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An arboreal spider protects its offspring by diving into the water of tank bromeliads

Une araignée arboricole utilise les réservoirs d'eau des broméliacées pour se protéger et protéger son cocon

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A R T I C L E I N F O

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A B S T R A C T

Cupiennius salei (Ctenidae) individuals frequently live in association with tank bromeliads, including *Aechmea bracteata*, in Quintana Roo (Mexico). Whereas *C. salei* females without egg sacs hunt over their entire host plant, females carrying egg sacs settle above the *A. bracteata* reservoirs they have partially sealed with silk. There they avoid predators that use sight to detect their prey, as is known for many bird species. Furthermore, if a danger is more acute, these females dive with their egg sacs into the bromeliad reservoir. An experiment showed that this is not the case for males or females without egg sacs. In addition to the likely abundance of prey found therein, the potential of diving into the tank to protect offspring may explain the close association of this spider with bromeliads. These results show that, although arboreal, *C. salei* evolved a protective behavior using the water of tank bromeliads to protect offspring.

Mots clés :
Aechmea bracteata
Cupiennius salei
Cocons
Eau utilisée dans un comportement protecteur

R É S U M É

L'araignée *Cupiennius salei* (Ctenidae) vit souvent en association avec la broméliacée à réservoir *Aechmea bracteata*. Dans le Quintana Roo (Mexique), les femelles qui transportent un cocon s'installent au-dessus d'un réservoir d'*A. bracteata* qu'elles obstruent partiellement de voiles de soie pour se camoufler des prédateurs. En présence de vibrations importantes et répétées, ces femelles plongent avec leur cocon dans l'eau du réservoir. Notre étude montre que les autres adultes (mâles et femelles sans cocon) n'utilisent pas les réservoirs d'eau. Ainsi, en plus de l'abondance de proies, la possibilité de

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pouvoir plonger pour protéger la descendance pourrait expliquer l'association entre cette espèce d'araignée et les broméliacées. Nos expériences montrent que les femelles porteuses d'un cocon manifestent une stratégie de protection vis-à-vis des cocons et d'elles-mêmes en s'immergeant durant 30, voire 90 minutes.

1. Introduction

Although most spider species are terrestrial, a gradient in their relationship with the aquatic environment does exist. The iconic example is seen in *Argyroneta aquatica* (Cybaeidae), whose individuals live almost entirely under water thanks to the ability of hydrophobic hairs to retain a bubble of air. Furthermore, they build silk structures that, like diving bells, retain air and permit them to remain submerged and even to detect prey that touch this silk net [1,2]. The bubble of air retained by the hydrophobic hairs or the silk of the diving bell allows respiration as gas exchanges with the surrounding water occur through differences in the partial pressure of oxygen and carbon dioxide [1,3].

Some other spider species hunt aquatic organisms, including insects, tadpoles, frogs, and fish on the surface of the water, and are thus called semi-aquatic spiders. This is the case for different species of the Pisauridae and Ctenidae whose hunting individuals stay in contact with a terrestrial substrate when hunting [4,5]. Diving was observed in the genus *Pirata* (Lycosidae) when, occasionally, individuals hunt aquatic prey such as larval mayflies and isopods [6]. Thanks to their hydrophobic hairs, semi-aquatic spiders most generally dive as a protective strategy, so that *Pirata* spp. can remain underwater for 24 h if disturbed [6] and *Dolomedes triton* (Pisauridae) for 90 min [7], whereas *Ancylometes rufus* (Ctenidae) individuals dive to escape predators, but the duration of the time spent underwater is not known [4].

As noted for certain other webless, arboreal spider species [8–10], *Cupiennius salei* (Ctenidae) individuals are frequently associated with epiphytic tank bromeliads that provide them with a suitable habitat [11]. In Quintana Roo, Mexico, the host tank bromeliad is *Aechmea bracteata* that has groups of shoots at different ontogenetic stages, each forming a rosette with numerous water reservoirs or phytotelmata [12]. Tank bromeliads shelter various terrestrial and aquatic organisms [12–15]; among them, emerging winged insects are potential prey for spiders [5].

Based on preliminary field observations, we aimed in this study to verify if bromeliad reservoirs serve as an aquatic refuge for *C. salei* individuals.

2. Material and methods

This study was conducted in an inundated Neotropical forest (Quintana Roo, Mexico; 18.426725° N; 88.804360° W; 120 meters a.s.l.). The identification of the spiders was based on voucher specimens deposited in the collection of the "Museo de Zoología" in Ecosur, Chetumal, Mexico.

Cupiennius salei, called the 'wandering tiger spider' due to dark stripes on its body and legs, originates from Central America. This is an arboreal, webless species with large individuals (10 cm legspan and 3.5 cm in body length for adult females, males measure up to 2.5 cm in length) [16]. Individuals are nocturnal, ambush predators that detect prey through the perception of vibrations and rely on a neurotoxic venom to paralyze prey [17–20].

Adult males and females without egg sacs as well as juveniles were observed wandering on *A. bracteata* during this study. Females with egg sacs build a thick coat of silk that partially seals one reservoir (height: 6–12 cm; diameter: 5–12 cm; volume of water: 110–250 ml) of the host bromeliad and stay behind this coat, carrying the egg sac behind their abdomen, ≈5 cm above the water (Fig. 1) [11].

We tested the reactions of adult males and females with or without an egg sac by having one experimenter rapidly, but lightly tap a 20-cm-long wooden stick on the plant with a force corresponding to knocking on a door (15 cm from the spiders; 5 times during 2 s repeated every 10 s, until the spiders reacted by fleeing). We noted the behavior of these male and female spiders (see Table 1). For females carrying an egg sac, prior to this experiment, we gently opened the coat of silk to observe their behavior and, after 1 min, as they seemed unalarmed, we used the same procedure as for the males and other females. This last experiment was conducted three times separated by ∼2 h to permit the spiders to calm down.

Two females that had remained underwater during more than 30 min with their egg sac were collected, taken to the laboratory and installed in a terrarium with a shoot of *A. bracteata* to verify if they and their brood survived this long immersion.

3. Results and discussion

In the experimental situation, all *C. salei* males and females devoid of an egg sac moved behind the shoot to hide. When the tapping continued, they fled the host bromeliad to seek another hiding place (see Table 1 for the number of observations). In two cases, they raised their forelegs and opened their chelicerae before fleeing.

When confronted with the disturbances, all six females with egg sacs first opened their chelicerae and raised their forelegs in a posture of intimidation. When disturbed again, they changed the position of their egg sacs, initially situated behind their body, grasping them with their forelegs to place them in front of the cephalothorax (Fig. 2A), and dived into the water with the egg sac (Fig. 2B and C; Table 1). All six females stayed underwater from 30 to 90 min. Later on, after these females left the water of the tank of the bromeliads and returned to their initial position, the same experiment was conducted, resulting in the same result. When this experiment was conducted for

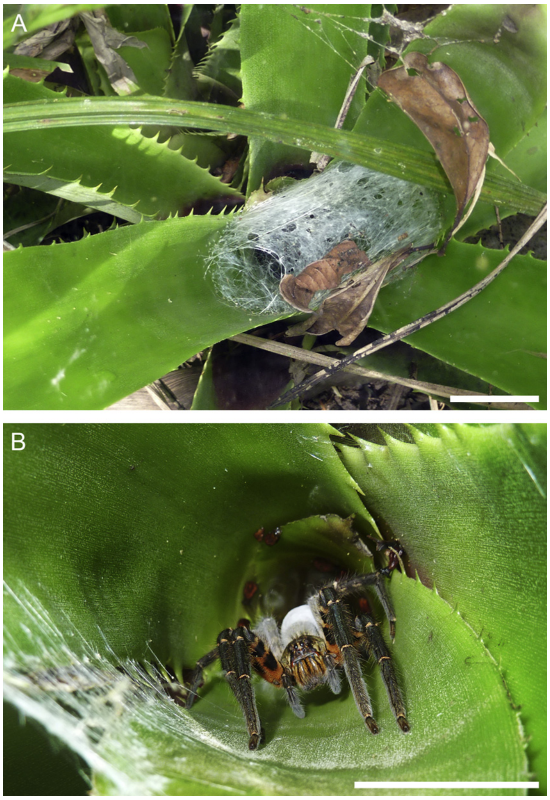

Fig. 1. Shoot of *Aechmea bracteata* with the coat of silk (A), the spider and behind, its egg sac (B). The white scales represent 5 cm.

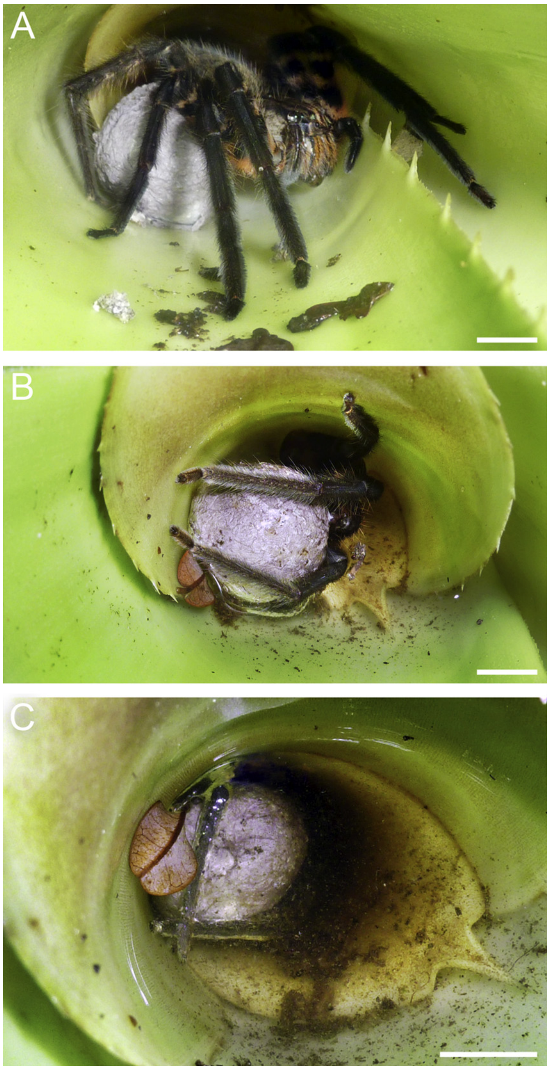

Fig. 2. Behavior of the spiders when carrying eggs. Moving the egg sacs, initially situated behind the spider, in front of the cephalothorax (A). Holding the egg sac, using the first legs (B), and diving into the water (C). The white scales represent 1 cm.

the third time, the female spiders quickly jumped out of the tank carrying their egg sacs, moved behind the shoot of the host bromeliad and jumped onto another plant as did spiders without egg sacs.

The two females bred in the laboratory continued to carry their egg sacs; after 4 and 5 days, respectively, spiderlings emerged. They remained on the external part of the bromeliad, the female always remaining close to them in a defensive posture. Therefore, as for the diving bells of *Argyroneta*, the silk of the egg sacs likely retains air through surface tension strengths.

Although terrestrial (i.e. neither aquatic nor semi-aquatic), *C. salei* females have adapted to diving, but, because in this experiment they dove only when they carried egg sacs, this behavior is specifically related to their fitness (i.e. offspring protection). Indeed, wandering Ctenidae are highly susceptible to being preyed upon by birds in forest canopies and females are more attractive to visual hunting predators when carrying an egg sac whose color contrasts with the spider body [21].

The previous known cases of spiders able to dive correspond to the aquatic *Argyroneta* that use a diving bell and semi-aquatic spiders that dive to avoid predation (and only occasionally to hunt) [1,4,6,7]. The present study adds the case of terrestrial female spiders diving with their egg

Table 1
Behavior of *Cupiennius salei* individuals noted on *Aechmea bracteata*. Comparisons of their reactions when left alone or when disturbed (see text). Statistical comparison of the reaction of disturbed females with or without an egg sac; Fisher's exact-test (Past software): $P = 4.34 \cdot 10^{-6}$.

Cupiennius salei individuals noted on tank bromeliads	Natural situation		After being disturbed	
	Hunt	Build a web above a well	Escape	Dive
Juveniles	15	0	–	–
Adult males	15	0	15	0
Adult females	20	0	20	0
Adult females with egg sacs	0	6	0	6

sacs to protect their offspring from predators thanks to their association with tank bromeliads. Because using the reservoirs of a tank bromeliad allows *C. salei* females to protect their offspring beyond the limits of their physical capacities (e.g., chelicera, legs), this use can be considered an 'extended phenotype' [22,23].

In conclusion, the relationship between *C. salei* and tank bromeliads is much more complex than previously known, the benefit for the spider being related both to prey availability [5] and its fitness (this study). Indeed, *C. salei* females bearing egg sacs protect their offspring through camouflage by purposely constructing a web above a reservoir of a tank bromeliad and escape threats by diving into that reservoir.

Disclosure of interest

The authors declare that they have no competing interest.

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