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# Creative problem solving in a jumping spider

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## ABSTRACT

Behavioural innovation, a key indicator of advanced cognition, has been well documented across animal taxa and manifests as creative problem-solving. Typical innovators such as apes and corvids can spontaneously solve complex, multi-step tasks individually without prior training. Innovative behaviours in arthropods—honeybees, bumblebees, and ants—are probably underestimated because their innovative behaviours are often considered products of associative learning, group-level processes, or one-step problem-solving. Here, we challenge this view by demonstrating spontaneous, individual-level innovation in nest construction by the social-living jumping spider *Toxeus maxillosus*, without prior training or external demonstration. Under four challenging laboratory conditions, *T. maxillosus* females exhibited the core components of typical innovative behaviours: environmental exploration, behavioural flexibility, insight, and action planning. Furthermore, in a vertical string-pulling task (a benchmark test of animal innovation), half of the spiders pulled an out-of-reach sponge upward and incorporated it into the inner wall of the device, thereby creating a suitable microstructure for nest construction. These behaviours demonstrate multi-step, goal-directed object manipulation. Our findings suggest that arthropods are capable of individual-level, spontaneous innovation involving planning and multi-step sequences, akin to those observed in typical innovators. We propose that a social lifestyle centred on prolonged maternal care—a trait shared by *T. maxillosus* and many vertebrate innovators—rather than large brain size or long lifespan, may be a critical evolutionary driver of such cognitive complexity. This study challenges the vertebrate-centric view of typical innovation and provides a new framework for understanding the evolution of cognition across phylogenetic scales.

**Keywords:** Innovative behaviour; Parental care; Problem-solving; Spider cognition; *Toxeus maxillosus*

## INTRODUCTION

Behavioural innovation (see Table 1) refers to the process by which individuals generate a solution to a novel challenge or a novel solution to an existing problem (Kummer & Goodall, 1985; Reader & Laland, 2003; Vezyrakis et al., 2026). Innovative propensity is associated with superior intelligence and enables individuals to solve problems creatively, adapt to uncertain adverse conditions, and increase access to potential food or reproductive resources, thus granting animals substantial ecological and evolutionary advantages (Kaufman & Kaufman, 2015). Innovative behaviour arises from a unified psycho-behavioural pathway: individuals first explore unfamiliar environments and manipulate novel objects (exploration), then—without any external model or template (spontaneously)—produce instantaneous, original solutions via insight and creative recombination (insight) (Reader & Laland, 2003). Although innovative behaviours are taxonomically widespread, five vertebrate clades—Primates (Bandini & Harrison, 2020), Proboscidea (Foerder et al., 2011), Cetacea (Marino, 2002), Passeriformes (Kabadayi &



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**Table 1 Operational definitions of cognitive and behavioural terms used in this study**

| Term | Definition | Reference(s) |
|---|---|---|
| Exploration | The gathering of information about the environment, which may or may not be associated with the acquisition of resources (e.g., food, shelter, mates). | Piper, 2011 |
| Learning | A modification of behaviour involving the nervous system that results from practice or specific experience with an external event. In this study, learning refers to the acquisition or modification of behavioural patterns through experience, characterised by: (a) adaptive changes in behavioural responses resulting from individual practice (self-learning) or social observation (social learning); (b) gradual improvement in task performance through repeated exposure or demonstration; and (c) retention and application of acquired information across temporal and spatial contexts, demonstrating behavioural plasticity and adaptive capacity under varying environmental conditions. | Tierney, 1986 |
| Training | The acquisition of a specific behavioural solution, characterised by: (a) repeated presentation of the complete target behaviour by a demonstrator; (b) provision of controlled reinforcement to shape the subject's performance; and (c) attainment of a prescribed performance criterion through structured guidance. | Mellen & Ellis, 1996 |
| Planning | An internal process of formulating a systematic and organised method for one's behaviour in advance. Planning involves higher mental processes, such as maintaining a representation of the goal of the actions and monitoring outcomes related to one's own behaviour. | Kaufmann, 2015 |
| Action planning | The organisation of an animal's behaviour into discrete units (actions) that are structured hierarchically to achieve a particular goal. | Shettleworth, 2023 |
| Intentional behaviour | Behaviour directed toward a goal, requiring the actor to: (a) represent the goal; (b) choose among potential actions based on their likely efficacy in achieving that goal; and (c) persist toward the goal while flexibly adjusting actions in response to obstacles or failure. | Tomasello et al., 2003 |
| Problem-solving | A cognitive activity involving the use of cues provided by a problem situation and knowledge accumulated through long-term experience to overcome a physical or conceptual barrier. | Clayton & Emery, 2015 |
| Multi-step problem-solving | A form of cognition in which an animal sequentially executes two or more non-overlapping actions, with each action prompted by cues generated by the preceding step rather than directly by the final goal, thereby bridging an initially inaccessible outcome through an indirect chain of causation. | Auersperg et al., 2013; Richter et al., 2016; Taylor et al., 2010 |
| Behavioural flexibility | An individual's capacity to modify its actions in response to changing conditions, characterised by: (a) utilisation of past experience, including learned information, prior trial-and-error outcomes, or cause-and-effect understanding; (b) adaptive modification of behaviour without external demonstration or structured guidance; and (c) spontaneous adjustment demonstrating integration of prior experience under changing environmental contexts. | Logan, 2016 |
| Insight | The sudden recombination of previously gathered information into a novel adaptive response that is produced without overt trial-and-error and can be immediately applied to structurally similar problems. | Shettleworth, 2023 |
| Innovation | A novel behavioural solution that may involve solving a new problem or finding a new solution to an existing problem, producing a novel communication signal or using an existing signal for a new purpose, or making a new ecological discovery, such as incorporating a previously unused food item into the diet. | Kummer & Goodall, 1985 |
| Group-level innovation | A persistent, group-wide shift in behaviour that emerges when most or all members of a population adopt a new solution to a recurrent ecological or social challenge (e.g., a colony-wide change in nest architecture among honeybees). | Gallo & Chittka, 2021; Ramsey et al., 2007 |
| Individual-level innovation | The generation or adoption of a novel behavioural solution—either to a new problem or to a familiar one—by a single member of a population, without concurrent change in the behaviour of other conspecifics. Subsequent acquisition of this solution by others requires observational or social learning from the original innovator. | Ramsey et al., 2007 |
| Typical innovation | A novel, adaptive behavioural sequence executed at the individual level, characterised by: (a) goal-directed actions involving two or more sequentially ordered steps; (b) successful task completion without external demonstration, prior learning opportunities, or trial-and-error experience; and (c) spontaneous emergence demonstrating cognitive flexibility and problem-solving capacity under ecologically relevant conditions. | This study |
| Creativity | The brain's capacity to integrate skills, knowledge, and motivations to generate entirely new ideas or solutions. It represents a biological basis that can enable an individual to exhibit innovation. | Kaufman & Kaufman, 2015 |
| Intelligence | A collection of sophisticated cognitive abilities, including problem-solving, complex social cognition, and future planning. | Amodio et al., 2019 |

Osvath, 2017), and Psittaciformes (O'Neill et al., 2021)—are consistently regarded as prominent non-human innovators.

Compared to these typical vertebrate innovators, arthropod innovators differ fundamentally in three aspects. First, typical innovators can often solve tasks spontaneously while arthropods often depend on training. For example, Asian elephants (*Elephas maximus*) spontaneously added water to a tube to retrieve floating food just after observing the setup (Barrett & Benson-Amram, 2020), while the majority of buff-tailed bumblebees (*Bombus terrestris*) could pull the string to gain a reward only after progressive training or social learning (Alem et al., 2016). This training-based innovativeness is often regarded as a simple and straightforward associative process (Kaufman & Kaufman, 2015). Second, typical innovators often solve problems independently (individual-level innovation), whereas arthropods often exhibit flexibility at the colony level (group-level innovation), such as the behavioural flexibility exhibited by honeybees (*Apis mellifera*) in comb construction (Gallo & Chittka, 2018) and by weaver ants (*Oecophylla smaragdina*) in leaf-nest-building (Hu, 2026), both of which

rely on the repetitive innate behaviours of individual workers (Gallo & Chittka, 2021). Third, only typical innovators are known to solve complex, multi-step tasks by integrating different objects (Bandini & Harrison, 2020; Taylor et al., 2010), which suggests planning ability—a mental action involving intentions that extend beyond immediate actions (Kaufmann, 2015). For example, New Caledonian crows (*Corvus moneduloides*) retrieved food from a hole by first pulling up a string to obtain a short stick, which they used as a meta-tool to extract a longer stick, and then used the long stick to reach the food (Taylor et al., 2010), suggesting that they understand object–object interactions and are able to reason about causality (Taylor et al., 2009). Arthropod innovators typically rely on trial-and-error or one-step problem-solving and have not been shown to have the capacity for non-immediate intentional planning, as seen in spontaneous nest-building in weaver ants (Hu, 2026). Consequently, although arthropods frequently exhibit innovative behaviours, it remains questionable whether they are genuine innovators given these three limitations compared to typical innovators.

Three core characteristics might account for the innovativeness of typical vertebrate innovators (Kaufman & Kaufman, 2015): (1) Complex sociality ("social intelligence hypothesis" (Johnson-Ulrich, 2017)) drives the evolution of sophisticated intelligence and nervous systems to cope with frequent conspecific recognition, competition, cooperation, and social status evaluation (Penna-Gonçalves et al., 2025; van Schaik & Pradhan, 2003); (2) A longer lifespan (Kaplan et al., 2000; Street et al., 2017) enables the accumulation of skills from previous trial-and-error learning, such as difficult-to-acquire food-procurement skills, which is considered vital in the performance of innovation; (3) Expanded neural substrates (absolute or relative brain size) provide the physical basis for superior cognitive abilities (Jin et al., 2025; Sol et al., 2005). Arthropods generally lack all three traits and are therefore not usually regarded as capable of performing typical innovative behaviours. Nevertheless, evolutionary history shows that complex cognition has arisen repeatedly through divergent neural substrates (Roth, 2015) and longevity varies widely among the five typical innovator lineages (crows ~20 yr, elephants ~60 yr, bowhead whales >200 yr). Hence, these two factors may not be restrictive for animal cognition. Yet, all of them face convergent socio-ecological selection imposed by sociality and prolonged parental care, favouring the independent evolution of innovative ability. Therefore, arthropod innovation is likely underestimated, especially in social species, such as spiders that perform prolonged parental care.

Unlike the majority of salticid spiders, which are solitary or exhibit low levels of subsociality, *Toxeus maxillosus* (previously identified as *Toxeus magnus*) demonstrates a remarkable case of extended maternal care-based sociality (Chen et al., 2018). This species exhibits a unique reproductive strategy wherein the female independently constructs a breeding nest and subsequently provides nutritive secretions (commonly referred to as "spider milk") until nutritional independence, while maintaining continuous non-nutritional maternal investment throughout offspring development to sexual maturity, such as nest cleaning, enhancement, and repair (Jiang et al., 2024). According to our field and laboratory observations of breeding nest construction (using silk and environmental materials) and the diversity of nest architectures (Supplementary Figure S1; see details in Methods), we predicted that females could be flexible and innovative in breeding nest construction, as it involves a range of challenging tasks (Lehtonen et al., 2023).

To test whether *T. maxillosus* exhibits innovative behaviour similar to typical innovators, we recorded the breeding nest construction processes in mated *T. maxillosus* females under a series of challenging conditions, which we expected might trigger innovative behaviours. Furthermore, we used a vertical string-pull test, a classical method for testing animal innovation (Jacobs & Osvath, 2015), to test whether female spiders could obtain an "out-of-reach" object and complete the multi-step sequence required to incorporate it into nest construction. The results could help determine whether equivalent ecological selection arising from extended parental care could drive the convergent evolution of typical innovation, further expanding the social intelligence hypothesis. Testing these dimensions of typical innovative behaviours in arthropods will challenge the vertebrate-centric view of innovation and provide a basis for comparing cognitive evolution across phylogenetic scales.

## MATERIALS AND METHODS

### Study species

*Toxeus maxillosus* (Araneae: Salticidae) exhibits a breeding nest-based matrilineal resident society, in which male offspring are expelled once they reach sexual maturity, whereas female offspring stay in the natal nests with their mother, even after sexual maturity, and then disperse for breeding (around three weeks after sexual maturity). Breeding nests are essential throughout the spiders' lives, and the spiders commonly use bamboo leaves to construct their breeding nests, even though occasionally other plant leaves are also employed (Supplementary Figure S1). In our lab, we found that male spiders are never involved in breeding nest construction. Adult female spiders choose a nest site to construct their breeding nest soon after mating, then lay and hatch egg clutches, and perform lactation and other maternal care for about two months. During the maternal-care period, mothers clean, repair, and enhance the nest frequently, and offspring sometimes assist their mother in accomplishing these tasks. Like other spiders, *T. maxillosus* has flexible spinnerets, which are functionally comparable to hands in primates or bills in birds, for nest construction and repair.

*Toxeus maxillosus* is widely distributed in tropical and subtropical Asia, including southern and southwestern China. We collected twelve *T. maxillosus* families in Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (E101.27238°, N21.91993°, 584 m above sea level (asl)) and JiNuo Mountain (E101.03383°, N22.03992°, 550 m asl) between October 2020 and February 2021. Each family included an adult female and her spiderlings in the nest. To avoid disturbance to the spiders, each family was collected by removing the branchlet with the nest, and the branchlet was put into a normal rearing box (the control condition in the formal experiments) consisting of a transparent plastic box (17 cm long×13 cm wide×7 cm high) with a transparent plastic tube (length: 9 cm; diameter: 2.3 cm) fixed to an inner wall as a nest site (Figure 1A). In the lab, we controlled the temperature (25±2℃), light:dark regime (controlled light: 0800h–1800h, two hours of natural light (1800h–2000h) to avoid sudden entry into the dark), and feeding (every two days we fed fruit flies *Drosophila melanogaster* and house flies

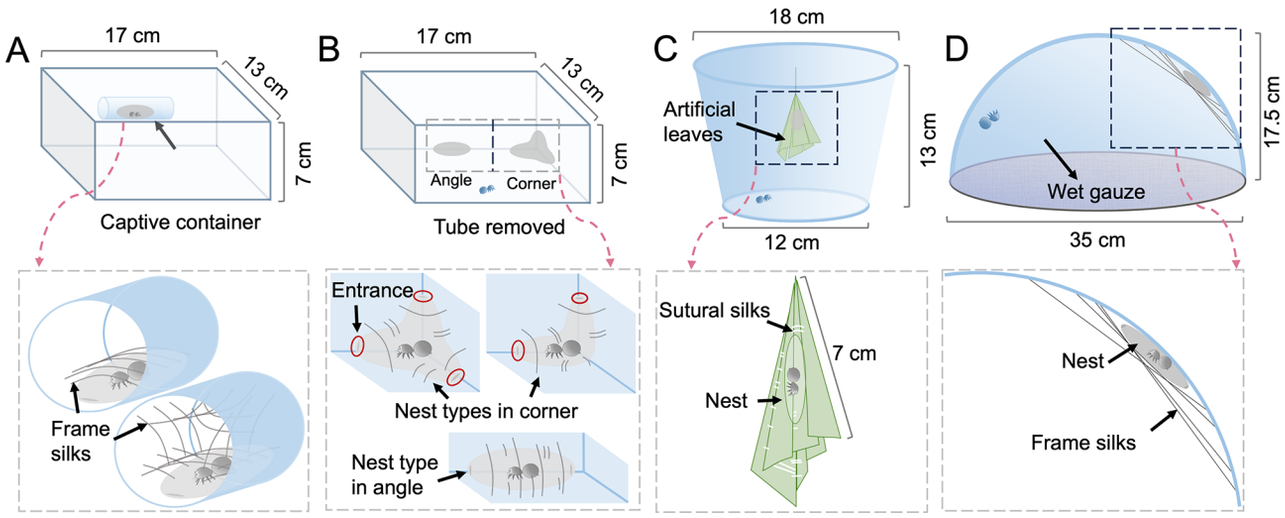


**Figure 1 Scheme of female *T. maxillosus* breeding nest construction in the Control and three challenging conditions**

A: Control condition, where each *T. maxillosus* female was kept in a transparent box with a plastic tube. Fifty-three females constructed nests within the tube and ten constructed nests in the corners of the boxes. B: Challenge 1, where each *T. maxillosus* female was tested in the same boxes as in the Control but without tubes. Eleven females constructed novel types of nests in three-sided corners and 35 females constructed novel types of nests in two-sided angles. C: Challenge 2, where each *T. maxillosus* female was tested in a transparent trapezoidal cylinder food box with artificial bamboo leaves hung in the middle. Twenty-four out of 43 tested females constructed nests with the artificial leaves, with nest structures resembling those in the wild. D: Challenge 3, where each *T. maxillosus* female was tested in a large transparent hemisphere placed over wet gauze to eliminate angles and corners that could be used for nesting. Thirty-six out of 38 tested females successfully constructed novel nest types that were never observed previously.

*Musca domestica*). We cleaned the rearing box every five to seven days. We removed the branchlet when all the spiders abandoned it. Once male offspring reached adulthood, we separated them from other offspring and reared them individually in smaller rearing boxes (5.4 cm long×5.4 cm wide×4.2 cm high) until mating. After mating, females were transferred to normal rearing boxes. To avoid inbreeding, mating pairs were from different families. The spiders collected from the field were named generation zero, and their offspring were called generation one and so on.

As we were limited by lab space and equipment, this study consisted of two rounds of experiments. In the first round, in 2023, we used 60 female spiders from generation three (each spider was only used once) to test their flexibility and innovativeness in breeding nest construction under four conditions (control condition and three challenging conditions, Figure 1) (Experiment 1), and 33 female spiders to test whether they possessed planning capacity by observing their breeding nest construction process in an arena with an "out-of-reach" sponge (potential nesting material) (Experiment 2). In the second experimental round, in 2024, we repeated Experiment 1 to further collect detailed data for analysing temporal and nest-shape parameters using 41 female spiders from generation seven or eight (some individuals were repeatedly used across the four conditions in a randomised order due to the limited number of spiders available in the laboratory, and randomisation was employed to exclude potential order effects on the results). Details of the sample sizes for Experiment 1 are presented in Supplementary Table S1.

**Experiment 1: Breeding nest construction under challenging conditions**

To test *T. maxillosus* females' flexibility and innovativeness in breeding nest construction, we used females raised in the laboratory (without any experience under natural conditions), and, in addition to the control condition, designed three challenging conditions under which the spiders were required to construct breeding nests; their nest-building performance was then recorded. Challenge 1—an empty rearing box (the same box used for normal rearing but with the plastic tube removed to increase the difficulty for nest building) (Figure 1B)—aimed to test whether female *T. maxillosus* could choose suitable sites (such as the box internal corners) to construct a nest in the box. Challenge 2—a transparent trapezoidal cylinder food box (bottom diameter: 12 cm, top diameter: 18 cm, height: 13 cm) with six top-tip-connected artificial bamboo leaves hanging in the middle from the top with a 1-cm-long string (Figure 1C)—was designed to test whether female spiders could inhibit the pre-existing nest construction behaviour in the normal rearing container and exhibit novel nesting behaviour using artificial bamboo leaves. To make the artificial bamboo leaves, we sewed the adjacent sides of a square piece of green cardboard (7.0 cm long×7.0 cm wide) into a cone with transparent tape and then divided it into six parts (a number of leaves similar to that used in the wild) along the generatrix, leaving 2 mm uncut at the top to maintain the cone shape. Challenge 3—a hemisphere arena without corners and other materials that spiders could use to construct a nest—was designed to further challenge their nest construction ability and test their innovation. The arena was set up by covering a large transparent acrylic hemisphere (diameter: 35 cm) on a brown melamine tray (diameter: 40 cm) which was filled with water and covered by white gauze (Figure 1D). We assumed the dome surface of the hemisphere would be flat (without any easy nesting sites) for the spiders, as their average body length is only 0.65 cm; the water-filled tray prevented the spiders from building a nest in the angle between the edge of the hemisphere and the tray, while maintaining a humid environment for the spiders.

During the experiment, spiders were introduced into experimental conditions the day after mating (1000h–1100h)

to record the nest-building processes and durations over seven days. Once the nest prototype (an ellipsoid-like chamber outline first became visible, Supplementary Figure S2) was formed, the spiders were transferred into a new normal rearing box (in 2023, the first-round experiment) or transferred into a new condition the next day for further testing (in 2024, the second experimental round), and prototype nest photos from two directions were taken to obtain nest parameters (camera type: Nikon DIGITAL CAMERA D750, Thailand, Supplementary Figure S2). The nest-building process and duration were checked and recorded each evening in 2023 and filmed in 2024 for detailed time allocation analysis (video camera type: SONY FDR-AX60, China). Time allocation in nest construction and nest morphological parameters obtained from videos and photos included: a) latency of nest construction, duration from entering the apparatus to the start of constructing the nest; b) nest construction duration, the accumulated time spent to construct the nest cell and frame structure; c) non-nest construction time, sum of the time in which the spider did not construct a nest since nest construction started, including sleeping, grooming, and eating periods; and d) total time, duration from being introduced into the apparatus to the completion of a preliminary prototype structure; e) length ($L$), width ($W$), height ($H$) of nest cell; and f) vertically projected area (measured in ImageJ, https://imagej.net/ij/) of each nest cell and its frame; and g) volume of the nest cell, considering it as an ellipsoid, using the formula: $V=(4/3)\pi\times(L/2)\times(W/2)\times(H/2)$ (Supplementary Figure S2). These parameters (measured by the same observer and following a strict video-review protocol) were used to evaluate the variation among the nests under different conditions. To obtain volume estimates, we treated each nest cell as an ellipsoid and applied the standard ellipsoid formula; this unavoidable simplification may introduce minor errors but enables consistent comparison across nests.

**Experiment 2: Breeding nest construction using "out-of-reach" sponge**

*Toxeus maxillosus* females often integrate easily accessible external materials into their nests, which may help reduce silk use, enhance nest stability, and improve nest concealment. To test whether and how they could incorporate an "out-of-reach" sponge into nest construction, we designed Challenge 4—a vertical string-pull test, a classical way of testing an animal's non-immediate intentional planning capacity in innovation (Jacobs & Osvath, 2015). In this experiment, we modified the arena of Challenge 3 by vertically suspending a piece of white sponge (size: 4.0 cm long×3.0 cm wide×0.3 cm high; average weight: 28.8 mg) with a white cotton string (diameter: 0.15 mm) 2 cm from the top middle of the hemisphere. We assumed that the "innovative" spiders would, first, pull the sponge upward; then, fix the sponge onto the inner face, thereby forming a stable micro-environment for nest construction. After that, spiders could construct a nest similar to those built in an empty box or tube (Figure 2A; Supplementary Figure S3A). We used 33 females in this experiment and checked daily for the following fourteen days to record whether and how the sponge pieces were used, and the nesting duration.

**Statistical analysis**

**Experiment 1: Breeding nest construction under challenging conditions**: To test *T. maxillosus* females' flexibility and innovativeness in breeding nest construction, first, we compared the durations of latency before nest construction, nest construction, non-nest construction activities, and total time among the four conditions using Aligned Ranks Transformation ANOVA (ART ANOVA) followed by pairwise comparisons with "Tukey" adjustment for

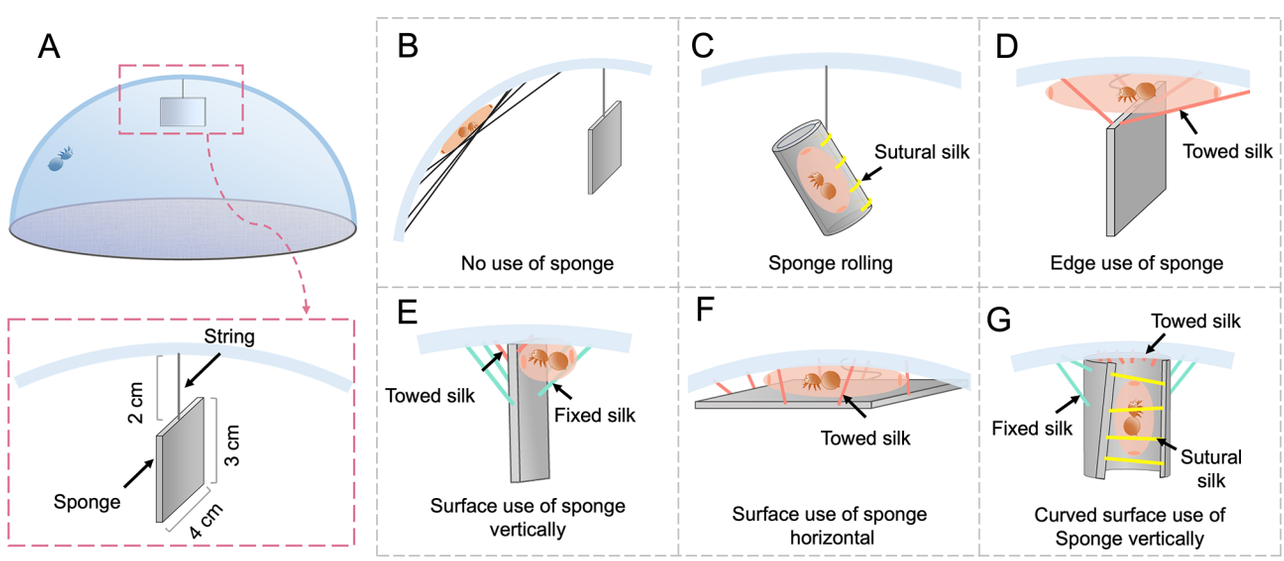


**Figure 2 Scheme of female *T. maxillosus* breeding nest construction using an "out-of-reach" object**

A: Experimental design for testing the use of an 'out-of-reach' object. A slice of sponge (size: 4.0 cm long×3.0 cm wide×0.3 cm high; average weight: 28.8 mg) was hung in the middle of the hemisphere placed over wet gauze. B: Nesting on the dome without using the sponge ($n$=15); C: Nesting inside of the sponge rolled directly using silk ($n$=1). D: Nesting in the space between the edge of the sponge and the dome surface created by lifting the sponge vertically upward to a position 0.5 cm from the top of the dome surface with silk ($n$=8). E: Nesting in the angle between the vertical surface of sponge and dome surface created by lifting the sponge vertically upward to and securing to the dome surface with silk ($n$=3). F: Nesting in the interlayer between the horizontal surface of sponge and dome surface created by lifting the sponge horizontally upward with silk ($n$=3). G: Nesting in the vertical cylinder-shaped sponge cavity created by lifting the sponge vertically to the dome surface, then half-rolling the sponge to create a vertical cylinder with a crevice which was sealed with silk ($n$=1).

*P*-values.

Second, we examined the variation in nest shape and size across different conditions by comparing nest shape parameters among the four conditions. We used a linear mixed-effects model (LMM) to analyse the length, width, height, and vertically projected area of the nest cell, as well as the calculated volume of the nest cell, separately. Each LMM included condition as a fixed effect and individual ID and family ID as random effects to account for potential non-independence among repeated measures. For the vertically projected area of the nest frame, diagnostic checks on the residuals of the initial LMM revealed significant deviations from normality; therefore, we analysed this parameter using ART ANOVA followed by pairwise comparisons with "Tukey" adjustment for *P*-values.

**Experiment 2: Breeding nest construction using "out-of-reach" sponge**: To test whether and how *T. maxillosus* females could incorporate an "out-of-reach" sponge into nest construction, we analysed the daily records of the nesting processes according to whether the sponge was used or not and, if used, how it was used and how long the spider spent on nesting. We also compared the nesting duration between sponge-using and non-sponge-using spiders with the Mann–Whitney test.

All schematic figures of the experimental design and breeding nest construction processes were illustrated in PowerPoint 2019. All data visualisations and analyses were performed in R v.4.3.2 through RStudio v.2023.9.1.494 (Posit Team, 2023; R Core Team, 2023). The package ggplot2 (Gómez-Rubio, 2017) was used for data visualisation. Mann–Whitney tests were conducted with the "wilcox.test" function from the built-in package stats (R Core Team, 2023). ART ANOVA was conducted with the "art" function and multiple comparisons were conducted with the "art.con" function in the package ARTool (Wobbrock et al., 2011). LMMs were fitted using the "lmer" function in the package lme4 (Bates et al., 2015).

## RESULTS

### Breeding nest construction under challenging conditions

In the control condition, 53 out of the 63 spiders constructed nests in tubes, with two distinct types of frame silk structure (Figure 1A; Supplementary Figure S4A, B), while the remaining ten spiders constructed nests in internal corners of the boxes (Figure 1B; Supplementary Figure S4C–E).

In Challenge 1, all 46 spiders constructed nests in internal box corners (Figure 1B). Specifically, 35 individuals constructed "I"-shaped nests (two entrances at opposite ends of the nest cell) in two-sided angles (Figure 1B; Supplementary Figure S4C), and the other eleven spiders constructed "L"-shaped (two perpendicularly offset entrances at opposite ends of the nest cell) or "T"-shaped (three mutually perpendicular entrances) nests in three-sided corners (Figure 1B; Supplementary Figure S4D, E). These results suggest that *T. maxillosus* females prefer nesting in angles and corners rather than on the flat surfaces of the box, and the variable nest structures reflect the spiders' behavioural flexibility in breeding nest construction.

In Challenge 2, spiders were reared in transparent trapezoidal cylindrical boxes. Results showed that 24 out of the 43 spiders constructed nests using the artificial leaves (Figure 1C; Supplementary Figure S4F, G), while the remaining nineteen individuals constructed nests in container internal angles. These nesting strategies reflect that the spiders can construct nests in the lab condition using only silk, while still being able to incorporate artificial materials in the same manner observed under field conditions, further revealing their behavioural flexibility in nest construction.

In Challenge 3, two spiders failed to build a nest, while the remaining 36 individuals solved the nesting tasks in a novel way. Specifically, the spiders first explored the hemisphere, chose an area, and stretched long frame silk filaments along its inner margin to create a flat layer (Figure 3A), then built the nest within this pre-formed space between the flat silk layer and the hemisphere (Figures 1D, 3B–D; Supplementary Figure S4H, I).

In terms of time allocation for nest construction (Supplementary Figure S5; Supplementary Table S2), control females began building after a time delay (latency: 8.4±7.8 h, $n$=23) and finalised the nest within one day, reflecting the urgent need for nest construction after mating. In the hemisphere treatment, however, they postponed the onset by an additional 10 h (latency: 18.7±17.1 h, $n$=25; ART-ANOVA: $t$.ratio=4.26, $P$<0.001). This extended delay, followed by an abrupt, continuous bout of silk deposition, is consistent with prolonged spatial assessment and prospective planning prior to an insight-like resolution. Once initiated, the total nest construction lasted 20 h longer than in the control (Challenge 3: 30.9±26.4 h, $n$=25; Control: 10.8±7.0 h, $n$=23; $t$.ratio=5.11, $P$<0.001), further underscoring the elevated difficulty of creating a nest within a hemisphere.

Moreover, nine out of the 25 females failed to complete a nest during their first attempt in the hemisphere; each abandoned the initial nest prototype and began constructing a new nest, and all successfully completed nests on the second attempt. This rapid abandonment–restart process indicates that the spiders recognised structural inadequacy and intentionally adjusted their behaviour. The other 16 spiders successfully built their nests on the first attempt, indicating effective advance planning of nest construction. These results further suggest that the female spiders need to 1) assess the site and size of the nest prior to starting nesting. For example, the spiders must have the capacity to evaluate the silk layer size, as the nest needs a certain height; the frame silk layer cannot be too large (although nest completion is still possible, it would waste precious silk, which is energetically and physiologically costly (Tanaka, 1989)) nor too small (insufficient distance between the hemisphere and the silk layer for spiders to enter and build nests); 2) understand relationships among objects (nest cell, hemisphere, and the layer); and 3) plan the sequential steps of the process. These involve gathering information and evaluating essential components of the situation. Therefore, the spiders need to have the ability to plan the entire nesting process. The capacity for planning can be considered a mental action that has causal mental antecedents (Kaufmann, 2015), which has often been associated with innovative problem-solving (Manrique et al., 2013; Reader & Laland, 2003).

The variability in nest sizes and shapes suggests that *T. maxillosus* females' nesting solutions were unlikely products of innate behaviour (Figure 4). Specifically, although the spiders achieved the same volume of the breeding nest cells under all three challenging conditions (Challenge 1: 2.1±0.5 $cm^3$, $n$=21; Challenge 2: 2.4±0.9 $cm^3$, $n$=19; Challenge 3: 2.0±0.9 $cm^3$, $n$=27) (Figure 4F; Supplementary Table S3), their nest cells

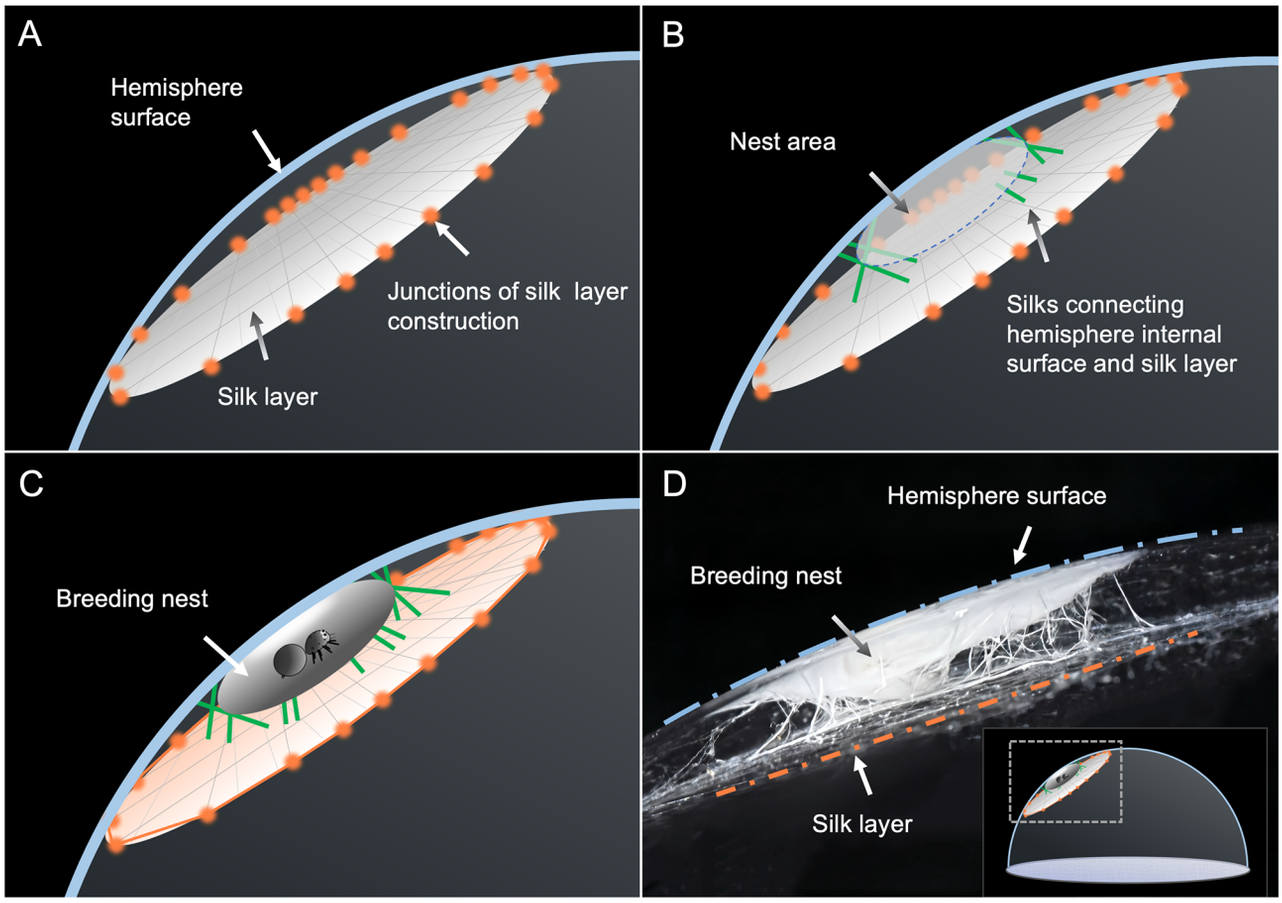


**Figure 3 Scheme of breeding nest construction process in Challenge 3**

A female spider constructed a nest following the sequence: A: Creating a silk layer with long frame silk filaments (mean±SD: 15.9±15.4 cm, *n*=16; from the two longest silk filaments in each of eight randomly selected nests); B: Connecting the silk layer to the dome surface to create a nesting space; C: Constructing the nest cell in the middle of the space; D: Lateral view of a completed nest within the hemisphere. Photos by Yi-Rong Wang.

showed notable differences in shape, and the nest frames exhibited condition-specific characteristics (Figure 4A–E; Supplementary Tables S3, S4). For example, in Challenge 3, the nest heights were significantly lower than those in other experimental conditions (Challenge 1: 0.75±0.11 cm, *n*=21; Challenge 2: 0.81±0.16 cm, *n*=19; Challenge 3: 0.58±0.10 cm, *n*=27) (Figure 4C; Supplementary Table S4), but the spiders increased their nest vertically projected areas (Challenge 1: 3.99±0.66 cm$^2$, *n*=21; Challenge 2: 3.74±1.17 cm$^2$, *n*=19; Challenge 3: 4.75±1.28 cm$^2$, *n*=27) (Figure 4D; Supplementary Table S3) by extending the nest width (Challenge 1: 1.62±0.21 cm, *n*=21; Challenge 2: 1.51±0.36 cm, *n*=19; Challenge 3: 1.87±0.36 cm, *n*=27) (Figure 4B; Supplementary Table S4). This nest-shape adjustment may reflect the spiders' planning ability: in all three challenges, they reduced the height of the nest cell to save silk (as discussed above), yet instead of accepting a smaller nest, they increased its width; thus, they enlarged the nest area and maintained a nest-cell volume equivalent to that achieved under the other challenges (Supplementary Tables S3, S4). The above experiments revealed that *T. maxillosus* females exhibited behavioural flexibility and innovation in the nesting task.

**Breeding nest construction using "out-of-reach" sponge**

The results showed that, of the 33 *T. maxillosus* females tested, two did not construct nests, and 15 constructed nests without the sponge (Figure 2B; Supplementary Figure S3B). However, the remaining 16 successfully incorporated the sponges into their nests (Figure 2C–G; Supplementary Figure S3C–G). We excluded one individual from the analysis because it directly used silk to roll the sponge into a barrel-shaped cylinder, resembling the typical leaf-rolling behaviour observed in the field (Figure 2C; Supplementary Figure S3C).

The remaining 15 sponge-using spiders exhibited four different strategies to create nesting microenvironments: a) using the edge of the sponge (*n*=8), where the sponge was lifted vertically by 1.5 cm with silk and positioned 0.5 cm from the top of the dome surface, and the spiders constructed nests in the gap between the sponge edge and the dome surface (Figure 2D; Supplementary Figure S3D); b) using the surface of the sponge vertically (*n*=3), where the sponge was lifted 2.0 cm vertically upward and secured to the dome surface with silk, creating an angle between the vertical face of the sponge and the dome surface; the spiders then constructed their nests within this corner, analogous to constructing inside the two-sided angle of an empty box (Figure 2E; Supplementary Figure S3E); c) using the surface of the sponge horizontally (*n*=3), where the spider lifted the sponge upward and, with silk, fixed it in a horizontal position, then constructed nests in the interlayer between the sponge and the dome surface—this procedure was similar to that used in Challenge 3, except that the original silk layer was replaced by the sponge, fully concealing the nest while simultaneously conserving silk (Figure 2F; Supplementary Figure S3F); and d) using the

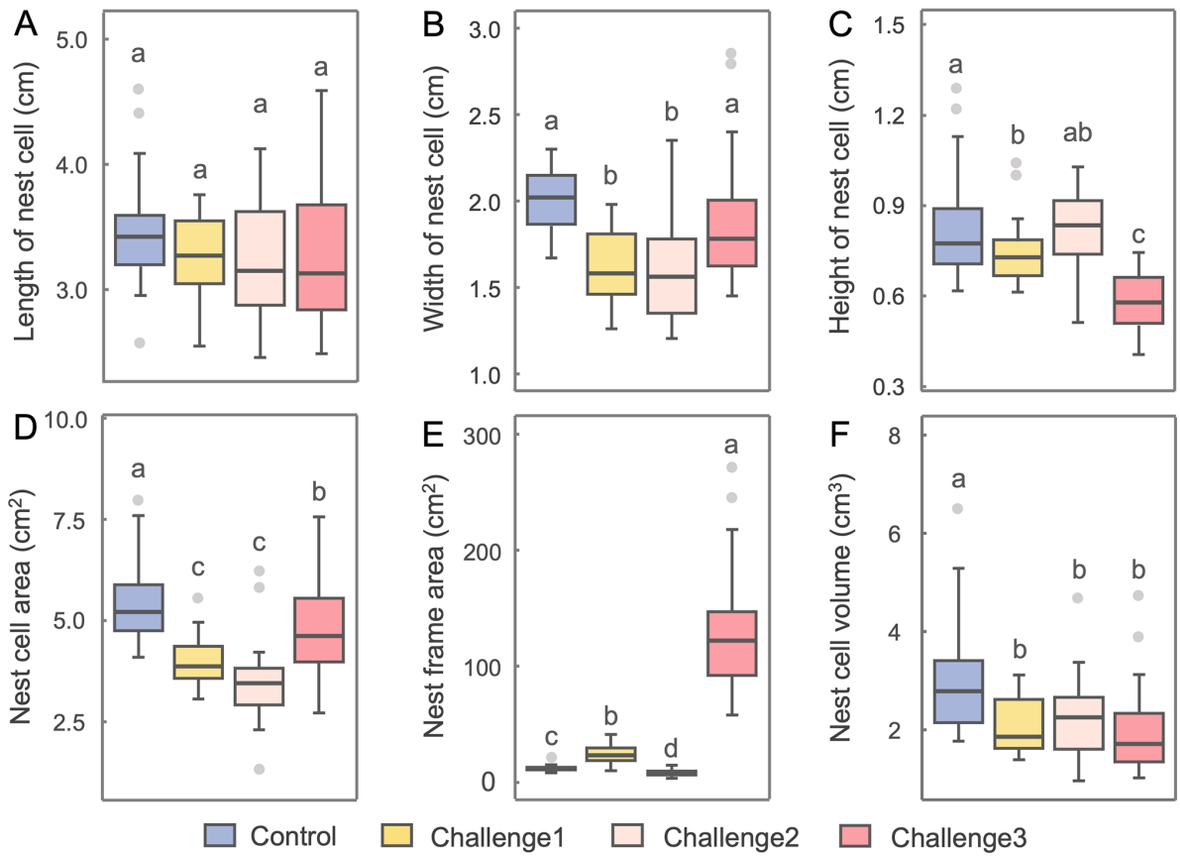


**Figure 4 Comparisons of breeding nest size and shape among Control and three challenging conditions**

A: Nest cell length. B: Nest cell width. C: Nest cell height. D: Vertically projected area of nest cell. E: Vertically projected area of nest frame. F: Nest cell volume. Note: Different lowercase letters in subfigures indicate significant intergroup differences ($P$<0.05, Dunn's multiple comparison test); identical letters indicate no significant difference.

curved surface of the sponge vertically ($n$=1), where the spider first lifted the sponge vertically to the dome surface, then half-rolled the sponge to create a vertical cylinder with a crevice that was sealed with silk, and finally constructed the nest inside the resulting sponge cavity (Figures 2G, 5; Supplementary Figure S3G). This method resembles the tube-nest construction observed under breeding conditions, with two key differences: first, the spider must create the tubular structure itself, incorporating its own silk to enlarge the inner diameter; second, it firmly fixes one end of the tube to the dome surface with silk, simultaneously stabilising the nest and providing ample space and concealment.

During this process, the spiders not only completed a multi-step task but also used the material to create a more suitable microenvironment (gaps, corners, planes, or tubular structures) for nesting under unfavourable conditions. Importantly, sponge use did not prolong construction time relative to nests built without sponges (sponge-using: 3.0 (median), 1.0–7.0 (IQR) days, $n$=15; non-sponge-using: 3.0, 2.0–4.0 days, $n$=15; Mann-Whitney test: $U$=106, $P$=0.801). This indicates that *T. maxillosus* may achieve high-quality nests (enhanced crypsis and stability) without incurring additional costs, which can be directly converted into an adaptive advantage when encountering adverse conditions or colonising new habitats. In addition, the variation observed among *T. maxillosus* females in their use of sponges may be attributed to differences in cognitive abilities or distinct personalities with different responses (Carere & Locurto, 2011; Reader & Laland, 2003).

## DISCUSSION

This study indicates that female *T. maxillosus* exhibited all the key components of typical innovation: 1) behavioural flexibility: in challenges 1 and 2, the spiders altered nest shape and structure in different locations; 2) exploration and insight: in challenge 3, prolonged latency suggests the spiders may need more time to explore the hemisphere and assess the nest-building process. After that, they abruptly initiated construction at one discrete time point, indicating that they achieved an "insight" that generated a viable nest-building plan and thus produced an innovative solution to the challenge. This all-or-none switching pattern is interpreted as cognitive insight—a necessary step in the innovation process (Reader & Laland, 2003); 3) action planning: Bratman (2013) contends that the capacity for action planning depends on two elements: temporally extended intentional agency and self-governance. In Challenge 3, spiders significantly prolonged nest-building time within the hemisphere, adjusted the length of the silk while conserving silk to maintain the height of the layer, and completed the nest according to the self-generated architectural plan. In other words, they realised that what they were doing served a later goal and was neither an isolated nor a random act. The same planning structure is evident in sponge use: earlier moves must set the stage for later ones so that the entire sequence converges on the objective; 4) multi-step problem-solving ability: female *T. maxillosus* could incorporate otherwise out-of-reach sponges through string-pulling into the nest construction sequence. These findings suggest that female *T. maxillosus* possess typical innovative

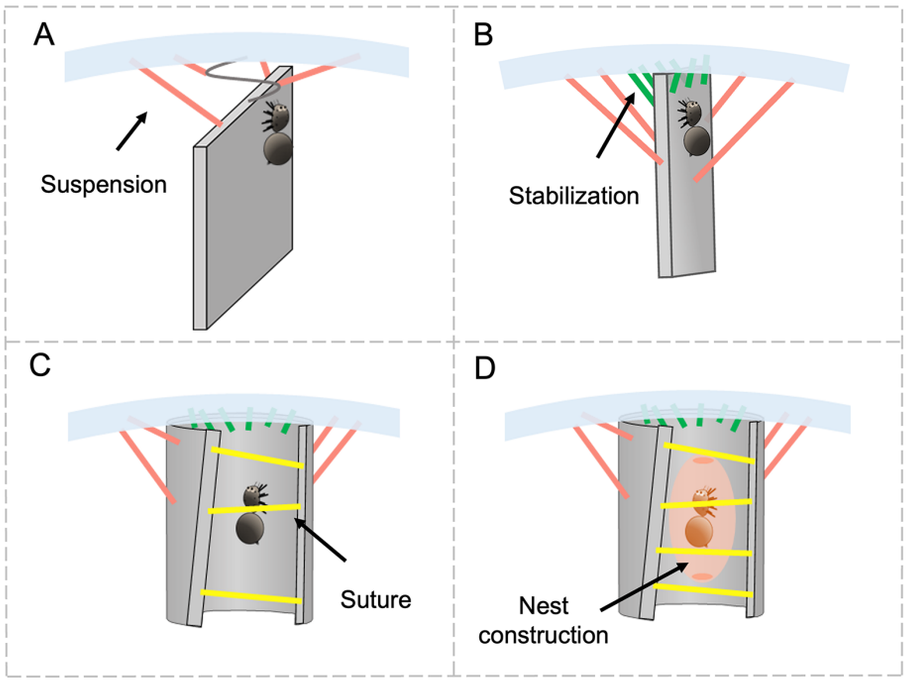


**Figure 5 Scheme of breeding nest construction process in the vertical cylinder-shaped sponge cavity**

A female spider constructed the nest following the sequence: A and B, Lifting the sponge vertically upward and fixing it to the dome surface; C: Half-rolling the sponge and sealing the crevice with silk; D: Constructing the breeding nest inside the cavity.

ability in nest construction.

What evolutionary factors enabled female *T. maxillosus* to evolve the capacity for typical innovation? Comparisons with traditional typical innovators suggest that the sociality of *T. maxillosus* might be the key driver. Previously, it was believed that social living, relatively longer lifespans, and larger numbers of neurons have been identified as the three core characteristics associated with the evolution of superior cognition (Kaufman & Kaufman, 2015; Street et al., 2017). Among these, the social lifestyle involving long-term mother–offspring interactions is the only common feature between *T. maxillosus* and vertebrate typical innovators, such as elephants. *Toxeus maxillosus* females spend almost their entire lives in social groups—they remain with their mothers and siblings in the natal nest until adulthood, then construct a breeding nest to complete their own reproduction, during which they care for the spiderlings until adulthood (Chen et al., 2018). Living in social environments requires sophisticated intelligence to cope with frequent conspecific recognition, competition, cooperation, and social status evaluation. These social interactions are considered to favour the evolution of cognitive capacities in social animals (van Schaik & Pradhan, 2003). Additionally, unlike some eusocial invertebrates, such as honeybees (Johnson, 2010) and ants (Robinson, 1992), which have evolved highly specialised individuals to perform specific tasks within groups, individuals of subsocial or social species must have the ability to perform a much wider range of tasks, such as foraging, nest construction, mate selection, offspring nursing, and skill transfer (Royle et al., 2014). Furthermore, social animals also collaborate more frequently than solitary animals, and their cooperation is general and flexible. These demands require individuals to possess sophisticated cognitive abilities to make decisions and find appropriate solutions in complex social environments while facing frequent unpredictable challenges. The conclusion that prolonged maternal-care sociality might be a key driver of typical innovation is a central thesis of the present paper; however, its validity awaits further evaluation through phylogenetic analysis.

Arthropods, especially some eusocial insects, exhibit a sophisticated behavioural repertoire despite their miniature brains, such as pessimistic cognitive biases (Bateson et al., 2011), social signal learning (Dong et al., 2023), concept learning (Giurfa et al., 2001), and learning about object affordance (Poissonnier et al., 2023). A colony of a eusocial species has often been seen as a superorganism, as tasks such as the honeybees' comb construction can be accomplished with flexibility through the collective efforts of hundreds of individuals (Gallo & Chittka, 2018; Hu, 2026). However, how these individuals make collective decisions remains mysterious. At the individual level, the diversity of comb morphology has been regarded as the product of the accumulation of instinctive behaviours following a repertoire of innate rules (Gallo & Chittka, 2021). The learning-based problem-solving (Loukola et al., 2017) and innovative skill accumulation (Bridges et al., 2024) in the bumblebee *B. terrestris*, as well as the hunting route planning in the jumping spider *Portia labiata* (Tarsitano, 2006), exhibit impressive intelligence at the individual level. These species exhibit either a low level of eusociality, characterised by relatively smaller colony sizes and lower labour division, as seen in bumblebees, or a subsocial lifestyle, where mothers care for hatchlings until they achieve nutritional independence, as observed in most jumping spiders. Individuals of subsocial species must cope with a greater variety of complex tasks than individuals of highly eusocial species. The overwhelming majority of arthropods adopt either solitary or eusocial lifestyles, which may explain why few species have evolved superior cognitive capacity at the individual level. For example, bumblebees have demonstrated problem-solving abilities in tasks such as string-pulling (Loukola et al., 2017) and social learning (Bridges et al., 2024). Similarly, ants

exhibit collective problem-solving in geometric puzzles (Dreyer et al., 2025). These studies, along with our findings, suggest that arthropods possess a range of cognitive abilities that can be harnessed under novel conditions.

We suggest that the similarity in social lifestyle between *T. maxillosus* and vertebrate innovators may be a core indicator of arthropod intelligence as revealed in this study. This hypothesis could be tested in additional arthropod species that exhibit a high level of subsociality. Yet, as intelligence may manifest in domain-specific ways across species, such as spatial memory in elephants (Hope et al., 2025; Polansky et al., 2015), causal reasoning in corvids (Taylor et al., 2009), and symbolic communication in parrots (Pepperberg, 2012), the precise domain in which subsocial arthropods express their cognitive signature remains to be uncovered. Furthermore, the innovative performance of *T. maxillosus* in breeding nest construction provides an opportunity to explore how its cognitive capacity is achieved despite a relatively short lifespan of approximately 10 months (Jiang et al., 2024) and a constrained brain size (the spiders' total body mass is ca. 0.025 g) (Chen et al., 2018). Finally, based on our experience, we expect *T. maxillosus*' innovative propensity to be heritable, which deserves further investigation.

This study has two potential limitations. First, the data were collected in two experimental rounds; we did not record some details in the first experimental round, such as the detailed duration of each step during nest construction and nest morphometric measurements (e.g., length, width, and height of the nest cell), which led to inconsistencies in sample sizes among analyses. Second, we were unable to directly and precisely measure the nest cell volume due to methodological constraints and thus approximated it using ellipsoids to ensure consistency in measurements and statistical methods among different conditions. Overall, our results show that *T. maxillosus* females are capable of individual-level behavioural flexibility and innovation in problem solving, and we hypothesise that maternal care-based sociality may be a critical evolutionary driver of individual innovation.

## DATA AVAILABILITY

All the original data used in analyses and figures have been deposited in the Science Data Bank (https://doi.org/10.57760/sciencedb.zrdc.0000y).

## COMPETING INTERESTS

The authors declare that they have no competing interests.

## AUTHORS' CONTRIBUTIONS

Conceptualisation, Z.C., Y.R.W., and X.J.; methodology, all authors; investigation, Y.R.W. and C.J.; visualisation, Y.R.W., C.J., Z.C. and J.X.L.; funding acquisition, Z.C.; project administration, Z.C. and X.J.; supervision, Z.C. and J.X.L.; writing – original draft, Z.C., Y.R.W., C.J. and J.X.L.; writing – review & editing, all authors. All authors read and approved the final version of the manuscript.

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