i>	September 4, 1997	Sapporo (Hokkaido)	<i>Sasa senanensis</i>
<i>Phytoseius tenuiformis</i>	May 12, 1997	Sapporo (Hokkaido)	<i>Sasa senanensis</i>
<i>Agistemus summersi</i>	May 12, 1997	Sapporo (Hokkaido)	<i>Sasa senanensis</i>
<i>Amblyseius</i> sp.1	August 4, 1997	Sapporo (Hokkaido)	<i>Sasa senanensis</i>

Table 3 Percentage of predator females (adults) and laid eggs inside nests (%).
 Numerals in parentheses are the numbers of females or eggs tested

Prey species	Predator stage	Predator species				
		<i>T. bambusae</i>	<i>A. iburiensis</i>	<i>P. tenuiformis</i>	<i>A. summersi</i>	<i>Amblyseius</i> sp.1
<i>Stigmaeopsis longus</i>	Adult	95.24 (21)	100 (22)	65 (20)	66.67 (18)	0 (13)
	Egg	100 (40)	100 (131)	88.24 (34)	70.97 (62)	0 (12)
<i>Stigmaeopsis celarius</i>	Adult	100 (12)	93.75 (16)	0 (10)	0 (14)	0 (14)
	Egg	100 (47)	100 (96)	0 (7)	0 (34)	0 (14)
<i>Stigmaeopsis takahashii</i>	Adult	94.74 (19)	100 (20)	0 (20)	0 (20)	0 (16)
	Egg	100 (58)	100 (123)	0 (7)	0 (43)	0 (6)
<i>Stigmaeopsis saharai</i>	Adult	93.75 (16)	100 (16)	0 (9)	0 (13)	0 (13)
	Egg	100 (62)	100 (80)	0 (3)	0 (23)	0 (6)

Fig. 1
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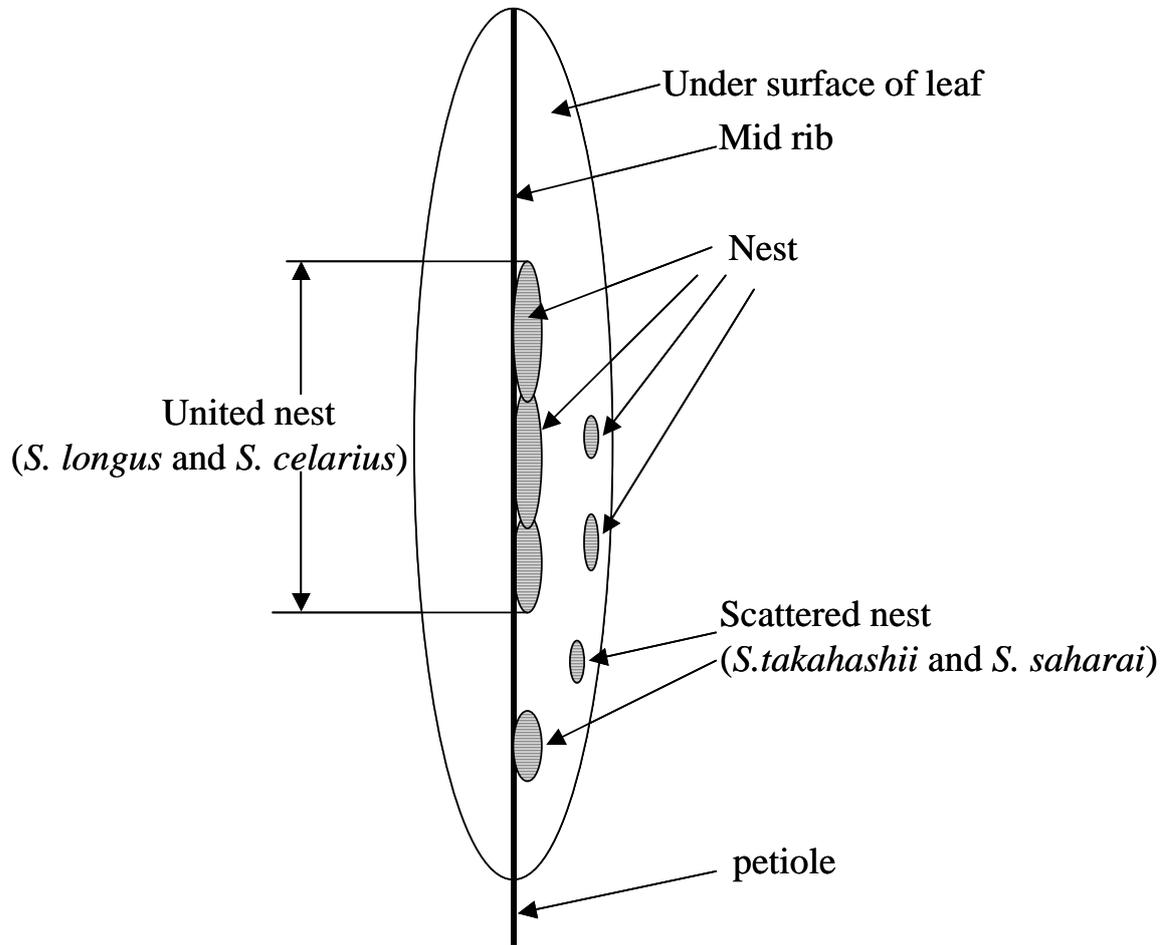


Fig. 2
K. Mori and Y.Saito

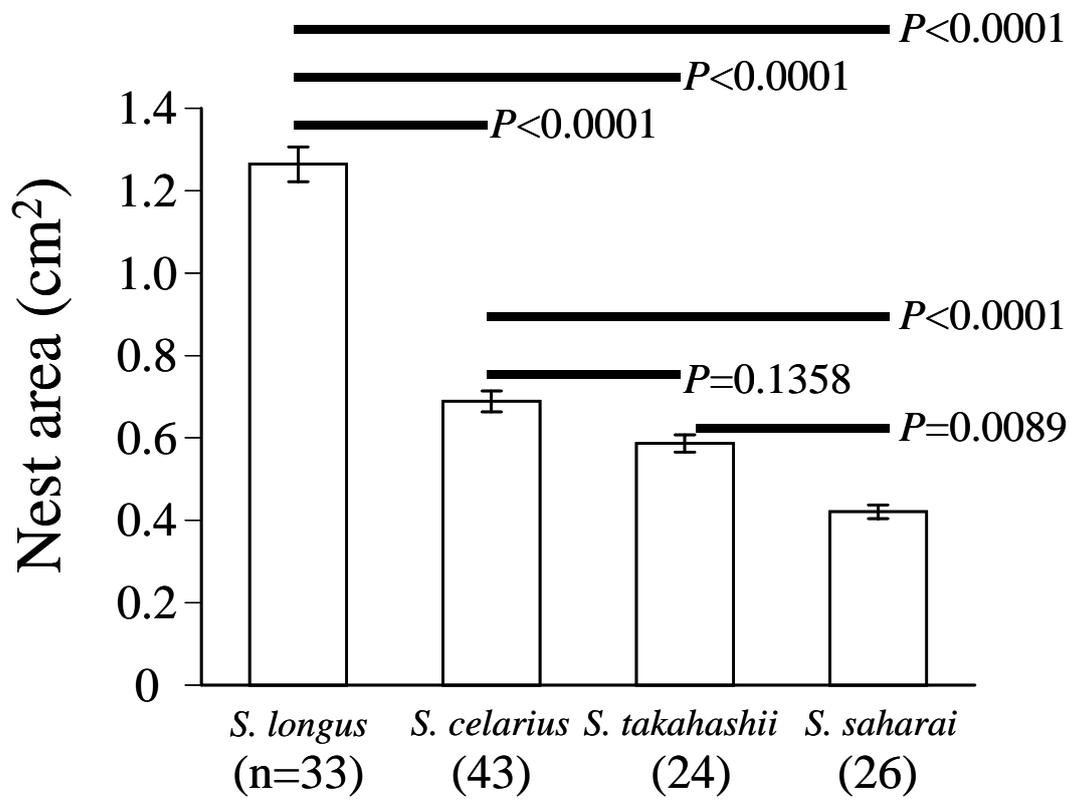


Fig. 3
K. Mori and Y.Saito

Predator species :

T. bambusae *A. iburiensis* *P. tenuiformis* *A. summersi* *Amblyseius sp. 1*

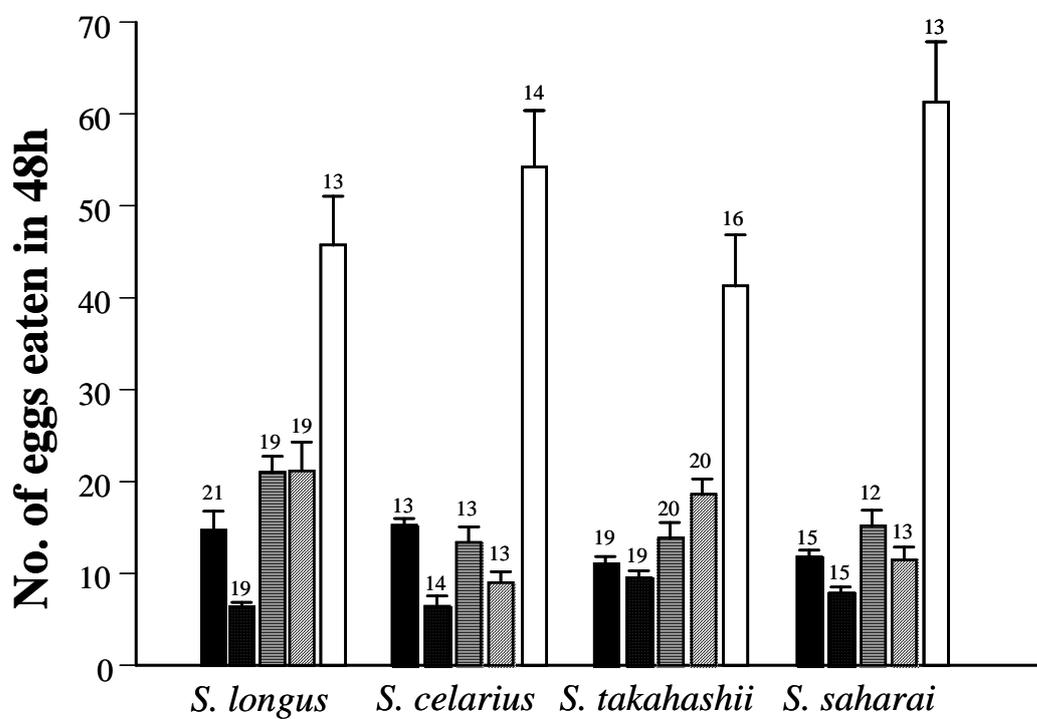


Fig. 4
K. Mori and Y.Saito

