# SPIDER SIZE AND LOCOMOTION ON THE WATER SURFACE (ARANEAE, PISAURIDAE)

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**ABSTRACT.**   Newly emerged fishing spiders, *Dolomedes triton* (Walckenaer 1837), can achieve rowing velocities as high as those of adults despite an approximately 600-fold difference in mass (1.7 mg *vs.* 1.1 g). In contrast, when velocity is measured in relative terms (body lengths/sec), small spiders move much more rapidly than adults, with $V_{rel} \propto mass^{-0.31}$. This surprising performance of very small spiders can be attributed both to their very high stride frequency ($f_{s} \propto mass -0.43$) and to the high angular velocity of their propulsive legs ($\omega \propto mass^{-0.33}$). Calculations of leg tip velocities, based on measurements of both angular velocities and leg lengths, reveal that maximum leg tip velocities are achieved by spiders of about 33 mg, nineteen times more massive than the smallest spiders we tested. Some very small spiders perform conspicuously and consistently less well than do others of the same size. A detailed dissection of the motion of these underachievers reveals that a disproportionate amount of their rowing effort goes into vertical as opposed to horizontal work: the ratio of vertical to horizontal work during rowing is $1.03 \pm 0.89 : 1$ in normal fishing spiders and $5.18 \pm 1.73 : 1$ in the underachievers.

**Keywords:**   Allometry, locomotion, size, spider, aquatic

Locomotion across the surface of water is performed both by fishing spiders (Arachnida, Araneae, Pisauridae) (McAlister 1959; Shultz 1987) and by water striders (Insecta, Hemiptera, Gerridae) (Anderson 1976). This form of locomotion involves not only support by the water's surface tension but also drag resistance to leg motion as the animals push backward to propel themselves forward. Crucial for the rowing gait in this semi-aquatic locomotion is the dimple formed in the water surface as the animal's leg pushes first down and then backward, because it is the leg with its dimple that encounters resistance as it moves horizontally, and it is that resistance against which the animal pushes to achieve forward acceleration (Suter et al. 1997). When the leg pushes too deeply into the water or moves horizontally too rapidly, the dimple disintegrates, leaving the leg alone, without the dimple, to provide forward thrust. The leg without the dimple encounters far less drag resistance because its effective frontal surface area is much smaller (Suter & Wildman 1999).

This unorthodox form of locomotion, available only to relatively small creatures, is performed by pisaurid spiders of all ages and consequently of all sizes. In one of the most common pisaurids in North America, *Dolomedes triton* (Walckenaer 1837), adult females

at about 1 g are approximately 600 times as massive as hatchlings, a difference that should, in theory, result in substantial differences in the efficacy of rowing locomotion. Is there a relatively simple allometric relationship between size and rowing efficacy in pisaurid spiders?

The allometric properties of aerial, terrestrial, and submerged locomotion have been studied in considerable detail (for references, see Pennycuick 1992; Calder 1984; Peters 1983). The allometry of locomotion on the water surface, however, has received very little attention: both Vogel (1994) and Denny (1993) have speculated about the difficulties that may be faced by very small organisms (e.g., juvenile water striders) attempting to push against a very slippery water surface, and we have published some data on allometric relationships (Suter et al. 1997; Suter & Wildman 1999) in support of specific arguments about the biomechanics of rowing in fishing spiders. Heretofore, there has been no explicit investigation of the relative efficacy of rowing locomotion for very small *vs.* much larger arthropods. Thus, the primary reason for undertaking the empirical studies on which we report here is the need to fill that gap in our knowledge. The secondary reason for these studies is derived from the observation

(Suter unpubl. obs.) that very young fishing spiders in the genus *Dolomedes* hunt primarily in terrestrial and emergent vegetation whereas adolescents and adults hunt more frequently at the water surface. The current study, if it demonstrates substantial size-specific differences in rowing efficiency, could help to explain the motivation for changing foraging behavior during maturation.

## METHODS

**Organisms.**—The species of fishing spider used in this study, *Dolomedes triton* (Araneae, Pisauridae), can become quite large (adult females: to 1.5 g, 2 cm body length, and 9 cm leg span), and normally inhabit marshes and the edges of ponds and streams throughout much of North America (Gertsch 1979). The larger subjects ($> 0.1$ g) for these experiments were collected from small ponds in Mississippi and held in our laboratory (maintenance and experimentation at 22–25 °C) in 3.8 liter plastic aquaria containing water (about 2 cm deep) and an inverted clay flower pot to provide a solid substrate. We fed these spiders assorted insects and changed their water approximately once a week. The smaller subjects (1.7–100 mg) were hatched in the laboratory from an egg case borne by an adult female captured (as above) in Mississippi. The locomotion of the smallest subjects (1.7 mg) was studied while they were still 2nd instar hatchlings and had not yet eaten. These and the other small spiders were first reared communally in a 19 liter aquarium containing 2 cm of water and several rocks to furnish solid substrate (although they seldom left the glass walls of the aquarium), and were provided with live fruit flies (*Drosophila melanogaster* and *D. virilis*) and each other *ad lib*.

The largest of the adult fishing spiders (1.05 g) was 610× as large as the smallest of the hatchling spiders (1.72 mg), providing us with more than 2.5 orders of magnitude in mass variation against which to scale the several parameters of surface locomotion.

**High-speed videography.**—Because most of the motion involved in the spiders' rowing movements across the surface of water occurs in the horizontal plane, we videotaped their locomotion from directly above. The arena used in videotaping the locomotion of all but the smallest spiders consisted of a white porcelain-surfaced tray, a smooth, circular plastic

barrier to prevent the spider's escape, and a layer of water at least twice as deep as the deepest dimple we had observed for a spider of the size of the test spider. We used the bottom section of a small petri dish (6.0 cm diameter) as the arena for videotaping the locomotion of the smallest spiders. The arenas were lit with an incandescent point source (subtending an angle of 0.28° when 60 cm from the spider), mounted at 45° above and to one side of the videotaped part of the arena. We adjusted the camera's aperture to obtain sufficient depth of field to allow both the spider and its shadow (on the porcelain surface of the arena or on a white sheet of paper under the petri dish) to be in sharp focus.

During a trial, we placed a test spider in the arena, recorded its movements at 1000 fps with a Kodak EktaPro EM-1000 video recorder, and stored the images in S-VHS format. We analyzed the spider's motion in the horizontal plane by using Image (NIH shareware) to digitize and record the coordinates of the anterior and posterior tips of the body and the angles of legs III and II (relative to the body's long axis) either every 1 ms (for small spiders) or every 5 ms. We used the body coordinates to measure the spider's length, to analyze the displacement of the spider through time in both absolute and relative terms, and to calculate the pitch ($p$, degrees) of the body $[p = \cos^{-1}$ (apparent length/true length)] as it changed during the rowing stride cycles. We used changes in leg angles over time to estimate the angular velocity of the leg and the velocity of its tip during the power phase of rowing locomotion.

To estimate the horizontal component of the force exerted by a spider during a rowing stroke, we graphed the spider's velocity (m/s) as a function of time (s) and used the slope of the linear part of the line as our estimate of acceleration (Suter et al. 1997). We then applied Newton's second law ($F = ma$) to calculate the average net force exerted by the spider during acceleration in the horizontal plane.

To estimate the horizontal work done during a rowing stroke, we multiplied the horizontal component of force by the distance the spider traveled during the application of the force ($w = mad$). To estimate the vertical work done during a rowing stroke, we used the measurements of pitch to calculate the maximum change in the height of the spider's
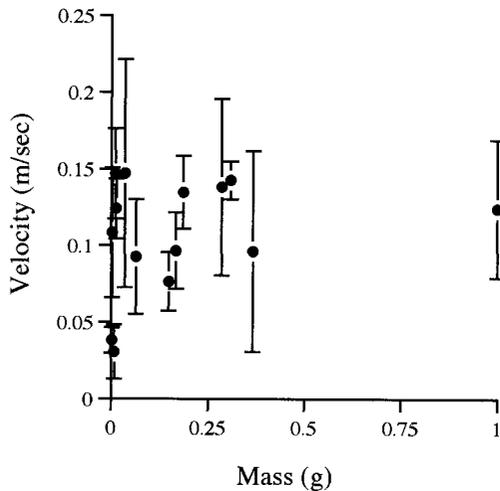
Figure 1.—The relationship between *Dolomedes triton* mass and velocity (mean ± SD). Especially for very small spiders, between-individual variance is high; standard deviations indicate substantial variability within individuals.
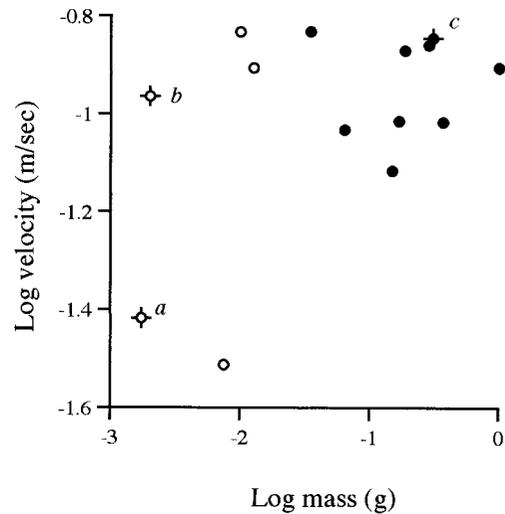


Figure 2.—The log-log relationship between spider mass and velocity. Spiders greater than 0.03 g (●) had mean rowing velocities $> -1.2$ log m/s whereas spiders with masses less than 0.03 g (○) had a bimodal distribution of mean rowing velocities with three individuals attaining velocities comparable to those of the larger spiders and two individuals having mean velocities $< -1.4$ log m/s. To elucidate the differences among the large and the two modes of small spiders, the rowing locomotion of three spiders (indicated by "+"; a, 1.7 mg; b, 2.0 mg; c, 308 mg) is characterized in detail in Figure 5 and is highlighted in Figures 3, 4, and 10).

center of mass (Fig. 9). That change in height required work against gravity ($w = mgh$).

## RESULTS

Actual horizontal velocities achieved by spiders rowing across the surface of distilled water averaged 0.107 ± 0.038 m/sec (mean ± SD of the means of 14 individuals, 51 trials total) and showed no obvious systematic changes with spider mass (Fig. 1). Within-individual variation was high for some spiders, likely a consequence of differences in effort as reflected in differences in the angular velocities of the propulsive legs (Suter et al. 1997; Suter & Wildman 1999). When the logarithms of velocities were plotted against the logs of spider masses, however, it became clear that inter-individual differences were substantially greater for very small spiders than for larger ones (Fig. 2). Two individuals, both with average velocities < 0.05 m/sec, were outliers in a population of spiders whose average velocities otherwise remained between 0.08 m/sec and 0.15 m/sec. Because the outliers had masses < 0.03 g, we included in our analysis a treatment of two groups that were defined by spider size (the five spiders with masses < 0.03 g, two of which were the outliers, and the nine larger spiders).

Although absolute rowing velocities did not vary systematically with mass, relative velocities, $V_{rel}$ (body lengths/sec), decreased substantially and significantly with increasing mass (Fig. 3). The relationship for only the larger spiders (> 0.03 g) was $V_{rel} = m^{-0.32}$ ($r^2 = 0.653$, $n = 9$, $P < 0.01$) and that relationship changed only slightly when the smaller spiders were included in the analysis ($V_{rel} = m^{-0.31}$; $r^2 = 0.785$, $n = 14$, $P < 0.01$). This strong relationship may be a consequence, in part, of the fact that stride frequency, $f_s$ (strides/sec), also decreased significantly with increasing mass (Fig. 4; for larger spiders, $f_s = m^{-0.36}$ and for all spiders, $f_s = m^{-0.43}$).

In an effort to understand the causes of the quantitatively very different performances of individuals of the same small mass and the very similar performances of individuals of divergent masses, we analyzed in detail the locomotor behavior of three spiders (*a–c* in Figs. 1–3). In this trio, *a, b,* and *c* had masses
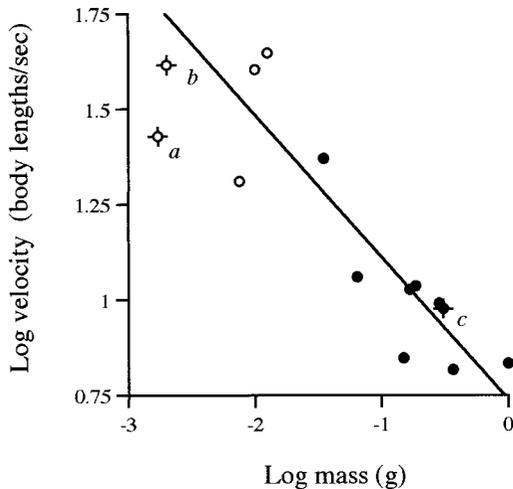
Figure 3.—The log-log relationship between spider mass and relative velocity measured in body lengths traveled per second. A linear fit to all points indicates $Log_{10}V = -0.305\ Log_{10}m$ ($n = 13$, $r^2 = 0.785$, $P < 0.01$). When we removed spiders smaller than 0.03 g from the analysis, the slope of the linear fit changed only slightly, to $-0.320$ ($n = 9$, $r^2 = 0.653$, $P < 0.01$).



Figure 4.—Stride frequency during rowing is closely related to spider mass. A linear fit to log-transformed data yields the equation $Log_{10}f_s = -0.432\ Log_{10}m + 0.145$ ($n = 13$, $r^2 = 0.877$, $P < 0.01$). When we removed spiders smaller than 0.03 g from the analysis, the slope of the linear fit changed to $-0.357$ ($n = 9$, $r^2 = 0.676$, $P < 0.01$).

of 1.7, 2.0, and 308 mg respectively, but had mean absolute velocities of 0.038, 0.109, and 0.143 m/sec respectively. The spiders' horizontal velocities varied over time, rising linearly during the propulsive phase of each stride and decreasing during the recovery phase (Fig. 5, top row). The acceleration was, in each case, accompanied by a rapid rise in the area of the shadows cast by the dimples made by legs III and II (Fig. 5, middle row), indicating a corresponding rise in the depth of each dimple (shadow area, in mm², is a nearly perfect linear correlate of dimple depth, in mm: for a 13.8 mm length of hydrophobic wire, for example, area = 34.6 depth − 6.2, $n = 8$, $r^2 = 1.00$). For the two smallest spiders (*a, b*), the horizontal acceleration was also accompanied by a distinct rise in body pitch (the angle between the animal's body and the water surface), but such an association was much less evident for the largest spider (*c*) (Fig. 5, bottom row).

Data from an earlier study indicated that leg length in these spiders is directly proportional to the log of mass (Fig. 6, modified from Suter & Wildman 1999, fig. 7A) and that the log of the angular velocities of the propulsive legs is
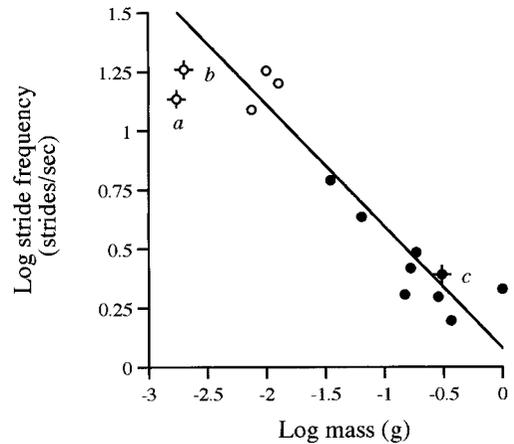
inversely proportional to the log of mass (Fig. 7, modified from Suter & Wildman 1999, fig. 7B). Further analysis of these data relating angular velocity to mass indicates that maximum (i.e., achievable) angular velocity is probably also a linear function of mass when both variables are log-transformed, but with a more steeply negative slope (Fig. 7). Because the propulsive force available during rowing is strongly dependent on the velocity of the leg tips, we used the equations relating mass to leg length and angular velocity (Figs. 6, 7) to elucidate the relationship between leg tip velocity and spider mass (Fig. 8). Achievable leg tip velocity rose steeply with mass until it reached its maximum at about 0.8 m/s in 33 mg spiders, and then fell with further increases in mass. In contrast, average leg tip velocity also rose rapidly to its peak (about 0.3 m/s) in 141 mg spiders but then declined only very slightly with further increases in mass.

## DISCUSSION

**General observations.**—The principles governing the relationships between size and locomotion remain controversial despite several decades of careful measurements (reviewed, for example, in Peters 1983; Garland 1983; Calder 1984; Pennycuick 1992). Much of the controversy revolves around the scaling
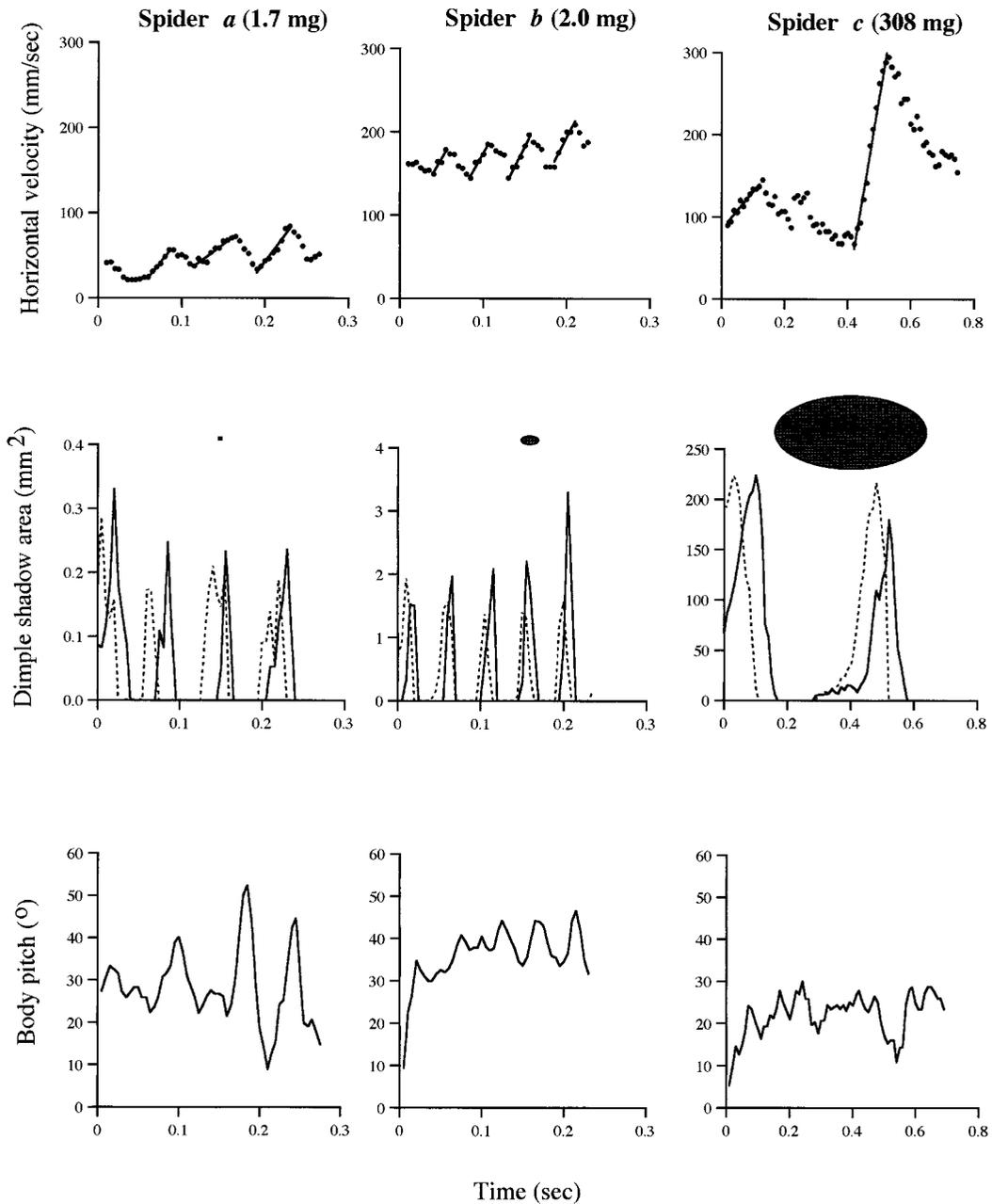
Figure 5.—Analysis of the rowing locomotion of the three spiders first identified in Figure 2. Velocities (top row of graphs; three-point running averages) vary periodically with time, indicating accelerations and decelerations that correspond to the propulsive and the glide phases of each rowing stroke; the horizontal acceleration during each stroke was calculated as the slope of the velocity versus time segment of the propulsive phase. The change in dimple shadow area (middle row of graphs) created by legs II (solid lines) and III (dashed lines) during the strokes graphed in the top row; ellipses indicate the relative sizes of maximum dimple shadows for the three different spiders. The change in body pitch (bottom row of graphs) during the same strokes; body pitch, referring to the angle formed between the body's long axis and the horizontal, varied substantially more during rowing by spider *a* than it did during the rowing of the other two spiders.
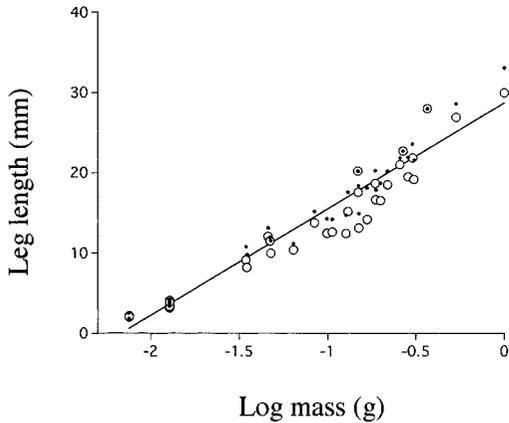
Figure 6.—Leg length in fishing spiders varies linearly with the log of mass. This relationship [$L_1$ = 13.22 $\log_{10}m$ + 28.73; $n$ = 62, two legs each (● and ○) for 31 spiders, $r^2$ = 0.946, $P$ < 0.001] is surprising because, for most other organisms in which it has been measured, it is the log-log relationship that is linear.



Figure 7.—Log-transformed angular velocities of the propulsive legs vary approximately linearly with the log-transformed masses of the spiders ($\log_{10}\omega$ = −0.328 $\log_{10}m$ − 0.256, $n$ = 50, $r^2$ = 0.379, $P$ < 0.01). In an effort to estimate the angular velocities of which spiders are capable, we fit a line to the maxima (circled data points; $\log_{10}\omega$ = − 0.623 $\log_{10}m$ − 0.266; $n$ = 9, $r^2$ = 0.991, $P$ < 0.01).

parameter that is to be held constant while other parameters are changed: different predictions follow from models based on geometric similarity, for example, than from those based on similarity of musculoskeletal elasticity or stress in the propulsive limbs. Not surprisingly, the reviewed literature concerns terrestrial locomotion, flying, and swimming, and ignores locomotion on the water surface. The present paper is the first to explore these relationships in an organism that regularly inhabits the water surface, although size and locomotion on the water surface by basilisk lizards has received some attention (Glasheen & McMahon 1996a, 1996b).

A comparison of the results of this study with expectations from other (principally vertebrate) studies reveals that models based on geometric similarity (Hill 1950) work well for rowing locomotion as performed by *D. triton* (Table 1): absolute velocity is approximately scale-invariant (Fig. 2) while relative velocity varies with mass$^{-0.31}$ (Fig. 3) and stride frequency varies with mass$^{-0.43}$ (Fig. 4). The absolute *vs.* relative velocity findings are particularly interesting for two reasons. First, the fact that very small spiders can achieve the same rowing velocities as adults despite a 610-fold difference in mass is remarkable. That achievement is made possible by both the rapid rise in stride frequency with decreas-
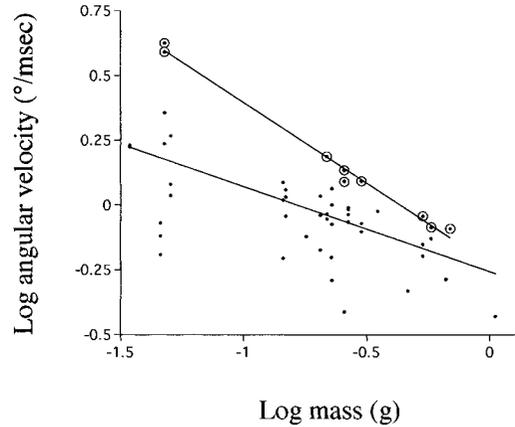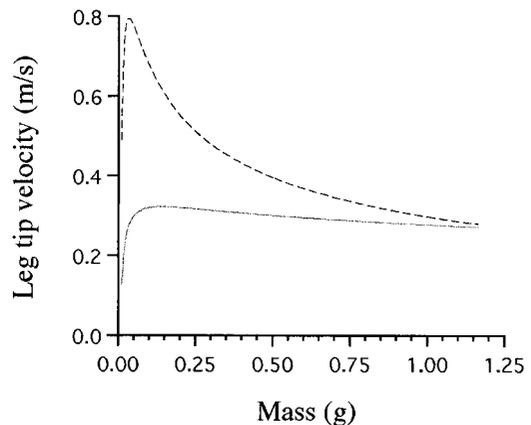


Figure 8.—Leg tip velocity is maximum when spiders are very small. The relationship between leg tip velocity and mass was calculated from the allometric relationships between leg length and mass (Fig. 6) and between leg angular velocity and mass (Fig. 7). The solid line indicates the relationship based upon average angular velocities (lower curve fit, Fig. 7) and the broken line indicates the relationship based upon maximum angular velocities (upper curve fit, Fig. 7). Peak leg tip velocities occurred at 0.141 g and 0.033 g for the solid and dashed lines, respectively.

Table 1.—Allometric relationships predicted in the literature and determined in this study.

| Relationship | Proportionality | | | |
| --- | --- | --- | --- | --- |
| | Expected | Source | Observed | Source |
| absolute velocity *vs.* mass | $V \propto m^0$ | Hill 1950 | $V \propto m^{0.02}$ | Fig. 2 |
| | $V \propto m^{0.24}$ | Heglund et al. 1974 | | |
| relative velocity *vs.* mass | $V \propto m^{-0.33}$ | Hill 1950 | $V \propto m^{-0.31}$ | Fig. 3 |
| | $V \propto m^{-0.09}$ | Calder 1984 | | |
| stride frequency *vs.* mass | $f_s \propto m^{-0.33}$ | Hill 1950 | $f_s \propto m^{-0.43}$ | Fig. 4 |
| | $f_s \propto m^{-0.17}$ | Alexander 1982 | | |

ing size (Fig. 4) and the fact that leg tip velocity is at a maximum in very small spiders (Fig. 8). The achievement also bespeaks the efficacy of the drag-based propulsive system used by even the smallest of the spiders (Suter & Wildman 1999). And second, relative velocity may be a better predictor of success at evading predation than is absolute velocity (Van Damme & Van Dooren 1999), hypothetically making newly hatched spiderlings far more difficult to capture than their parents since the spiderlings' relative velocities can be up to $10\times$ as great (Fig. 3).

**Conspicuous differences among small spiders.**—The generalizations discussed above ignore the conspicuously poor performances of the two very small spiders with average rowing velocities < 0.05 m/sec (Fig. 2).

To understand their relative deficit, we analyzed one of them (Figs. 2–4) in detail, and compared the results to those of a similarly small but fast spiders (*b*) and to those of a much larger adult (*c*). In theory, the low velocity of *a* could be caused by any number of physiological or biomechanical deficits such as low power output by the muscles that move the legs, low stride frequency due to muscular or neural deficits, sub-optimal stroke direction, and so forth.

The difference between *a* and *b* in stride frequency (Figs. 4, 5), although in the right direction, is only about 12%, far too little to account for the more than three-fold difference in absolute velocity (Fig. 5, top row: *a*, 0.046 m/s; *b*, 0.16 m/s). In contrast, there are substantial and revealing differences between
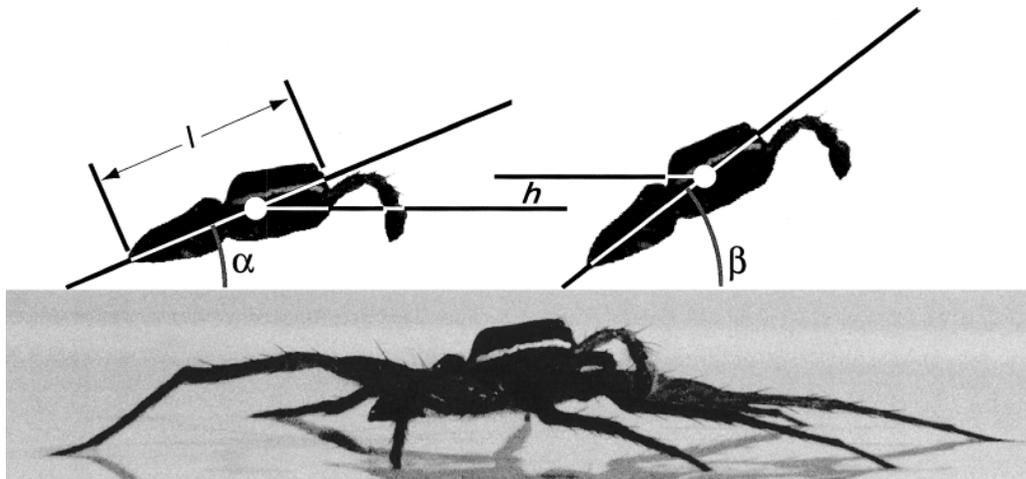


Figure 9.—The change in pitch of the long axis of the spider's body was measured both at the beginning of the rowing stroke (angle α) and at the peak of thrust production (angle β). The change in pitch allowed us to estimate the change in height of a spider's center of mass [$h \propto l\,(\sin\beta - \sin\alpha)$ where $l$ is the length of the body] and therefore to calculate the vertical work done during the rowing stroke. Because a spider can raise its body without changing the body's pitch (Suter 1999), the use of pitch changes to estimate work done against gravity underestimates vertical work.

the dimple areas recorded during the power strokes of the three spiders in this comparison (Fig. 5, middle row): the 308 mg spider (*c*) made dimples in the water surface that were approximately 100× as large (in the horizontal plane) as those of the 2.0 mg spider (*b*), but this 2.0 mg spider's dimples were about 10× as large as those of the 1.7 mg spider (*a*). Because *a* is the outlier in performance (Fig. 2), we took the relationship between spider mass and dimple area to be best indicated by the data from *b* and *c*. From that perspective, the dimple area of *a* is low by a factor of between 7 and 8 (expected maximum dimple area, 2.01 mm$^2$; observed maximum dimple area, 0.26 mm$^2$).

Because the relationship between dimple area and dimple depth is linear (see Results), the observed deficit in dimple area for *a* corresponds to a seven- to eight-fold deficit in dimple depth. That difference, in turn, is more than enough to account for the observed velocity difference between spiders *a* and *b*, because the horizontal thrust force that can be generated by a spider on the water surface is strongly influenced by dimple depth (Suter et al. 1997; Suter & Wildman 1999). To spider *a*, therefore, the water surface would appear to be very slippery, offering much less resistance to the backward motion of the propulsive legs than would be encountered if the dimples were deeper. The spider could compensate behaviorally for the deficit in dimple depth (and resistance) in either of two ways: it could increase the angular velocities of the propulsive legs or it could deflect some of its leg displacement downward in an attempt to increase dimple depth, either of which would have the effect of increasing drag (Suter & Wildman 1999). Our estimates of the ratios of vertical to horizontal work during rowing strokes (Fig. 10, derived from pitch measurements like those in Fig. 5, bottom row) indicate that spider *a* was doing about four times as much work to raise itself against gravity as it was to propel itself forward, confirming its attempts to increase dimple depth. Not surprisingly, the spider with the highest ratio of vertical to horizontal work, *d* (Fig. 10), was also very small and the slowest of all of the spiders tested (Fig. 2).

The underlying cause of the difference in dimple sizes that appears to be at the root of the locomotor difficulties experienced by spi-
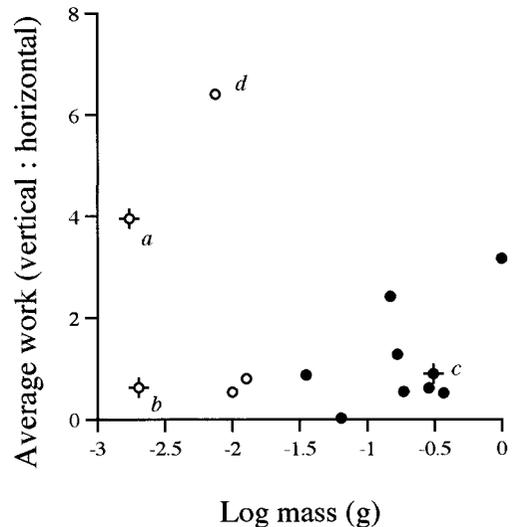


Figure 10.—The ratio of vertical work ($w = mgh$, mJ) to horizontal work ($w = mad$, mJ) in relation to the log of spider mass. The high ratio measured for spider *a* (four times as much work going into vertical displacement as into horizontal locomotion during each rowing stroke) provides an explanation for the conspicuously slow horizontal locomotion of that spider (Fig. 2). That inefficiency is surpassed by only one spider (*d*), which is similarly conspicuous in horizontal velocity (Fig. 2, lowest velocity).

der *a* but not by spider *b* remains obscure. Because the two spiders differed little in mass (1.7 *vs.* 2.0 mg), the mass difference is unlikely to explain the differences in dimple sizes. We suspect, instead, that variations either in the hydrophobicity of the spider cuticle or in the structures of hairs on the tarsi (J. Rovner and P. Sierwald, pers. comm.) may account for the unexplained differences.

### ACKNOWLEDGMENTS

Appendix 1.—Symbols used in the text and figures.

| Symbol | Meaning | Units |
| --- | --- | --- |
| $a$ | acceleration | m/s$^2$ |
| $d$ | distance | m |
| $F$ | force | mN |
| $f_s$ | stride frequency | strides/sec |
| $g$ | acceleration due to gravity | m/s$^2$ |
| $h$ | height | m |
| $l$ | length of body | m |
| $m$ | mass | g |
| $P$ | pitch of longitudinal axis | degrees |
| $V_{rel}$ | relative velocity | body lengths/sec |
| $w$ | work | mJ |

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