

Egg capsule architecture and siting in a leaf-curling sac spider, *Clubiona riparia* (Araneae: Clubionidae)

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Abstract. Females of the leaf-curling sac spider *Clubiona riparia* build three-sided capsules, in which they enclose both themselves and their eggs. A capsule is usually constructed by bending a single blade of grass or other leaf twice, each time causing a fold that is perpendicular to the long axis of the blade, and joining the edges with silk. When constructed with monocot leaf blades, the resulting capsule is roughly triangular in cross section and 2–4 times as long as it is wide. We sampled occupied capsules from a 0.16-hectare marsh in central Ontario, Canada. Although we found capsules built with the leaves of cattails (*Typha latifolia*), iris (*Iris versicolor*), a grass (*Calamagrostis* sp.), and an unidentified willow shrub (*Salix* sp.), for the current analysis we concentrated on the monocots because of their structural similarity. Capsules built on cattails (2.13 ± 0.14 ml) were more voluminous than those on iris (1.63 ± 0.14 ml), and capsules made of grass blades (0.67 ± 0.08 ml) were the smallest. Nearly 70% of the total variation in capsule volume was associated with differences between the plant species. Only among capsules built on cattails was there a significant positive relationship between pre-oviposition spider mass and capsule volume; it accounted for about 37% of the variability in capsule volume. On willow leaves, spiders always constructed capsules with the lower surface of the leaf to the inside of the capsule; and on cattail blades, spiders always made their bends in a clockwise direction. We discuss the implications of our findings for an understanding of the choices these spiders make just prior to oviposition.

Keywords: Reproductive ecology, parental care, oviposition site choice, clutch mass

Animal architecture has been extensively studied (von Frisch 1974; Collias & Collias 1976; Jones et al. 1997; Hansell 2005; Gould & Gould 2007), with particular attention paid to the structures built by birds (e.g., Hansell 2000), social insects (e.g., Jones & Oldroyd 2007), and web-building spiders (e.g., Kaston 1964; Blackledge & Eliason 2007; Harmer & Herberstein 2009). Among spiders, web building is only one of several architectural modes and at least two of these, burrow excavation and the construction of aerial shelters made with non-silk “decorations” or by leaf curling, involve the use of environmental (as opposed to secreted) materials. Unlike webs, which always serve foraging functions (Eberhard 1990; Foelix 1996) and frequently double as intraspecific communication channels (Witt & Rovner 1982; Foelix 1996), burrows and aerial retreats are usually defensive, serving to protect against predators and parasitoids, excessive thermal load, desiccation, and other threats to the spiders’ well being (Morse 1985, 1988; Konigswald et al. 1990; Lubin et al. 1991, 1993; Ward & Lubin 1993).

Aerial shelters or retreats are particularly interesting because, relative to retreats constructed at the soil surface or under rocks or logs, they display the interplay between added exposure to wind, insolation, and visually orienting predators and parasitoids on the one hand, and on the other hand reduced exposure to ground-foraging predators, high soil-surface temperatures, some potential prey items and, possibly, prospective mates (Henschel et al. 1992; Ward & Henschel 1992; Ward & Lubin 1993; Konigswald et al. 1990; Morse 1985, 1988, 2007).

The leaf-curling sac spider, *Clubiona riparia* L. Koch 1866 (Araneae: Clubionidae), is known among arachnologists

largely because of the elegant and simple capsule that the female constructs as a shelter for herself and her eggs (Fig. 1: Comstock 1948; Edwards 1958; Dondale & Redner 1982; Paquin & Dupérré 2003). These retreats are constructed by bending a leaf (often of a monocot) twice, thereby forming a chamber that is roughly triangular in cross section, and sealing its seams with silk, with the eggs and female inside (Comstock 1948). The capsule takes time and energy to construct and ultimately bears all of the spider’s lifetime reproductive output, assuming the validity of Comstock’s assertion that it serves “as a nursery for the spiderlings and a coffin for the parent” (Comstock 1948:581). In that context, the capsule can be viewed as the consummation of a series of choices made by the gravid female — what plant to use as substrate; how high on the plant to build; how large to make the capsule; how tightly to seal its edges with silk — all interconnected and presumably all under the influence of natural selection.

We report here on *C. riparia*’s use of the leaves of three monocots (cattail, *Typha latifolia*, iris, *Iris versicolor*, and a grass, *Calamagrostis* sp.), and to some extent on their use of the leaves of a dicot (an unidentified willow, *Salix* sp.), in constructing enclosed capsules suitable for egg development and protection. Our emphasis here is on capsule volume and its correlates — subsequent papers will cover the energetics of capsule construction and the possibility that the gravid spiders show preferences among the available plant species.

METHODS

Field site and sampling.—The study site was an elongated marsh, 0.16 ha in area, on a small island located at 45°27′33.1″ N, 80°25′52.7″W, about 2.7 km off the northeast shore of

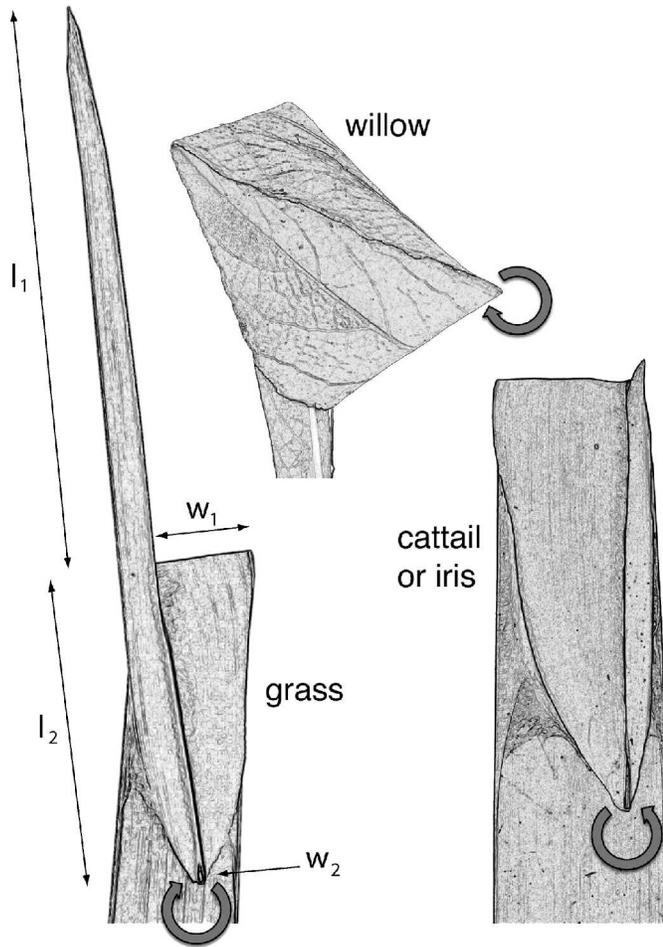


Figure 1.—Capsules of *C. riparia* showing their typical three-sided structure. The circular arrows are included to clarify the convention used to distinguish capsules that are built using clockwise bends (in these examples, grass and willow) from those built using counterclockwise bends (in this example, cattail or iris). The linear dimensions associated with the grass image are those we used to indicate where on a monocot blade the capsule was constructed and to calculate the volume of the capsule (see text).

Georgian Bay, Ontario, Canada. The water of the marsh was confluent with the open waters of Georgian Bay, but sheltered from any wave action. The site was about 10% open, with the remainder covered by vegetation. In terms of plant coverage, the dominant plant was a grass, *Calamagrostis* sp. (monocot, Poaceae). At the north end of the marsh was a stand of cattails, *Typha latifolia* L. (monocot, Typhaceae), covering about 16 m², and at various sites in the marsh were clumps of iris, *Iris versicolor* L. (monocot, Iridaceae) and individuals of an unidentified willow shrub, *Salix* sp. (dicot, Salicaceae). Sedges (Cyperaceae) and rushes (Juncaceae), as well as at least one other species of grass (Poaceae), were also present. Each cattail, each iris, and each willow was surrounded by *Calamagrostis* sp., although across much of the area of the marsh, each individual *Calamagrostis* sp. was surrounded only by others of the same species.

Our visual search for the egg capsules of *C. riparia* was careful but not structured. We found capsules on each of the dominant plant species (above), but none on the other

grasses, sedges, or rushes. We marked each capsule site with flagging tape and did not return to it until we had searched the entire marsh. Then, as we collected each capsule, we recorded the plant species and the capsule's height above the water surface.

Measurements and analyses.—In the laboratory, we photographed each capsule and used a caliper to measure its linear dimensions to the nearest 0.1 mm. For capsules constructed on monocot blades, these were: leaf tip to capsule, width of the leaf at the first bend, width at the second bend, and capsule length (Fig. 1). We also noted whether the capsule was constructed using a pair of clockwise bends or a pair of counterclockwise bends (Fig. 1) and whether the bends were made in such a way that the top surface of the leaf formed the inside or, conversely, that it formed the external surface of the chamber (we did not score this attribute for cattail or iris blades because we could not differentiate the two surfaces). Finally, we opened each capsule and weighed the spider and the clutch of eggs, each to the nearest mg. In a few cases, the spider had not yet laid its eggs, so for these we recorded gravid female mass as the combined mass of egg clutch and spider (in our analyses, we considered gravid female mass as being equivalent to the sum of egg clutch mass and spider mass when the latter were measured separately).

In calculating the volume of each of the capsules constructed with monocot blades, we first applied Heron's Formula for the area of a triangle (Dunham 1990), assuming the cross-section of the capsule to be an equilateral triangle with side lengths equal to the average of the two widths measured above. We then multiplied this area by the capsule length to get an estimate of the volume. This was an estimate because a) the monocot blades are somewhat tapered, more toward their tips than further down the leaf; b) near the ends of the capsule two sides of the structure converge, giving the cross-section a far less equilateral shape; and c) away from the ends of a capsule, the sides bulge slightly, giving the capsule's cross-section a shape similar to a Reuleaux triangle (i.e., slightly convex on each side; Weisstein 2009).

The most regular of the capsules constructed of willow leaves are approximately tetrahedral in shape (Fig. 1), but many were quite irregular, sometimes more conical or even cylindrical. To measure their volumes, we preserved them in 95% alcohol, then dried them and lightly coated them with silicone (Ace® Silicone Lubricant) to render their surfaces hydrophobic. Finally, we submerged each in a graduated cylinder containing distilled water and measured its volume directly. These volumes are reported below, but in our subsequent analyses we concentrated on the chambers of the three monocot species, both because their similar shapes make comparisons among them more meaningful and because we used a very different technique to measure the volumes of willow capsules and were reluctant to treat the two techniques as if they were comparable.

Our two primary analytical tools were one-way ANOVA, with plant species as the grouping variable and using Sokal and Rohlf's (1987) method for determining the relative importance of within vs. between treatment variance; and linear regression, with spider or clutch mass as the independent variable. In both statistical contexts, our interest was in elucidating the sources of variation in capsule volume.

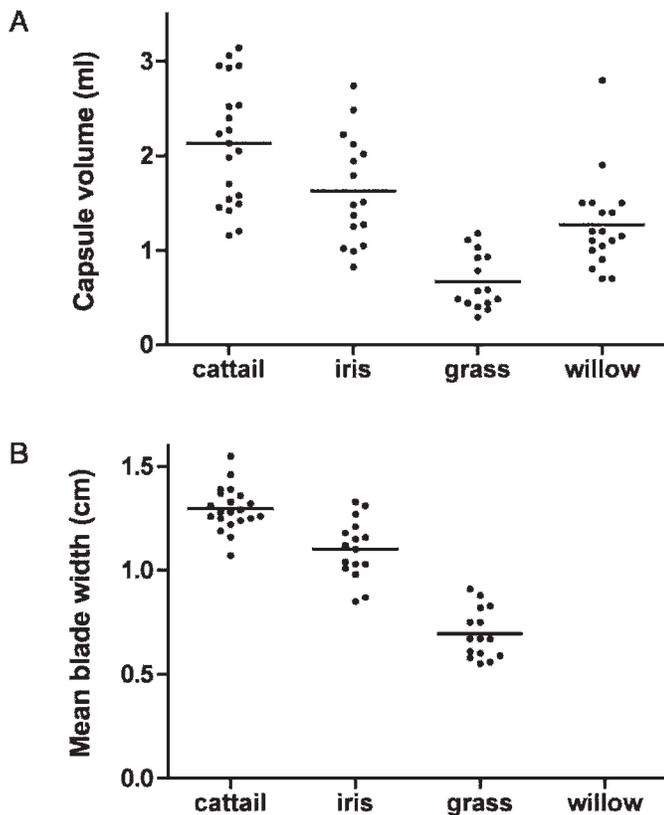


Figure 2.—A. Capsule volumes varied significantly depending on which plant leaves were used in construction. ANOVA was applied only to the monocots (willow capsule volumes were measured using different methods), and among them all pair-wise differences were significant. B. Mean blade widths, analyzed with ANOVA, also varied significantly among the three monocot plant species, and pair-wise tests were all significant. The most voluminous capsules were constructed with cattail blades and were so large in part because the mean blade width of cattails was large.

RESULTS

Among the monocots, capsule volume varied more than ten-fold, the smallest being a grass capsule with a volume of 0.29 ml and the largest being a 3.14-ml capsule made from a cattail leaf. The mean capsule volume (\pm SE) on cattails was 2.13 ± 0.14 ml, on iris 1.63 ± 0.14 ml, and on grass 0.67 ± 0.08 ml (Fig. 2A). ANOVA revealed that this variation was significantly associated with host plant species ($F_{2,39} = 32.04$, $P < 0.0001$), and Tukey's Multiple Comparison Test showed that all three pair-wise differences between the mean volumes were significant (cattail vs. iris, $P < 0.05$; cattail vs. grass, $P < 0.001$; iris vs. grass, $P < 0.001$). About 69.2% of the total variation (Fig. 2A) was attributable to differences among host plant species. Capsules constructed of willow, the only dicot, were intermediate in volume (1.27 ± 0.11 ml) between those on iris and those on grass (Fig. 2A).

An important component of capsule volume in monocots is the width of the blade where it becomes incorporated into the capsule, in this case measured at the two bends (Fig. 1). Given the significant differences in capsule volumes (above), it is unsurprising that blade widths were also significantly different, and with the same pattern (Fig. 2B). ANOVA showed that the differences among the mean widths of cattail ($1.30 \pm$

Table 1.—Spiders constructed their capsules without regard to handedness on iris, grass, and willow, and without regard to which leaf surface became the external surface of the capsule on grass. In contrast, spiders on cattail built only clockwise capsules, and spiders on willow always left the upper surface of the leaf on the outside of the capsule. * Top and bottom surfaces were anatomically indistinguishable on the leaves of cattail and iris, rendering these distinctions not applicable.

	Proportion clockwise	<i>P</i>	Proportion with top surface outside*	<i>P</i>
Cattail	21/21	< 0.0001	NA	
Iris	6/16	0.227	NA	
Grass	7/13	0.500	6/13	0.500
Willow	11/18	0.240	18/18	< 0.0001

0.02 cm), iris (1.10 ± 0.04 cm), and grass (0.70 ± 0.03 cm) were highly significant both in aggregate ($F_{2,49} = 108.4$, $P < 0.0001$) and in pair-wise tests ($P < 0.001$ for each).

Capsules constructed on cattails were substantially higher above the water (112.4 ± 5.0 cm) than were capsules on iris (51.1 ± 2.1 cm), grass (59.9 ± 2.1 cm), or willow (53.8 ± 3.0). ANOVA showed these differences to be highly significant ($F_{3,65} = 76.1$, $P < 0.0001$), but in pair-wise tests, heights on iris, grass, and willow were indistinguishable from one another, and heights on cattails were significantly different from the others ($P < 0.001$ in each case).

Capsules on the four plant species also differed with respect to handedness, the direction of the two bends used to form the capsule (Fig. 1), and with respect to whether the top or the bottom surface of the leaf became the outside surface of the capsule (Table 1). Notably, spiders on cattail built only clockwise capsules, and spiders on willow always left the upper surface of the leaf on the outside of the capsule. Spiders on iris, grass, and willow showed no preference with respect to handedness, and spiders building on grass appeared to have no preference for one side of a leaf or the other as the outside surface of the capsule. We could not distinguish which side of a cattail or iris blade was top, so we did not score this attribute of capsules constructed on those two plant species.

In looking beyond host species for the sources of variation in capsule volume, we regressed capsule volume on spider mass, egg clutch mass, and pre-oviposition spider mass (the sum of spider and egg clutch masses). In doing this, we were aware that, because of its constituent components, pre-oviposition mass would be correlated with spider mass and with egg clutch mass. We also knew that many studies have found a strong direct effect of spider mass on egg clutch mass both among species (Marshall and Gittleman 1994; Nicholas et al. 2011) and within species (e.g., Killebrew & Ford 1985; Brown et al. 2003), a relationship that we also saw in our own data (Fig. 3; $r^2 = 0.221$, $F_{1,40} = 11.32$, $P = 0.0017$). Thus we knew that our several regressions were not independent of each other.

In our regression analysis (Fig. 4), capsule volumes (when pooled across plant species) were significantly influenced by spider mass, egg clutch mass, and pre-oviposition spider mass ($P = 0.050$, 0.023 , 0.012 , respectively). The strongest relationship was between pre-oviposition spider mass and capsule volume ($F_{1,40} = 6.90$; $r^2 = 0.15$). When the data were

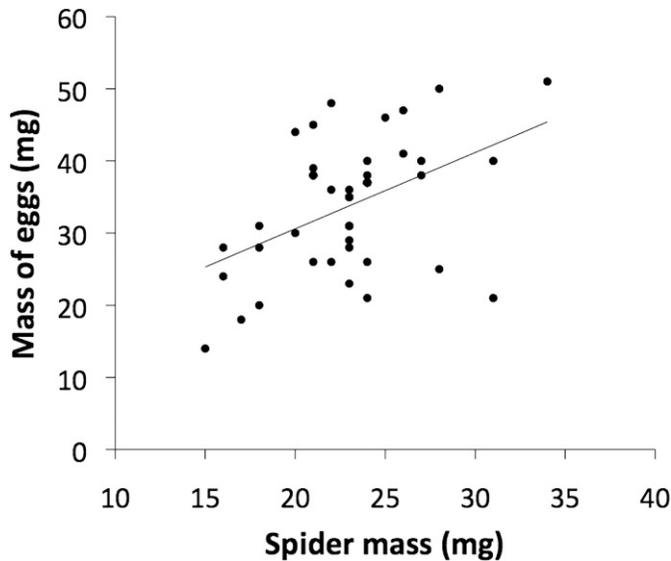


Figure 3.—About 22% of the variation in clutch mass was attributable to differences in spider mass ($r^2 = 0.221$, $F_{1,40} = 11.32$, $P = 0.0017$).

broken down by plant species, only among capsules built on cattails were there significant influences of the independent variables on capsule volume. And again there, the strongest relationship was between pre-oviposition spider mass and capsule volume ($F_{1,15} = 8.63$; $r^2 = 0.37$).

Despite a strong relationship between spider size and capsule volume, especially among capsules on cattails, we found no evidence that larger spiders were predisposed to build on cattails or, conversely, that smaller spiders chose to construct capsules on grass leaves (Fig. 5). ANOVA revealed that mean pre-oviposition spider mass did not vary significantly across the three monocot plant species ($F_{2,47} = 1.05$, $P = 0.358$).

DISCUSSION

Many *C. riparia* construct their capsules on cattail, iris, or willow, despite the fact that grass blades, on which they can also construct capsules, are close by and in abundance. This suggests that suitable building sites were not a limiting resource in this area, but more importantly, it suggests that predisposition and choice could be involved. Choosing cattail, for example, means having the option to make a substantially larger capsule than could be constructed on a grass blade (Fig. 2), and that might well be advantageous for a large spider gravid with a large clutch of eggs. The data on pre-oviposition spider mass contradict that suggestion: the plant species on which a spider constructed a capsule was unrelated to the spider's size (Fig. 5). Moreover, at least for spiders that constructed capsules on iris or grass, the size of the spider appears not to have influenced the size of the capsule that it made (Fig. 4).

In contrast, we have strong evidence that spider size influenced the volume of capsules that were constructed on cattails: more than a third of the variation in capsule volume on cattails was attributable to the pre-oviposition masses of the spiders, with a doubling in spider size resulting in about a 20% increase in capsule volume (using the slope of the line in

the bottom graph in Fig. 4). We also now know (Table 1) that these spiders always bend willow leaves to fashion a capsule that has the upper surface of the leaf to the outside, and that when they build on a cattail blade they always turn the blade in a clockwise direction (according to the convention we have adopted: see Fig. 1). What do these three observations — 1) the spider's scaling of the volume of its capsule to the spider's own mass, 2) the spider's consistent attention to willow leaf surface properties, and 3) the spider's proclivity for clockwise handedness when building on cattail but not elsewhere — imply about the kinds of pressures a gravid female *C. riparia* faces? We consider these questions in order below.

Scaling capsule volume to spider mass.—Although architectural feats are not often analyzed in this way, it is very clear that many spiders know how to measure, and that they adjust the sizes of their structures to fit their needs. As araneids grow, for example, so do their webs, presumably both because they are able to build larger webs and because they have greater metabolic needs, and larger webs intersect larger numbers of prey (Eberhard 1990). Similarly, burrowing wolf spiders increase the diameter of their burrows as they grow (Carrel 2003), and desert widow spiders increase a number of web and retreat dimensions as the spiders grow (Lubin et al. 1991). In that context, the spider size/capsule size relationship in *C. riparia*, and the spider's implied ability to measure, are not surprising.

Moreover, the scaling of capsule volume to spider mass makes sense from a biomechanical perspective. First, capsule volume must be sufficient to enclose both the spider and its eggs as separate entities (Fig. 6: not just as the single gravid organism that constructed and first inhabited the capsule) and to allow for the spider's movements while sealing the capsule from the inside and while laying eggs. Second, if predation by animals that would breach the capsule by cutting through the plant material (Fig. 6: as opposed to tearing the silk where two leaf edges meet) is important, then larger capsule size is better because, at least in the monocots, the leaf blade gets thicker as it gets wider. Third, a larger spider's size means that it can exert greater forces and, perhaps, can expend more energy during capsule construction (R.B. Suter et al. unpublished data) than can a smaller spider, allowing it to bend wider and stiffer leaves and thereby enclose more volume.

If larger leaf-curling sac spiders are able to construct larger capsules, and if there are advantages to doing so, why was the scaling of capsule volume to spider mass only observed when the spiders build on cattails? Statistically, this is not a trivial dichotomy: on cattails, the relationship is robust, explaining more than 36% of the variation in capsule volume; on iris and grass, the relationship is insignificant, and not just marginally so (Fig. 4). The leaves of the grass, *Calamagrostis* sp., at their widest, where the spiders bend them to make capsules, are about half the width of the part of the blades of cattails that the spiders use (Fig. 2B). That means that, were a spider to try to make a more voluminous capsule on a blade of grass, it would have to do so by elongating the capsule; but that would not appreciably improve the spiders maneuverability inside the narrow capsule and, because the spider was already doing its construction at the widest part of the blade, the resulting long capsule would not be more resistant to the depredations of gnawing animals.

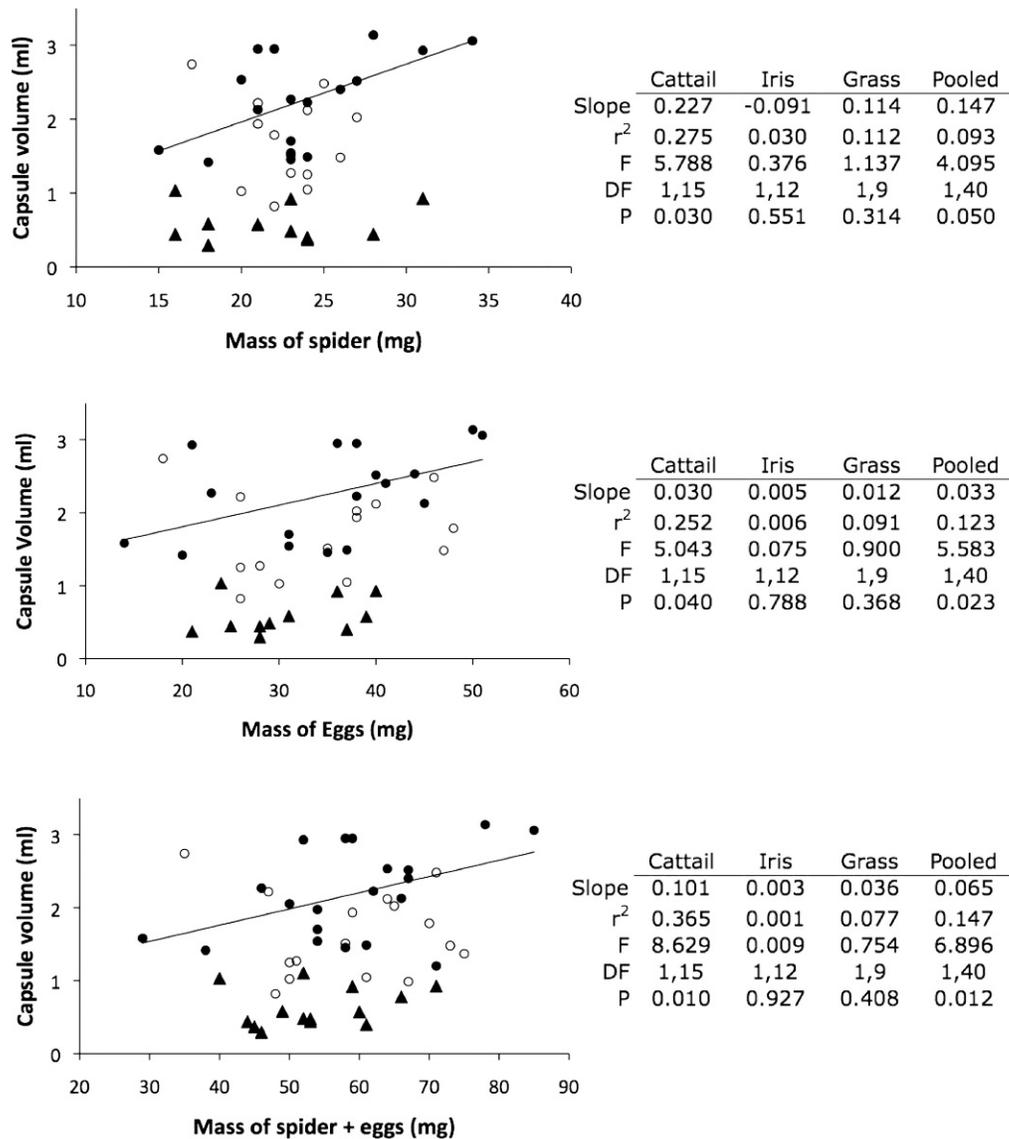


Figure 4.—On cattail (filled circles; regression line), capsule volume varied significantly with spider mass, egg clutch mass and pre-oviposition spider mass (the sum of spider mass and clutch mass). Those relationships were not found with capsules built on iris (open circles) or grass (triangles). On cattail, the strongest relationship was between capsule volume and pre-oviposition spider mass, where differences in mass accounted for 36.5% of the variation in capsule volume.

That line of reasoning, which provides a tenable explanation for the constrained volumes of capsules on grass blades, irrespective of spider size, does not serve well for capsules on iris blades. These blades, though about 15% narrower than cattail blades, are of much the same shape and share with cattail blades the property of becoming thicker and stiffer as one moves down the blade from the tip. Thus, as they do on cattails, larger spiders could make more voluminous capsules on iris, but they do not. We do not currently have a way to explain why the scaling of capsule volume to spider mass does not happen on iris.

Bending willow leaves to put the top surface outside.—When a spider constructs its capsule using a willow leaf, it does so by bending the leaf toward its lower side, resulting in a chamber that has the lower surface of the leaf on the inside and the upper surface of the leaf on the outside (Table 1). The willow

leaves used by spiders at our study site were strongly asymmetrical, with a relatively smooth, shiny, dark upper surface that was devoid of stomata, and a much more textured and lighter lower surface with vascular tissue in relief and many stomata (R.B. Suter unpublished data). The presence of gas exchange pores, the stomata, consistently on the interior faces of the capsule walls suggests that the consequent differences in humidity and possibly respiratory gases are important to the spiders.

Desiccation is surely a problem for spiders and their eggs (Gillespie 1987; Hieber 1992; DeVito & Formanowicz 2003), and probably led to the evolution of known behavioral and architectural solutions (Humphreys 1975; Suter et al. 1987; DeVito & Formanowicz 2003). We presume that capsule construction by *C. riparia* also serves to reduce desiccation, both of the spider and of its egg clutch. Part of that function,

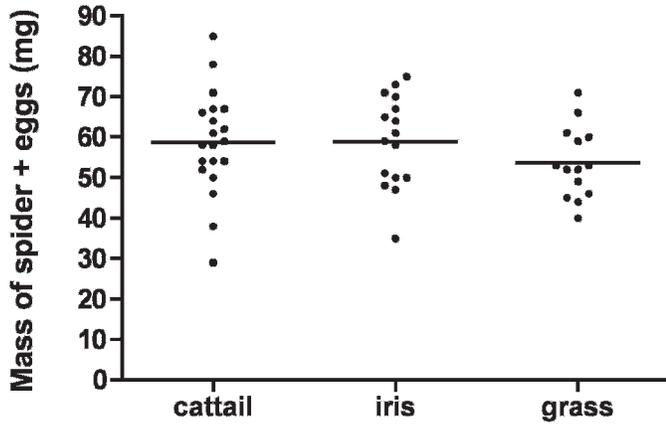


Figure 5.—Pre-oviposition spider masses did not vary significantly depending on which plant leaves were used in construction ($F_{2,47} = 1.05$, $P = 0.358$), an indication that a spider’s choice of one plant species over another was not biased by the spider’s mass.

the provision of shelter from the forced convection of winds and from insolation, would be provided even if the sides of the capsules were made of willow leaves that had no stomata. But the presence of stomata on the inside means that water vapor lost from the plant during normal transpiration would dwell inside the capsule until it diffused outward through the spaces between the silk-joined edges of the leaves, thus keeping the relative humidity of the capsule’s interior at close to 100%.

This hypothesis is mildly supported by the observation that the spiders do not favor one side or the other of the grass (Table 1) because the species of *Calamagrostis* on which we found the spider capsules was amphistomatal, with stomata on both surfaces of each blade (R.B. Suter unpublished data), as is usual in this grass genus (Ma et al. 2005).

We have no direct evidence concerning the relative humidity inside the capsules on any of the host plants, so a test of our contention that the particular structure of willow capsules functions to boost interior humidity must await further study. Three alternative hypotheses about the topside-outside construction of willow capsules relate to the fact that the underside of the willow leaf is much more reflective than the top side: building a capsule with the underside inside a) makes the capsule less conspicuous to visually orienting predators; b) causes the capsule to absorb more solar energy under sunny conditions, thereby raising internal temperature; and c) keeps the more photosynthetic layers of the leaf exposed, thereby possibly inhibiting abscission and prolonging the life of the leaf (Taylor & Whitelaw 2001).

Bending cattail blades clockwise.—Our data on cattail capsules show a striking and highly significant handedness: all of the spider-bearing capsules on cattails were constructed by bending the blade clockwise (Table 1), whereas on the other three plant species there was no evidence of handedness. Asymmetries of this sort, in which an animal’s morphology or behavior is in some way chiral, have received much attention in recent years, particularly as researchers have demonstrated that some chirality at the level of gross morphology, brain laterality, and behavior, is a consequence of chirality at the molecular and early developmental levels (Levin & Palmer 2007; Okumura et al. 2008; Davison et al. 2009). In the current case, we do not know whether the asymmetry resides in the gravid spider or in the cattail leaf.

Our working hypothesis is that the amphistomatal (Kaul 1974) cattail leaf is asymmetrical with respect to how easily it bends — that it is somewhat less energetically costly for the spider to bend it with a clockwise bias than with a counterclockwise bias, and that this difference is large enough to matter in the evolutionary calculus leading to an optimum architecture. Support for this hypothesis could come from measurements of the work required to bend cattails clockwise vs. counterclockwise, and that study is underway. To make good sense, however, that support would have to be paired with similar measurements of iris blades, because they are superficially nearly identical to cattail blades but are not treated as identical by the spiders (Table 1).

Despite the structural simplicity of the elegant capsules built by *C. riparia*, our analyses of their sizes and their locations revealed substantial complexity. The gravid spiders that constructed the capsules did so not only on narrow-bladed grass leaves and on the broader blades of iris and cattails but also on willow leaves. Given this variety of construction sites, it is not surprising that capsule volume varied widely (the smallest had a tenth of the volume of the largest), but it is surprising that only on cattails was there a significant relationship between spider size and capsule volume. Capsules found on cattail blades were also unusual in having been consistently constructed by bending the blades clockwise, while no chiral preference was seen in capsules built on the

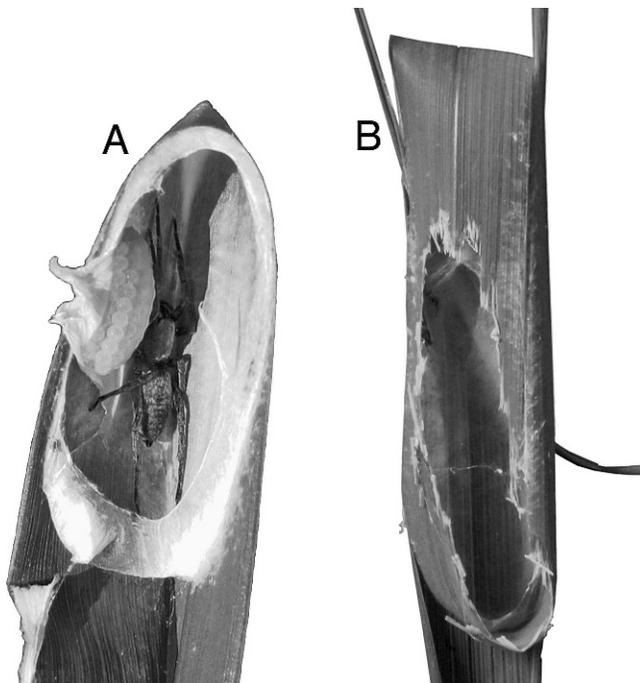


Figure 6.—Two opened capsules, shown approximately to scale. A. An inhabited capsule, opened by the authors, shows the female *C. riparia* with its egg mass and portrays the relationship of their size to the volume of the capsule. B. An empty capsule showing damage probably caused by a predator that gained access to the spider and eggs by tearing through the plant material rather than by separating the grass blades at a silk-closed seam.

other three plant species. Finally, the spiders always folded a willow leaf so that its stomata-bearing surface faced, and could perhaps modify or modulate, the enclosed atmosphere of the capsule.

This account is only a beginning. We are currently conducting four related studies: measuring the energetics of capsule construction, testing the spiders for preferences among the available plant species, analyzing the ways in which the microenvironment inside a capsule differs from external conditions, and seeking the source(s) of the chirality in capsule construction on cattails.

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