THE EFFECT OF FOOD AND SILK RESERVE MANIPULATION ON DECORATION-BUILDING OF ARGIOPE AETHEROIDES

by

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Summary
In this study I investigated how decoration-building of *Argiope aetheroides* is proximately controlled. Since decoration silk is produced from the aciniform glands and these glands' secretion is also used in prey-wrapping, I tested if manipulating the amount of silk in the aciniform glands would lead to changes in the building of decorations. When the aciniform glands of *A. aetheroides* were supplemented by giving spiders ample prey and silk was not depleted, a significant increase in total area and number of arms of decorations was found. When the aciniform glands were intensively depleted by repeatedly removing the wrapped prey from webs, the size of decorations in subsequent webs was significantly reduced. Spiders building webs with small or no decorations were still able to produce plenty of silk to wrap prey. Therefore, the presence of undecorated webs seemed to result from the silk reserve, which the spiders may invest on decoration-building, being depleted, rather than the aciniform glands being completely emptied. Based on the results, I propose that there is a threshold point in the aciniform glands, and the amount of silk reserve in the glands relative to that threshold determines the size of decorations.

Introduction

After constructing a regular web, many orb-weaving spiders incorporate extra structures called decorations or stabilimenta on their webs (Nentwig & Heimer, 1987). Investigators have reported several types of decorations made

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of various material such as silk, egg sacs, prey remain and detritus from at least 12 genera of orb-weaving spiders (Eberhard, 1973; 1990; Levi, 1983; Nentwig & Heimer, 1987). Among various types of decorations the functions of those composed entirely of silk were the focus of most studies. Traditionally the functions of silk decorations had been proposed to be stabilizing the web, adjusting web tension, serving as a moulting platform, aiding in thermoregulation, defending against predators and attracting visually-oriented insects (reviewed in Herberstein *et al.*, 2000a). Among them, the predator defense and prey attraction hypotheses have received the most attention. Many studies demonstrated that decorated webs built by various species of *Argiope* (Craig & Bernard, 1990; Tso, 1996; 1998a; Herberstein, 2000; Bruce *et al.*, 2001; Craig *et al.*, 2001), *Cyclosa* (Tso, 1998b) and *Octonoba* (Watanabe, 1999) caught significantly more prey than undecorated ones. Such results are usually attributed to the web decoration's colour signals being similar to those of the food resources, and thus attractive to insects (Craig & Bernard, 1990; Craig, 1991, 1994; Zschokke, 2002). However, some researchers did not find decorated webs built by *Argiope* spiders to catch more prey than undecorated ones (Blackledge & Wenzel, 1999). These authors suggested that web decorations were included to function as warning signals to prevent webs from being destroyed by birds or as defense devices against parasitoid predators (Blackledge, 1998a; Blackledge & Wenzel, 1999, 2000, 2001). After evaluating many empirical studies, Starks (2002) suggested that the prey attraction and predator defense hypotheses were not mutually exclusive and web decoration might have multiple functions.

Although the functions of decorations built by *Argiope* spiders are well studied, it remains unclear how their building is proximately controlled. Individual *Argiope* spiders do not always decorate their webs, and the number and size of silk bands on webs varies considerably on a daily basis (Seah & Li, 2002). If the presence of web decorations really benefits the spiders as proposed by various hypotheses, then why do the spiders not always incorporate such structures on their webs? To determine how decorating behaviour is involved in the ecology of *Argiope* spiders, an understanding of how the inconsistent pattern is proximately generated is essential. In the past two decades, researchers have tried to provide answers on different levels. Craig (1994) found the inconsistent pattern to be able to prevent hymenopteran prey from learning to associate the decorations with danger and then concluded that inconsistent building of decorations (in both shape and frequency) is beneficial to *Argiope* spiders, thus is favored and maintained by natural selection. However, the work by Craig (1994) did not answer how the inconsistent building of decorations is controlled. Other researchers tried to identify the proximate factors regulating the building of decorations. Nentwig & Rogg (1988) examined the influence of numerous abiotic and biotic factors, and only found factors such as extreme temperatures, moulting and age to be effective. Elgar *et al.* (1996) found the level of ambient light to significantly affect the size of decorations built by *Argiope aetheroides*. However, both a field survey and a laboratory experiment conducted by Nentwig & Rogg (1988) found this factor to be ineffective. Decorations may attract insects to webs, thus they can be considered as one form of foraging efforts exhibited by *Argiope* spiders. Several researchers examined whether size of decorations and past foraging success have a negative relationship, as do spiders' other foraging efforts (Blackledge, 1998b; Tso, 1999; Herberstein *et al.*, 2000b). The food treatments used in these studies did generate significant effects, but the results were inconsistent with the predictions. Food deprivation had either no (Tso, 1999) or a negative effect (Blackledge, 1998b; Herberstein *et al.*, 2000b), while food satiation generated an enhanced decoration-building. Concluding from these results, there must be some factors other than those examined in the aforementioned studies that are involved in the proximate control of decoration-building.

A finding by Peters (1993) suggested that the content of the decoration silk-producing gland may be one of the key factors influencing building of decorations. Peters (1993) found the aciniform glands to be responsible for the production of decoration silk. However, silk produced in the aciniform glands was also used in prey wrapping (Foelix, 1996). Since the amount of silk reserve in other silk glands greatly affects the size of orb webs (Eberhard, 1988; 1990; Zschokke, 1997), perhaps the size of decorations is determined by the amount of silk reserve in the aciniform glands, which in turn is affected by the intensity of prey wrapping. In this study, I tested the effect of manipulating the silk reserve in the aciniform glands on decoration-building of *Argiope aetheroides*. By subjecting spiders to various degrees of prey wrapping and food intake, I evaluated the following two predictions:

(1) Spiders receiving high food intake and low aciniform gland depletion will increase decoration-building.
(2) Spiders receiving intermediate food intake and intensive aciniform gland depletion will decrease decoration-building.

Materials and methods

Thirteen female *Argiope aetheroides* (Walckenaer, 1841) were collected and were released into two insectaries ($3 \times 3 \times 3$ m). Each spider was individually marked by applying enamel paint of a different colour on the dorsum of the abdomen. The experiments began three days after the spiders were released into the insectaries to allow them to recover from stress. During this time the spiders were given one mealworm in the first day and nothing in the other two days. The experiment was divided into two stages. In the first stage, I tested whether high food intake and low silk depletion would lead to enhanced decoration-building. In the second stage I tested whether intermediate food intake and intensive aciniform gland depletion would lead to a reduction in decoration-building.

The effect of high food intake and low aciniform gland depletion

At the beginning of the experiment each marked spider was given two mealworms (size between 20 to 30 mm) daily until four consecutive webs were constructed. Before being introduced to the web the mealworms were pressed with tweezers on the head region to temporarily immobilize them. When subduing the introduced immobilized mealworms the spiders usually only symbolically wrapped several thin strands of silk and then carried the prey back to the hub without further wrapping. Each day, the total area and number of arms of decorations of each web were recorded. The variables measured and the equations used in calculating decoration area followed Tso (1999). To evaluate spiders' responses in other web characteristics such as total silk output and catching area, I also recorded the following variables: number of radii; web radius, hub radius and number of spirals of four cardinal points. I used the formulae given in Tso (1999) to calculate total silk output and the 'adjusted radii-hub' formulae given in Herberstein & Tso (2000) to calculate catching area. Wilcoxon Paired Rank tests were used to compare area and number of silk arms, total silk output and catching area recorded from webs built before (web 1) and after receiving the treatments (webs 2, 3 and 4, respectively).

The effect of intermediate food intake and high aciniform gland depletion

Spiders completing the first stage of the experiment were given two mealworms daily until three more consecutive webs (web 5, 6 and 7) were built. This pre-depletion feeding was conducted to build up the silk reserve in the aciniform glands. Beginning on web 7, I reduced the food intake to half, and began the depletion treatment. Tso (1999) found *Argiope trifasciata* to invest a great amount of silk in decorations when they received a high prey intake. Therefore, in this study I gave spiders an intermediate amount of prey to prevent the effect of the depletion treatment being reduced by an enhanced decoration building generated by high prey intake. Aciniform gland depletion was achieved by placing a mealworm on the web, allowing spiders to wrap silk around the prey, then removing the wrapped prey from the web. When the spiders approached and began to subdue the mealworms I slightly shook the worms with tweezers to further enhance the prey-wrapping behavior of the spiders. When receiving this stimulus the spiders usually wrapped the mealworms with a great amount of silk and the whole prey was completely covered by several layers of silk. This procedure was repeated three to five times on each spider each day until four consecutive webs were built. From each web built during this stage the aforementioned web variables were measured and Wilcoxon paired rank tests were used to compare these web variables recorded from webs built before (web 7) and after receiving aciniform gland depletion (webs 8, 9 and 10, respectively).

During the depletion treatment, more than half of the spiders switched web sites, which made the data inappropriate for web characteristic assessment. Therefore, the effects of silk depletion and intermediate food supplement on silk length and catching area were not examined in the analyses.

Results

The effect of high food intake and low aciniform gland depletion

Complete data were available from 7 out of 13 marked spiders. The manipulations used in this part of the study successfully and promptly affected *Argiope aetheroides*'s decoration and web-building in a manner similar to those of previous studies (Blackledge, 1998b; Tso, 1999; Herberstein *et al.*, 2000b). After the first day of feeding (web 2), the area of decoration increased slightly but did not reach statistical significance (Fig. 1a). The subsequent feeding further increased the mean decoration area of *A. aetheroides* and that of web 3 and web 4 were both significantly higher than web 1. After three days of high prey intake and little aciniform gland use, the average number of decoration arms recorded from web 4 nearly doubled compared to that recorded from web 1 (Fig. 1b). In contrast to an elevated decoration building, web silk output decreased dramatically (Fig. 2). High food intake resulted in a significant decrease in total silk length and catching area even after the first round of feeding. Compared to those recorded from web 1, the average total silk length recorded from web 4 reduced 53%, and catching area reduced 60% (Fig. 2).

The effect of intermediate food intake and high aciniform gland depletion

In the second stage of the experiment, aciniform gland depletion generated a severe reduction in decoration-building. Although decoration size varied among individual spiders, decoration-building during the treatment gradually decreased following successive gland depletion (Fig. 3a). After the successive rounds of silk depletion, the area of decoration decreased considerably (Fig. 3a). After receiving successive aciniform gland depletions the decoration area of web 10 was significantly smaller than that of web 7. The average decoration area recorded from web 10 was one-fourth the average

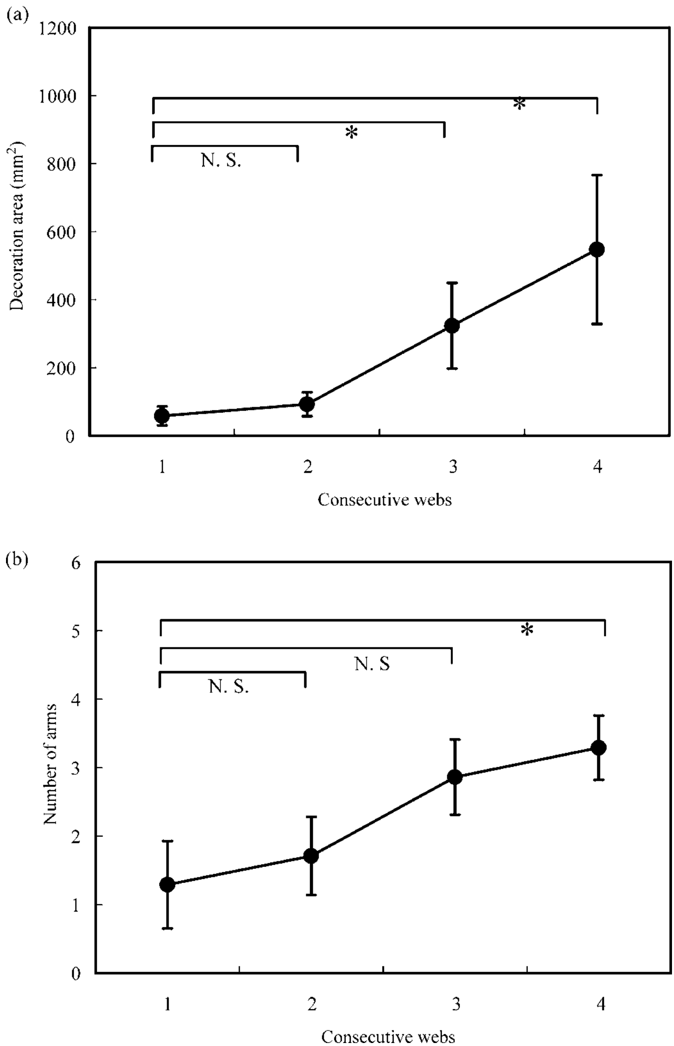

Fig. 1. Mean (±SE) total area (mm^2) (a) and number of arms of decorations (b) recorded from webs built during high food supplement and low silk depletion.

area recorded from web 7 (Fig. 3a). Most webs were decorated with four arms before silk depletion, but after the treatment webs decorated with two or three arms were the most frequently built. However, the number of arms did not differ significantly before and after depletion (Fig. 3b).

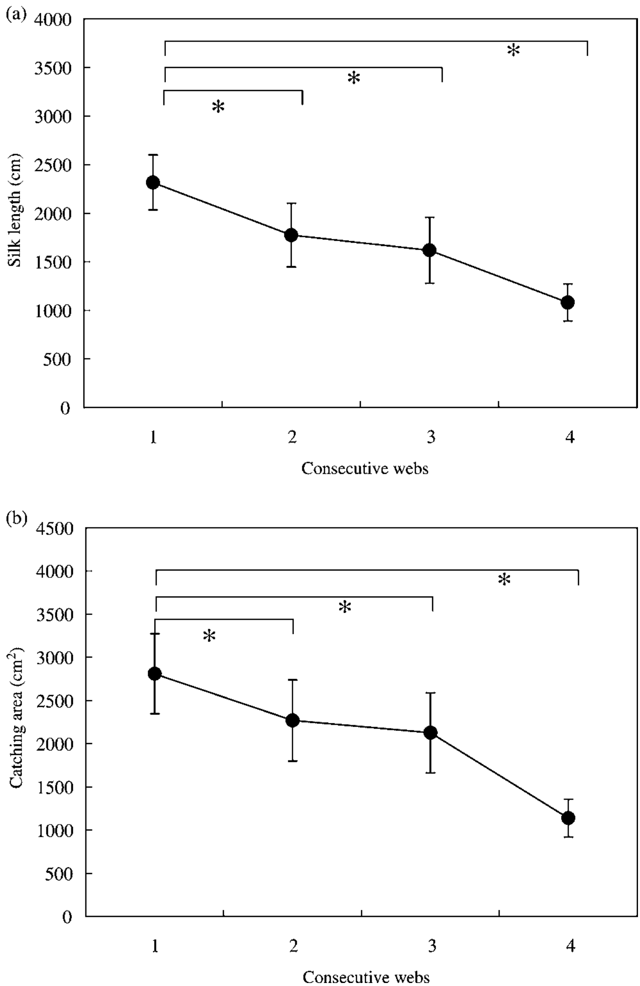

Fig. 2. Mean (±SE) total silk length (cm) (a) and catching area (mm^2) (b) recorded from webs built during high food supplement and low silk depletion.

Discussion

This manipulative study provides evidence that the amount of silk reserve in the aciniform glands greatly influences the building of decorations in subsequent webs. In the beginning of the first stage of experiment, less than half of *Argiope aetheroides* decorated their webs. As the treatment continued, eventually all spiders decorated their webs and significantly increased the size and number of arms of decorations. This result suggests that *A. aetheroides*

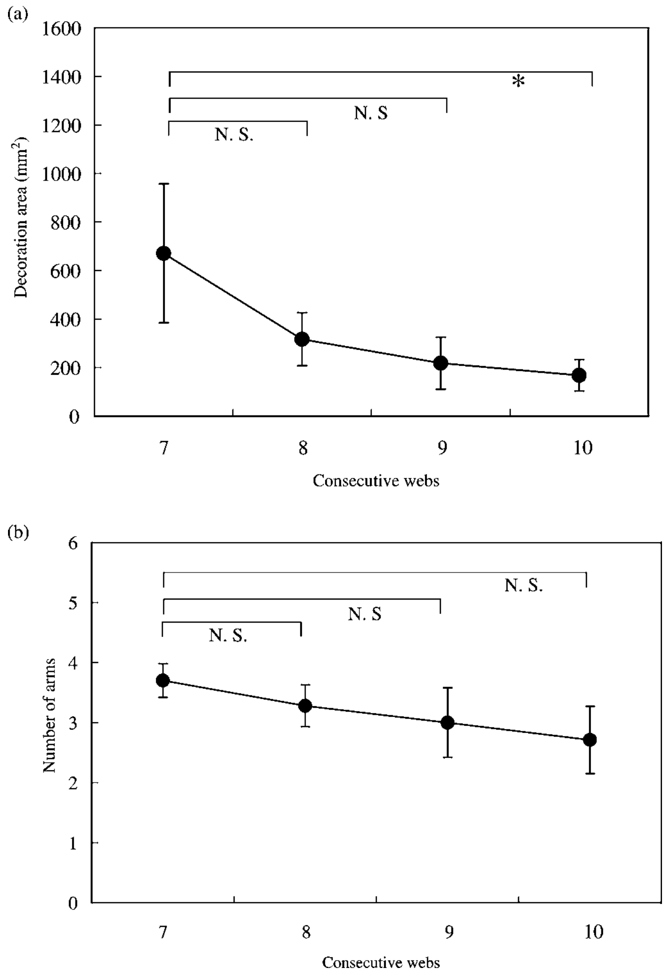

Fig. 3. Mean (±SE) total area (mm^2) (a) and number of arms of decorations (b) recorded from webs built during intermediate food supplement and high silk depletion.

will always build decorated webs to increase their prey intake as long as there is enough silk in the aciniform glands. After intensive silk depletion, the size of decorations was much reduced. In the field, various species of *Argiope* spiders building undecorated webs are still able to pull out enough silk to subdue prey. Such a phenomenon indicates that even spiders that do not invest silk in decoration-building still have enough reserves in the aciniform glands. Therefore, the building of undecorated webs does not seem to result from spiders' aciniform glands being completely depleted, but from the con-

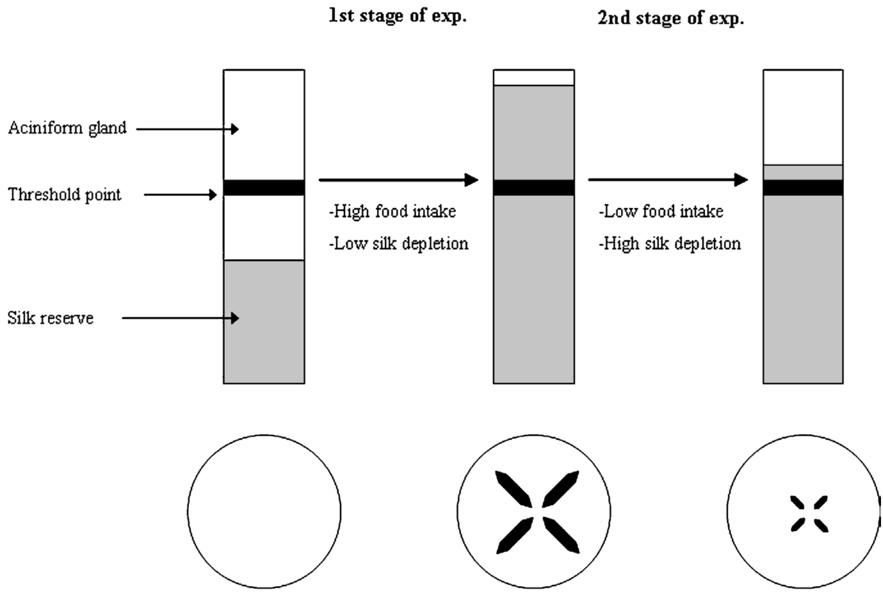

Fig. 4. A schematic diagram illustrating how the recorded decoration-building pattern can be generated by the treatments used in this study via the hypothetical changes in the amount of silk reserve in the aciniform glands.

tent of the glands being reduced to below a certain threshold. Based on these results, I propose that there is a threshold in the aciniform glands, and that the amount of silk reserve in the glands relative to that threshold determines the size of decorations (Fig. 4). If this hypothetical threshold does exist, the silk depletion employed in this study seemed unable to reduce the silk content to the level below the threshold point, but only reduced the amount of silk *A. aetheroides* might invest in decoration-building.

In the field, *Argiope* spiders are frequently observed building undecorated webs, which suggests that the amount of silk reserve in their aciniform gland content is frequently reduced to below the hypothesized threshold. This suggestion seems valid considering *Argiope* spiders' unique prey-subduing behavior and low catching success. *Argiope* spiders use 'wrap attack' as the major way of subduing insects (Olive, 1980), which takes a considerable amount of silk. For instance, an adult *Argiope aurantia* needs to spend an average of 20 to 30 seconds of wrapping to subdue an orthopteran (Harwood, 1973). Moreover, *Argiope* spiders' catching success of prey intercepted by the webs is low (17 to 53% reported by Olive, 1980; 25% reported by Pasquet & Leborgne, 1990). These facts indicate that spiders may frequently spend lots of silk with only little energy return, rendering the amount of silk reserve in the aciniform glands frequently below the threshold. In this study, *A. aetheroides* received ample food for more than a week before they received depletion treatment. This high level of food intake, which is rarely received by field spiders, provided spiders with lots of nutrient. Those well-fed spiders may in turn significantly increase aciniform gland secretion and thus could rapidly make up the amount of silk lost to the treatment. In future studies, the appearance of undecorated webs should be expected when spiders whose silk reserve is depleted also receive a lower level of food.

During the depletion treatment several spiders shifted their web sites. Because the physical complexity of a web site greatly affects the dimensions of a web (Enders, 1976; 1977; Janetos, 1986; Vollrath *et al.*, 1997), and because the size of the first web after relocation is reduced (Zschokke & Vollrath, 2000), web characteristics recorded from webs built on different sites were not suitable for assessing the effect of the treatment. However, decoration-building was unlikely to be affected by the relocation of web sites for two reasons. First, although spiders may spend some energy when searching for new web sites, this process should not severely affect the activity of the aciniform glands and their silk reserve. Secondly, Edmunds (1986) and Nentwig & Rogg (1988) both demonstrated that no correlation was found between size of decorations and web or web site characteristics. Therefore, web site switching should not seriously affect decoration-building of *A. aetheroides*.

Although web characteristics and decoration-building both greatly affect foraging of *Argiope* spiders, they seem to be influenced by different ecological factors. Web characteristics are greatly affected by past food intake. Results from Higgins & Buskirk (1992), Sherman (1994) and Tso (1999) all demonstrated that orb-weaving spiders increase silk output and catching area when experiencing low foraging success and reduce them when experiencing high foraging success. However, Blackledge (1998b), Tso (1999) and Herberstein *et al.* (2000b) all found that *Argiope* spiders' decorating behaviour in response to food treatments did not follow the predictions. The amount of silk reserve in the aciniform glands not being well controlled might be responsible for the unexpected results of these studies. Although spiders receiving food-deprivation treatment may have a slightly reduced silk secretion, the amount of silk reserve in the aciniform glands is not significantly affected, thus decoration-building is unchanged or only slightly reduced. Although spiders receiving excessive food may spend lots of silk in wrapping prey, an enhanced aciniform secretion resulting from a great increase of nutrient inflow may rapidly make up the loss of the aciniform gland, thus lead to enhanced decoration-building. Therefore, while web characteristics are greatly affected by past food intake, decoration-building seems to be determined by ecological factors capable of generating a change in the amount of silk reserve in the aciniform glands. The stochastic distribution of prey (Craig, 1989), plus *Argiope* spiders' wrap-attack prey-subduing behaviour and low catching success, may create a dramatic undulation in the content of the aciniform glands, and thus generate the unpredictable decoration pattern characteristic of those spiders.

In addition to ecological factors, decorating behaviour seems also to be influenced by the genetic makeup of the spiders. Edmunds (1986) investigated the effect of heredity by comparing the building patterns between adults and offspring of *A. trifasciata*. A higher similarity between related individuals was found, suggesting some degree of genetic linkage. But the sample size and experimental design were insufficient to determine the role genetic makeup plays in controlling decoration building. Craig *et al.* (2001) also examined the effect of heredity on decorating behaviour of *A. argentata* with a larger sample size and more sophisticated statistical analyses. They found that decorating behaviour was significantly affected by that of both parents. These results indicated that depending on the genetic makeup, individual *Argiope* spiders already vary in extent of decoration building to a certain degree. The aforementioned ecological factors and their effects on the aciniform gland content further generate an unpredictable and inconsistent decoration pattern, which is favored by natural selection because this impedes the learning of both prey and predators. Considering the results of all relevant studies, the observed inconsistent building pattern of decorations seems to be generated by the complicated interactions between genetic makeup, stochastic prey abundance, amount of silk reserve in the aciniform glands and natural selection mediated by cognitive behaviours of prey and predators.

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