Fast acrobatic maneuvers enable arboreal spiders to hunt dangerous prey

Alfonso Aceves-Aparicio[a,b,c,1] [ID], Ajay Narendra[a], Donald James McLean[a] [ID], Elizabeth C. Lowe[a], Marcelo Christian[b] [ID], Jonas O. Wolff[a,d] [ID], Jutta M. Schneider[b] [ID], and Marie E. Herberstein[a] [ID]

Spiders, the most specious taxon of predators, have evolved an astounding range of predatory strategies, including group hunting, specialized silk traps, pheromone-loaded bolas, and aggressive mimicry. Spiders that hunt prey defended with behavioral, mechanical, or chemical means are under additional selection pressure to avoid injury and death. Ants are considered dangerous because they can harm or kill their predators, but some groups of spiders, such as the Theridiidae, have a very high diversification of ant-hunting species and strategies [J. Liu et al., *Mol. Phylogenet. Evol.* 94, 658–675 (2016)]. Here, we provide detailed behavioral analyses of the highly acrobatic Australian ant-slayer spider, *Euryopis umbilicata* (Theridiidae), that captures much larger and defended *Camponotus* ants on vertical tree trunks. The hunting sequence consists of ritualized steps performed within split seconds, resulting in an exceptionally high prey capture success rate.

diet | coevolution | silk | Australia

Euryopis umbilicata hide under the bark of *Eucalyptus* trees during the day and emerge at evening twilight. With no capture web, they adopt a downward-facing position, flush against the trunk surface waiting for prey (Fig. 1*C*). The hunting sequence starts with a sit-and-wait period, followed by an acrobatic strike to the prey and successful capture by immobilizing the prey. As they settle, the spiders attach a silk line (dragline) to the tree trunk surface. Then, they use a continuous line of adhesive viscid silk (Fig. 1 *G–I* and Movies S1 and S2) to strike and immobilize their prey, the crepuscular banded sugar ants, *Camponotus consobrinus*, that also forage on *Eucalyptus* trees (1). We surveyed multiple trees and found up to nine spiders actively hunting on a single tree. We collected all prey items captured by spiders and found that the spiders almost exclusively captured ants (99.45%, *n* = 181/182), predominantly a single species, *C. consobrinus* (90.60%, *n* = 164/181). Such extreme prey specialization is unusual, since predators typically feed on diverse prey types (2). Moreover, most predators feed on relatively smaller prey. However, the ants measured approximately twice the body length of the spiders, but with similar mass (*SI Appendix*). Ants are considered dangerous, and only ~0.3% of known spider species feed on ants (3). Myrmecophagy is rare among most other taxa too, likely because ants have strong mandibles, the ability to spray formic acid, and strength in numbers (4). However, the spider family Theridiidae likely diversified together with ants during the Cretaceous (5), resulting in relatively numerous myrmecophagous species and hunting strategies as seen in the genus *Euryopis* (6, 7).

The analysis of the spider's capture strategy started when the spider first moved from the sit-and-wait position. A successful capture event involved two distinct phases. The first phase was an acrobatic strike during which the spider tumbled from its resting hunting position over the ant, irrespective of which direction the ant was approaching the spider from (ø = 306.17° ± 11.76, *r* = 0.101, *n* = 38, Rayleigh test, Z = 0.385, *P* = 0.68; Fig. 1*D*). The sudden initiation of attack was triggered either by contact (*n* = 55) or when prey was at close range (*n* = 5), possibly triggered by ants contacting silk lines. During these tumbles, the spider used its hind legs to pull viscid silk (Fig. 1*G*) from its spinnerets and attached it to the ant, preventing its escape (Fig. 1 *A* and *B*, *1–3*). The spider then dropped off the tree trunk and was secured by the viscid silk line attached to both the ant and the trunk. During this acrobatic choreography, the spider reached a maximum speed of 25.47 ± 2.29 cm/s (mean ± SEM) within milliseconds (74 ± 4 ms, *n* = 22; Fig. 1 *E* and *F*). Maximum speed was independent of spider size (generalized linear model, *P* = 0.07, explained deviance 16.78%) and the direction of the attack ($R^2_{x\theta}$ = 0.12, *P* = 0.27). The acrobatic strike ended when the spider reestablished contact with the tree trunk, still holding the viscid line (Fig. 1 *A* and *B*, *4* and *5* and Movies S1 and S2).
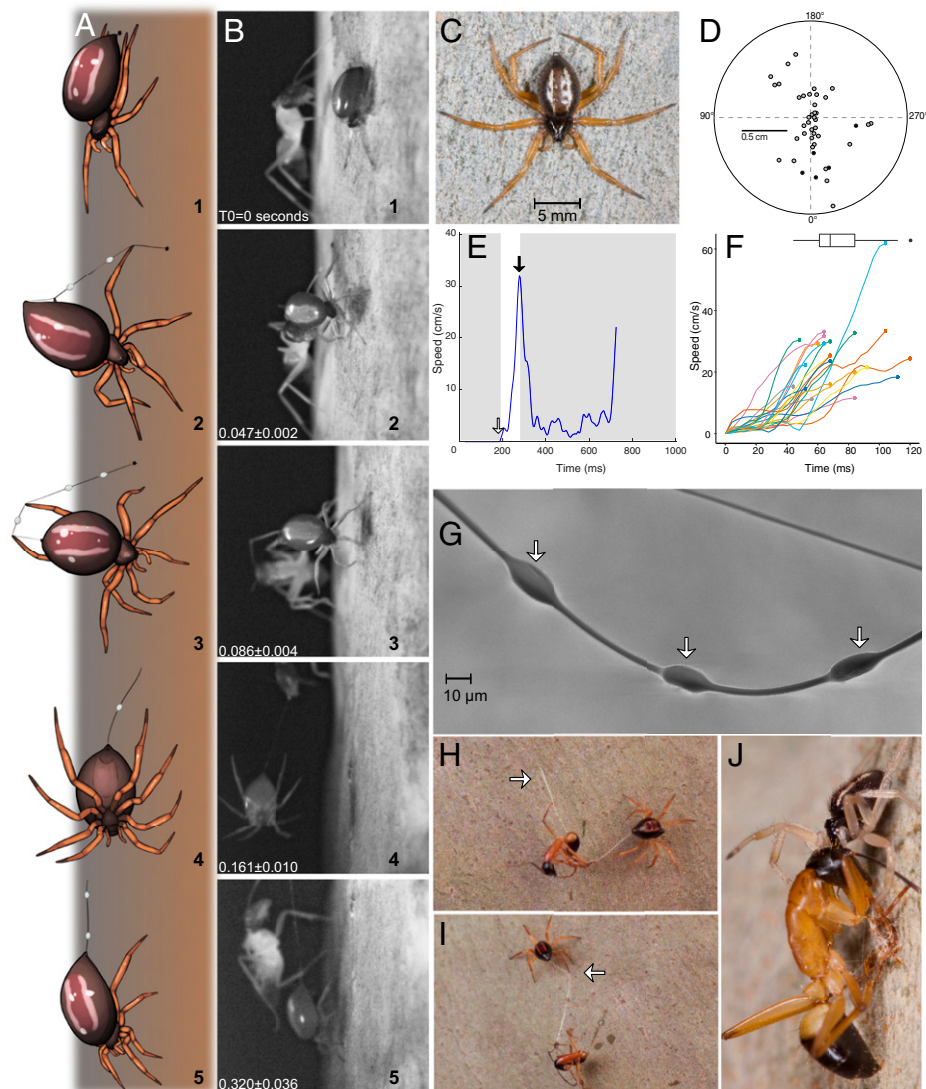
Fig. 1. Hunting choreography of the Australian ant-slayer spider, *E. umbilicata*. (*A*) Images *1–5* illustrate spider poses (prey not shown) at the five critical steps during the ant-slayers' strike (illustrations: Zoe Wild). (*B*) Images *1–5* show corresponding frames from high-speed videos: (*1*) waiting flat position, (*2*) deploying viscid silk using hind legs, (*3*) directing silk toward the potential prey, (*4*) drop-off from trunk surface, and (*5*) resettling on the trunk. Each frame displays the average elapsed time and SEM in seconds between stages (*n* = 22). (*C*) *E. umbilicata*—dorsal view of the Australian ant-slayer spider in a hunting position (photo credit: A.A.-A.). (*D*) Circular plot showing the direction and distance at which spiders attack the ants, with the center representing the spider position (0 = downward in the plane of the trunk). Successful attacks are shown in gray circles (*n* = 38), and unsuccessful attacks are shown in black circles (*n* = 5). (*E*) An example speed profile of a spider during the capture sequence (unshaded area, strike phase; white arrow, last resting position; black arrow, maximum speed reached during strike). (*F*) Individual strike profiles (normalized t starts at 0 s) of different spiders during the tumble. (*Inset*) Boxplot (5th to 95th percentile and median) of time taken from resting phase to top speed. (*G*) SEM of the adhesive droplets on the viscid silk used during captures. Arrows point to glue droplets. (*H* and *I*) Two stills from high-speed video recordings of the ant-slayer circling (clockwise) the ant (*C. consobrinus*). A line of viscid silk keeps the ant attached to the tree trunk (white arrow in *H*). The spider holds the silk line with its right hind leg (white arrow in *I*) while the other end of the silk is attached to the ant. (*J*) Image of the ant-slayer feeding on *C. consobrinus* ant.

In the second phase, the spider circled the ant, entangling it in viscid silk before biting it. It is possible the spider switched to dry silk during at this stage, as proposed by Carico (6) for *Euryopis funebris*. However, the resolution of our high-speed video does not allow us to determine this with confidence. Finally, the ant was detached from the trunk and carried away to be fed upon, often while dangling from a strand of silk (see also ref. 6). While the acrobatic strikes took less than a second, spiders spent significant time immobilizing and killing the prey during the second phase (637 ± 371 s, *n* = 22). The success of each attack was determined within the first few hundred milliseconds of the strike phase (323 ± 38 ms) when the spider tagged (i.e., contacted with sticky silk) and restrained the ant with the viscid silk. All ants that were successfully tagged during the initial acrobatic tumble (85% of all encounters, *n* = 51/60)

were captured (100%, *n* = 51/51). Upon contact, the viscid silk effectively held the ant, and the spider continued the capture into phase 2 of the attack (Fig. 1 *H–J*). The silk itself did hold the ant for a considerable amount of time, but not indefinitely—when we prevented the spider from biting the ant after tagging, the ant eventually escaped from the viscid silk (time from being tagged to dropping free, *n* = 15, mean ± SEM = 280.8 ± 31 s). Only in five instances were spider attacks unsuccessful (black circles in Fig. 1*D* and Movie S2). These typically occurred when ants fell from the trees before the viscid silk contacted their body. In one instance, the attack was unsuccessful because the ant changed its heading direction immediately after the spider initiated the attack.

Among theridiid spiders, the evolution of gum-footed silk lines and wrapping of prey with adhesive silk has likely enhanced

the access to abundant but dangerous prey such as ants (3, 5, 6, 8). Selection on traits that improve capture rates and avoid harm is predicted to be strong (9), as failure when hunting dangerous prey can potentially incur the greatest fitness cost (death). However, we never observed the ant-slayer being harmed or killed during prey capture ($n = 60$), despite the lack of a web. Most ant-eating spiders either use a web that immobilizes the ants from a safe distance (2, 3), which has evolved multiple times among spiders (10), or they cautiously approach ants from behind with substantial attack distance before attacking (e.g., the jump attack of a jumping spider). Instead, the behavioral precision of the ant-slayer's attack within hundreds of milliseconds combined with adhesive viscid silk appear to be essential for the successful retention of the ants.

Generally, ants are very abundant, with few predators, and, therefore, neutralizing the risk from hunting ants gives access to virtually unlimited prey with little competition (3). The ant-slayer is remarkable, as it almost exclusively captures a single species of ant—*C. consobrinus* at our study site. This extreme degree of prey specialization may reflect local *C. consobrinus* abundance, and/or it may be common to the genus (6). The precise evolution of this complex behavioral sequence could have resulted from the synergistic effects of ant abundance and basal predatory traits in theridiids such as sticky silk (5, 6, 8). The ant-slayer attaches its adhesive silk with a strike speed comparable to that of other non-web-building spiders such as wolf (0.05m/s to 0.3m/s) and jumping (1.5m/s) spiders that rely on moving the entire body toward prey, although not as fast as the slingshot spider (4.2 m/s) that catapults itself and its web toward approaching prey (11, 12).

Compared to other Australian ant predator specialists, the ant-slayer has an extraordinarily high prey capture success rate. For example, the feather-legged assassin bug also hunts large venomous jumper ants (*Myrmecia pilosula*) on tree trunks, but only 2.5% of their ant encounters result in successful captures (13). The ant-slayer's capture success is also high on a per encounter basis, far surpassing apex predators, such as solitary cheetahs and group hunting lions and wolves that usually succeed in less than 50% of their encounters with prey (14–16). Ant-slayers are even more impressive, as they forage solitarily and attack larger and dangerous prey (4, 9).

The evolution of specialized diets is uncommon among predators, and even less common when it involves large and dangerous prey (9). However, due to technological advances allowing for infrared high-speed videography, we have been able to describe what appears to be an almost flawless strategy to capture dangerous prey. While relatively fast and easy access to unlimited prey is the likely main benefit, the potential costs of this strategy remain elusive. Further research is needed to understand the physiological components that enable 1) the spiders to recognize particular prey types (e.g., chemosensory structures) or avoid recognition (e.g., chemical camouflage), 2) the mechanics of executing and modulating each movement within hundreds of milliseconds, and 3) the achievement of rapid and efficient viscid silk adhesion to the ant cuticle. For example, how and when does the spider adjust the position of its body or leg joints to precisely target prey, and is its silk adapted to adhere to the cuticle of ants? A detailed comparison of hunting strategies among congenerics (6) might reveal convergent strategies as well as species-specific solutions to a similar foraging niche.

Methods

Using field observations and experiments, we determine how these small arboreal spiders capture such large and defended prey. We used high-speed videography and scanning electron microscopy to characterize the spider attack and silk use during staged attack sequences in their natural habitat. We collected their preferred prey, *C. consobrinus* ants, and released them individually a few centimeters from the spiders. We filmed the acrobatic strikes at 250 frames per s (fps; $n = 38$ for assessment of strategy steps; from these, we analyzed the attack speed from sequences where the spider remained within the field of view throughout the whole strike, $n = 22$) and the entire capture sequence at 25 fps ($n = 22$) and carried out a frame-by-frame analysis of the spider movement in two dimensions (*SI Appendix*). Each ant and spider was only included once in staged encounters.

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