SUBMERSION SURVIVAL IN AERIAL WEB-WEAVING SPIDERS FROM A TROPICAL WET FOREST

INTRODUCTION AND METHODS

Previously I found that several species of temperate zone, web-weaving spiders that dwell beneath stones possess morphological and behavioral adaptations that enhance underwater survival (Rovner 1986). These spiders retain large air stores on the body surface in their dense setal coats; furthermore, they usually show minimal or no locomotor activity when submerged. Both factors adapt them for surviving rain-caused flooding. On the other hand, the aerial web-weavers I tested—*Achaearanea tepidariorum* (C. L. Koch), *Araneus marmoreus* Clerck, *Micrathena gracilis* (Walckenaer), and *Prolinyphia marginata* (C. L. Koch)—were less able to resist drowning. This may have resulted from the fact that their setal coats retained either a small ventral air store or none at all. Also, the araneids showed intense locomotor activity at the beginning of the test, which was followed by immotility very early in the test period. After removal from the water, these four species either became active only after a relatively long time or not at all, i.e., they had drowned. The high metabolic rate of araneids (Anderson 1970) may have played a role in their drowning so quickly. However, the relative size of the air store on the body surface and the level of activity were the only factors I examined.

I subsequently hypothesized that these two factors that conferred drowning resistance are sufficiently plastic within spider families as to be significantly modified by selection imposed by local conditions. I anticipated that aerial web-weaving spiders from a life zone typified by frequent, heavy rainfall (with possible local flooding) would possess greater drowning resistance than temperate deciduous forest species.

Here I tested seven species from a lowland tropical wet forest site; six were araneids and one a theridiid. Work was conducted during a 6-week stay at the Organization for Tropical Studies' La Selva station near Puerto Viejo de Sarapiqui, Heredia Province, Costa Rica (mid-November to late December, 1987). Female spiders were collected near trails in the forest—*Micrathena brevipes* (O. P. Cambridge), *Micrathena molesta* Chickering, *Micrathena schreibersi* (Perty), *Nephila clavipes* (Linn.), and *Achaearanea toeniata* (Keyserling); in the clearing surrounding the station buildings—*Argiope savignyi* Levi and *N. clavipes*; and on a footbridge over the river—*Metazygia* sp. Voucher specimens are deposited in Harvard University's Museum of Comparative Zoology.

Within a few days of capture, 10 individuals of each species were submersed one at a time for 1 h in 25°C distilled water, aerated prior to use. This occurred in a completely filled, covered, all-glass miniature aquarium of an appropriate size (27 or 70 ml) for the species being tested. (The inside bottom and back wall had a white paper liner that provided a surface to which the spider could cling). Adult *N. clavipes* were tested in a 260-ml paper cup with a plastic lid.

Each spider was anesthetized with CO_2 to facilitate placement in the water; timing began when the spider resumed movement. As pointed out by J. F. Anderson (pers. comm.) the use of CO_2 for anesthesia complicates the analysis since the gas affects respiratory processes. However, CO_2 anesthesia was the only means available to me to achieve a uniform initiation of each test. Grasping an unanesthetized spider to hold it beneath the water during placement of the lid on the aquarium could have caused overexcitement or even injury in some spiders. (An aquarium with a bottom inlet and top outlet to allow filling after placement of the spider and lid closure would prevent the need for anesthesia in future studies.)

I also wished to conduct some preliminary observations on species differences in reaction to contact with water and in buoyancy. For this purpose, several individuals of each species were placed on the surface of water contained in a plastic basin. After observing the nature of possible behaviors that would improve

Table 1.—Activity, typical behaviors, and mortality of spiders subjected to a 1-h submersion (25° C), listed in rough order of increasing likelihood of drowning after submersion. Percent of h spent in locomotion is given as $\bar{x} \pm$ SD (range); N = 10.

Species	Percent locomotion	Typical behaviors	Deaths
Micrathena molesta	3.6 ± 2.7 (0.8 − 7.8)	rapid crawl/inactive; mobile < 15 min	2/10
Metazygia sp.	6.1 ± 4.1 (0.1 − 13.2)	rapid crawl/inactive; mobile < 25 min	6/10
Achaearanea taeniata	3.6 ± 2.2 (1.4 − 8.8)	rapid crawl/inactive; mobile < 15	7/10
Micrathena brevipes	3.1 ± 0.8 (2.2 − 4.5)	thrash on bottom; mobile < 10	7/10
Micrathena schreibersi	2.7 ± 0.8 (1.5 − 4.0)	thrash on bottom; mobile − 10	7/10
Argiope savignyi	2.2 ± 1.1 (0.6 − 4.0)	slow or rapid crawl; mobile < 10 min	7/10
Nephila clavipes juv.	2.3 ± 1.9 (0.1 − 5.4)	slow crawl or thrash; mobile < 10 min	9/10
Nephila clavipes adult	0.9 ± 0.9 (0.1 − 2.4)	slow crawl or thrash; mobile < 5 min	9/10

survival, I gently pushed each spider beneath the surface to see if it showed buoyancy after losing contact with the surface film.

RESULTS AND DISCUSSION

In six of the seven species, more than half of the individuals drowned as a result of the 1-h submersion (Table 1). Such high mortality levels had occurred in only one of the four temperate zone aerial web-weavers (*Micrathena gracilis*) that I tested previously. On this basis, it is evident that the aerial web weavers that I tested from the tropical wet forest are not any better adapted for drowning resistance than are those tested from the temperate deciduous forest biome.

During submersion, most of the wet forest species were motile for less than 15 min (Table 1), a level of endurance similar to that shown by the two temperate zone araneids tested previously. *Metazygia* sp., which had built webs on a footbridge above the river, was able to remain motile the longest and, of all the species tested here, spent the greatest percentage of the hour in locomotion. *Micrathena molesta* was the most resistant of the spiders to drowning during submersion; however, there was no obvious factor to account for its superior endurance. Least resistant to drowning were adult *Nephila clavipes*, which became immotile after a very brief initial period of slow crawling or very slow thrashing. If submerged during rain-caused flooding in the field, adults of this species would survive only briefly while attempting to climb above the water's surface. Juvenile *N. clavipes* showed longer periods of motility but nonetheless drowned as often as the adults in the 1-h test (Table 1). The remaining araneids—*M. brevipes, M. schreibersi*, and *A. savignyi*—fared little better than *N. clavipes*. The single theridiid tested, *A. taeniata*, was similar to the best-adapted araneid, *M. molesta*, as to percent locomotion and duration of motility but drowned as frequently as the last-mentioned group of araneid species.

I also studied the effects of placing individuals of the seven species on the surface of an open pool of water in a basin. Pushing each floating spider beneath the surface revealed a difference in buoyancy between two groups of species. The three *Micrathena* species, *Metazygia* sp., and *N. clavipes* sank to the bottom, whereas *Argiope savignyi* and *Achaearaneataeniata* usually were buoyed up, apparently by having a temporary air store on the body surface of relatively large size for the mass of the spider. The gas store in the booklungs and the hydrophobic nature of the cuticle also may have influenced buoyancy (J. F. Anderson pers. comm.).

Of additional interest were differences among the species' responses to contact with the water's surface film. Three species—*A. taeniata, Metazygia* sp., and *N. clavipes*—floated on their sides with their legs drawn in, a behavior that kept one or both lung slits exposed to the air. The three *Micrathena* species and *A. savignyi* usually floated upright, with their lung slits below the surface. Although *A. savignyi* had an opisthosomal air film that probably maintained an air supply channel from its slits to the air above the water, that did not seem to be the case for the three *Micrathena* species, which have relatively few opisthosomal setae. However, one of these, *M. brevipes*, showed a behavior that solved the dilemma. By lifting its massive opisthosoma to a position above the carapace, the spider then further rolled into a partial "flip" and ended up in an inverted position. Thus, now floating on its dorsal surface, the spider avoided drowning.

The data presented here and in my previous study (Rovner 1986) suggest that araneids—even those of tropical wet forests—can withstand only relatively brief periods of submersion, compared to web-weavers that dwell beneath stones. Apparently, the features that provide drowning resistance in spiders are general to the families possessing them and cannot be readily modified to adapt species of other families to local conditions. Indeed, the marsh-dwelling araneid *Acanthepeira venusta* (Banks) in Florida, which climbs down into the water when disturbed, has relatively brief submersion periods of 3 min or less (Folkerts and Mullen 1987). On the other hand, the absence of adaptations for aquatic conditions in aerial web weavers of the tropical wet forest may suggest that these spiders are usually able to avoid falling into floodwaters during heavy rain and that, if they do fall onto the water, they may have adaptations reducing the possibility of submersion or drowning after being trapped in the surface film.

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Jerome S. Rovner, Department of Zoological Sciences, Ohio University, Athens, Ohio 45701 USA.

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