

## Gait characteristics of two fast-running spider species (*Hololena adnexa* and *Hololena curta*), including an aerial phase (Araneae: Agelenidae)

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**Abstract.** Funnel-web spinning spiders of the genus *Hololena* are capable of fast movements in a horizontal plane across a variety of challenging surfaces. We used two species, *H. curta* (McCook 1894) and *H. adnexa* (Chamberlin & Gertsch 1929), in experiments designed to reveal how they achieve remarkable speeds, occasionally exceeding 70 body lengths (~50 cm) per second. In high-speed recordings we found that spiders used their legs in alternating sets of four, distributed in staggered pairs along the body axis, resulting in an alternating-tetrapod gait. Increases in speed showed positive linear relationships with both frequency and stride length. There were also inverse, linear relationships in both species between speed and duty factor, meaning that increases in speed are associated with a decrease in the relative amount of time spent by the legs on the ground during each full leg cycle. By examining their duty factor vs. speed regressions, we found that spiders of both species were capable of aerial phases during high-speed running, with the transitional speed occurring at an average of 54 body lengths per second. We conclude that further experimentation with high-speed spiders and insects will likely show that a variety of species exhibits dynamically stable locomotion, including aerial phases.

**Keywords:** Kinematics, locomotion, duty factor

Running ability can save an animal from predation, help procure its next meal or help it find and interact with a prospective mate. Neural control, kinematics, dynamics and energetics of locomotion have all been studied extensively in a variety of arthropod taxa, including cockroaches (Full & Ahn 1995; Full & Tu 1990; Jindrich & Full 2002), flying insects (e.g., Dickinson & Götz 1993; Lehmann & Dickinson 1998), stick insects (e.g., Frantsevich & Cruse 1997) and aquatic beetles (Nachtigall 1980). These cover a range of locomotion strategies and underlying mechanisms, including fast running, slow walking, flying and swimming (Dickinson et al. 2000). Information on spider biomechanics is largely limited to the energetics of courtship and walking and to the running kinematics of large mygalomorph spiders such as tarantulas (Wilson 1967; Shillington & Peterson 2002) and other spiders (Lighton & Gillespie 1989; Watson & Lighton 1994). Additional research has concentrated on the contribution of spring- and hydraulically-based mechanisms and related functional morphology to movement in a variety of arachnids, as well as general jumping ability (Parry & Brown 1959; Anderson & Prestwich 1975; Sensenig & Shultz 2003; Shultz 1989; Suter & Gruenwald 2000; Weihmann et al. 2010). Other mechanical studies focus on abilities unusual for spiders or arthropods in general, such as swimming or water-walking ability (Shultz 1987; Suter et al. 1997; Suter et al. 2003). Still others highlight the mechanisms of spiders' web construction and use (Opell 1994, 1996; Naftilan 1999; Foelix 1996).

Despite the manifest importance of speed for small predatory animals, the gait kinematics of fast-running spiders has not been treated thoroughly in the literature. One exception is Foelix's (1996) description of locomotion of spiders as a pair of alternating tetrapods that become more synchronous (tighter temporal linkage between all four legs of a single tetrapod) at higher speeds. There are few published data and no model put forth to support his assertion; however, it provides a testable hypothesis for evaluation. Because of the differences between and difficulty of comparing gait patterns

across and even within different animal taxa (Blickhan et al. 1993), it is important to characterize a wide range of animals' kinematics to understand the general principles that can be used to model terrestrial locomotion.

**Speed and stability.**—With their plurality of legs, arthropods are notably adept at movement by means of careful placement of legs at slow speeds. Various species can climb obstacles, scale inclines and vertical surfaces (reviewed in Delcomyn 1985) and even bridge gaps exceeding their own body lengths via careful leg extension (Blaesing & Cruse 2004). Such behavior can be termed 'static stability.' At no point would the animal 'fall down' if motion were somehow to be temporarily suspended. But running is better modeled as a "spring-loaded inverted pendulum" (or SLIP; Alexander 1988, 2003; Holmes et al. 2006). This means that at the lowest point in an individual step, the leg acts as a spring or a bouncing ball, storing and releasing energy such that at the top of each step (when the leg is off the ground, or in swing phase), both kinetic and potential energy are maximized and in phase. This results in aerial phases in many animals, where a normal step-cycle includes a portion where there is no leg contact with the ground. These gaits require dynamic stability, for which kinetic energy both helps prevent falling, and, along with forward momentum, allows fast-moving animals to bridge gaps in the substrate that would impede slower animals relying on static stability (Ferris et al. 1998; Daley et al. 2006; Spagna et al. 2007).

Recent comparative work has been performed to characterize foot-surface interactions on challenging surfaces (Spagna et al. 2007) using spiders (*Hololena adnexa* [Chamberlin & Gertsch 1929]) along with insects, crustaceans, and robots. This research demonstrated that the spiders were capable of fast, stable locomotion ( $\geq 50$  cm/s, 70 body lengths/s) on mesh surfaces with varying probabilities of contact. The purpose of the present study is to characterize more thoroughly the gait characteristics of two fast moving, horizontally oriented spiders, *Hololena adnexa* and *Hololena*

*curta* (McCook 1894), on flat surfaces. This is done by examining gait parameters, including speed, duty factor and same-side limb phase for these species. This will provide a description of gait in fast-moving spider species and test Foelix's (1996) hypothesis of a positive correlation between running speed and tetrapod synchrony. This work also provides data from fast-running chelicerates for comparative work on kinematics and dynamics of terrestrial arthropods.

**Terms used.**—The typical gait of running spiders uses eight legs in two groups of four, alternating along the spider's anterior-posterior axis; for example, left legs I and III would be on the ground at the same time as right legs II and IV, while the other four legs would be off the ground, in motion (Foelix 1996). It is analogous to the 'alternating tripod' gait of fast-moving cockroaches and other insects (Full & Tu 1990), with an additional pair of legs behaving as additions to the tripods. For these reasons, this gait is referred to as an alternating tetrapod gait, with tetrapod referring to a set of four synchronous legs, not to a four-legged animal.

Swing phase is defined as the portion of a step cycle in which the leg (or the entire tetrapod) is moving toward another point of contact with the ground. Stance phase is the portion of a step cycle in which the leg or legs in question are in contact with the ground and providing a point upon which the animal can pivot the limb, or generate an acceleration force. Same-side limb phase is the mean fraction of a full step-cycle (stance phase plus swing phase) that passes before the opposite tetrapod touches down. Duty factor is defined as the mean amount of time each tetrapod spends in stance phase, normalized by the length of the full step cycle. The same-side limb phase convention is adapted from the study of quadrupedal animals (Hildebrand 1976), but instead of referring to the relative phasing of single legs, it describes relative phasing of the pairs of legs (I and III, II and IV) that move in phase in the alternating tetrapod gait.

## METHODS

Samples of *Hololena adnexa* were collected from the shrubbery around the campus of the University of California, Berkeley, Alameda County, California, and *Hololena curta* specimens were collected from various locations in Riverside, Riverside County, California. The spiders were housed in 9-dram vials and fed small crickets after experimental runs. The spiders were made to leave the vials by gentle prodding with a pipe cleaner, which prompted them to disengage from the webbing in the container and drop into the filming arena. The drop (~10–20 cm total) provoked an escape response, causing the animals to run across the filming arena.

Spiders were filmed with two high-speed digital video cameras set orthogonally to each other (one from the top; the other from the side) (Redlake Imaging MotionScopes) with lenses of variable focal length (10–25 mm) at 500 or 1000 frames per second. More than two duplicate runs were not allowed during a single experimental session to prevent individuals from fatiguing (Foelix 1996), so that each spider experienced only one or two runs per day. After experimental trials, the spider was collected and placed back into its vial and allowed to recover overnight. Following the experiments, spiders were weighed, measured (cephalothorax plus abdomen

length) and vouchers stored at  $-20^{\circ}$  C at William Paterson University.

To calculate gait parameters, we measured speed by counting the number of frames (at 1 or 2 ms per frame, depending on recording speed) required to cross the test surface. Gait analysis was performed by mapping gait phase for each leg manually on graph paper. Placing phase graphs for all eight legs on the same set of axes allowed estimates of the relative phase of and overlap between the animals' leg placement. Duty factor (the fraction of time spent by a single tetrapod in contact with the ground during a full step-cycle, including both stance and swing phases) for each run was calculated by dividing the number of frames in stance phase (for both tetrapods) by the mean sum of frames in stance and frames in swing for leg pair I. Leg pair I was chosen arbitrarily, as legs are similar in length in this family and, with a symmetrical gait, should spend a similar amount of time on the ground.

Linear regression was performed to determine the relationship between speed and duty factor, speed and stride length, speed and stride frequency, and speed and synchrony factor. Comparisons were only made between runs with at least one complete stance phase of a tetrapod, so that the full swing/stance cycle for one tetrapod could be calculated. Stance phase was averaged when multiple tetrapod stances were recorded from a single run. Runs were disqualified where one or more legs were not in the frame long enough to provide data for tetrapod characterization or comparison.

Period was measured as the total time in stance plus swing for leg I, and frequency as its inverse. Stride length was measured as total distance between the surface contact points for leg I in the first two visible stance-phases.

Tetrapod synchrony was calculated by dividing the number of frames in which all four legs in a single tetrapod were in stance phase, from the total number of frames in stance by any of the legs in that tetrapod. This calculation gave a fractional factor between 1, representing perfect synchrony between all four legs in a tetrapod, and 0, for a situation in which no frames contained all four legs in stance phase. To test the Foelix hypothesis that synchrony increases with speed, we plotted synchrony against speed and carried out regression analysis on the paired data from each spider. For an additional test of synchrony, we performed a linear regression between speed and same-side limb factor and then performed a regression of the residuals on speed.

Same-side limb phase was calculated as the mean point during limb phase of leg I (as above, the sum of all frames from beginning of stance through swing phase of leg I) at which any leg in the second tetrapod of legs made ground contact. Duty factor and leg phase were then plotted against each other and mapped on a Hildebrand Plot to characterize the type of gait or gaits used by the spiders (Hildebrand 1976, 1985).

**Statistics.**—All statistics were calculated using Minitab v. 13 (Minitab Inc., State College, Pennsylvania) and are expressed as (mean  $\pm$  SD). Significance level for all statistical tests was set at  $P < 0.05$ , with a Bonferroni adjustment to account for all tests being performed twice (once for each species) resulting in a critical  $P$  of 0.025. Linear regression was used to calculate the relationships between duty factor and speed, stride length

and speed, frequency and speed, and leg synchrony and speed for each species. Regression slopes were subsequently tested for significant differences between species via ANCOVA.

## RESULTS

Spiders ran using an alternating tetrapod gait, for which legs I and III on one side made contact with the ground in imperfect synchrony with legs II and IV on the other side, and vice versa, followed by the same pattern from the opposite side. A total of 28 runs was analyzed from 24 different individuals (1–3 runs per individual) of *Hololena adnexa*, and 19 runs from 5 individuals (1–6 runs per individual) from *Hololena curta*. Runs were included in the following analyses based on visual quality (staying in the focal plane of the cameras) and upon determination that the animal proceeded through at least 2 full step cycles while in frame without stopping or turning, to allow calculations of all the kinematic variables. Mean speeds of runs were 51.6 body lengths/s for *H. adnexa*, and 48.6 for *H. curta*, not significant (*t*-test assuming unequal variances,  $P = 0.40$ ). Additionally, ANOVAs of running performance by individual were performed to determine whether pseudoreplication (multiple runs by individual specimens) was a significant factor, and no effect was found for either species ( $P = 0.30$  and  $0.29$  for *H. adnexa* and *H. curta*, respectively).

**Speed, duty factor and aerial phase.**—Mean duty factors for runs by *Hololena adnexa* and *Hololena curta* were  $0.53 \pm 0.10$  and  $0.58 \pm 0.13$ , respectively. A two-tailed *t*-test assuming unequal variances showed no significant difference between mean duty factors between the two species ( $P = 0.13$ ). Duty factor was inversely correlated with speed for both species (Fig. 2). Linear regression analysis yielded relationships between duty factor and linear speed for the two species, with a slope of  $-96.88$  and an intercept of  $102.81$  for *H. adnexa* and a slope of  $-61.89$  and an intercept of  $84.45$  for *H. curta*;  $P < 0.001$  for both species. ANCOVA revealed no significant effect ( $P = 0.736$ ) on these regressions by species. A duty factor less than 0.5 indicates that the animal has an aerial phase in its leg placement patterns. Such duty factors were seen in both species, and happened in 39% (11 of 28) of *H. adnexa* runs and 32% (6 of 19) of *H. curta* runs (see Fig. 1 for an example of a step cycle in which all legs are visually clear of the surface for multiple frames). Aerial phases in the animals ranged from 1–10 ms in length.

**Speed, frequency, stride length and tetrapod synchrony.**—The spiders showed statistically significant linear regressions (Table 1) between both speed and stride length (normalized for body size of the individual), as well as between speed and stride frequency (total stance phase plus total swing phase; Figs. 3A, B). No abrupt transitions or changes in slope were seen in these distributions for either set of regressions. ANCOVA showed no significant differences between regressions of speed on stride frequency ( $P = 0.236$ ) or stride length ( $P = 0.160$ ) by species. The mean synchrony factors were  $0.30 \pm 0.17$  for *H. adnexa* and  $0.30 \pm 0.12$  for *H. curta*. Linear regression relating speed and synchrony factor were not significant for either species ( $P = 0.06$  and  $0.42$ , respectively; see Fig. 4 and Table 1). No abrupt transitions were seen in the amount of synchrony by either species. Testing the hypothesis another way, we examined same-side leg phase to see if the

phasing between leg-pairs became more consistent with speed. There was no significant relationship between the magnitude of the residuals for leg-phasing for either species ( $P = 0.50$  for *H. adnexa*;  $P = 0.30$  for *H. curta*).

**Gait description.**—A modified Hildebrand Plot considering opposing tetrapods rather than mammalian leg pairs (Fig. 5) shows that the spiders use a symmetrical gait that can be described as a trot, with just over a third of them in a running trot with aerial phase (17 out of 47 runs, see above), while the rest maintain a walking trot, with both sets of four legs on the ground for a fraction of each step (Hildebrand 1976). All the data points from both species cluster around 40% same-side leg phase and 50% duty factor.

## DISCUSSION

**Transition to aerial phase.**—Setting duty factor regression equations equal to 0.5, the point below which aerial phase occurs, and solving for speed gives normalized body speeds of 54.38 and 53.50 body lengths/sec for *Hololena adnexa* and *Hololena curta*, respectively. Although legs in swing phase are not in contact with the ground in most studies of gait, this relationship may not always occur in these spiders. While the front leg pairs (I, II and III) clearly swing free of the substrate, it is not always visually evident that the rearmost legs (pair IV) are in the air during the swing phase. Rather, at times they appear to be dragging the tarsi of the rear pair of legs, maintaining contact with the ground while pulling them to their next foothold, so that their swing phase more closely resembles a slide or shuffle in its early stages. *Hololena* spiders, like other spiders in the family Agelenidae (C.L. Koch 1837), have large setae extending at a  $\sim 70^\circ$  angle from the leg axis, and with the tarsus positioned parallel to the ground, these hairs may still contact the surface while the shaft of the tarsus is above the surface. However, they bend easily toward the leg axis, allowing the leg to be dragged past obstacles without being impeded (Spagna et al. 2007). This strategy of shuffling the rear legs may provide added stability, though such a shuffling gait does not appear to be addressed or modeled in the kinematic literature of arthropods. The spiders' dragline silk, which is sometimes but not always tacked down to the substrate during runs, may also pull down or otherwise orient their abdomen or rear legs, possibly limiting their ability to lift their rear legs clear of the substrate in the early stages of swing phase. The production of dragline was not controlled in these experiments. Although aerial phases in gait have been reported for spiders galloping on the surface of water (Gorb & Barth 1994; Suter & Wildman 1999; Stratton et al. 2004), this study appears to be the first report of aerial phases achieved by a spider in a purely terrestrial context.

**Speed and synchrony.**—The hypothesis of increased synchrony between legs within the two alternating tetrapods (after Foelix 1996) at increased speed is plausible, given subjective viewings of the high-speed video of spider runs. However, it is not supported by the data presented here, since a statistically significant relationship between speed and leg synchrony is not seen in either species. The raw number of frames in which individual legs appear at least partially out of phase with the rest of a tetrapod is clearly greater in the slower runs of both species, but normalization of these measurements by duration of stance phase reduces that relationship to insignificance. It

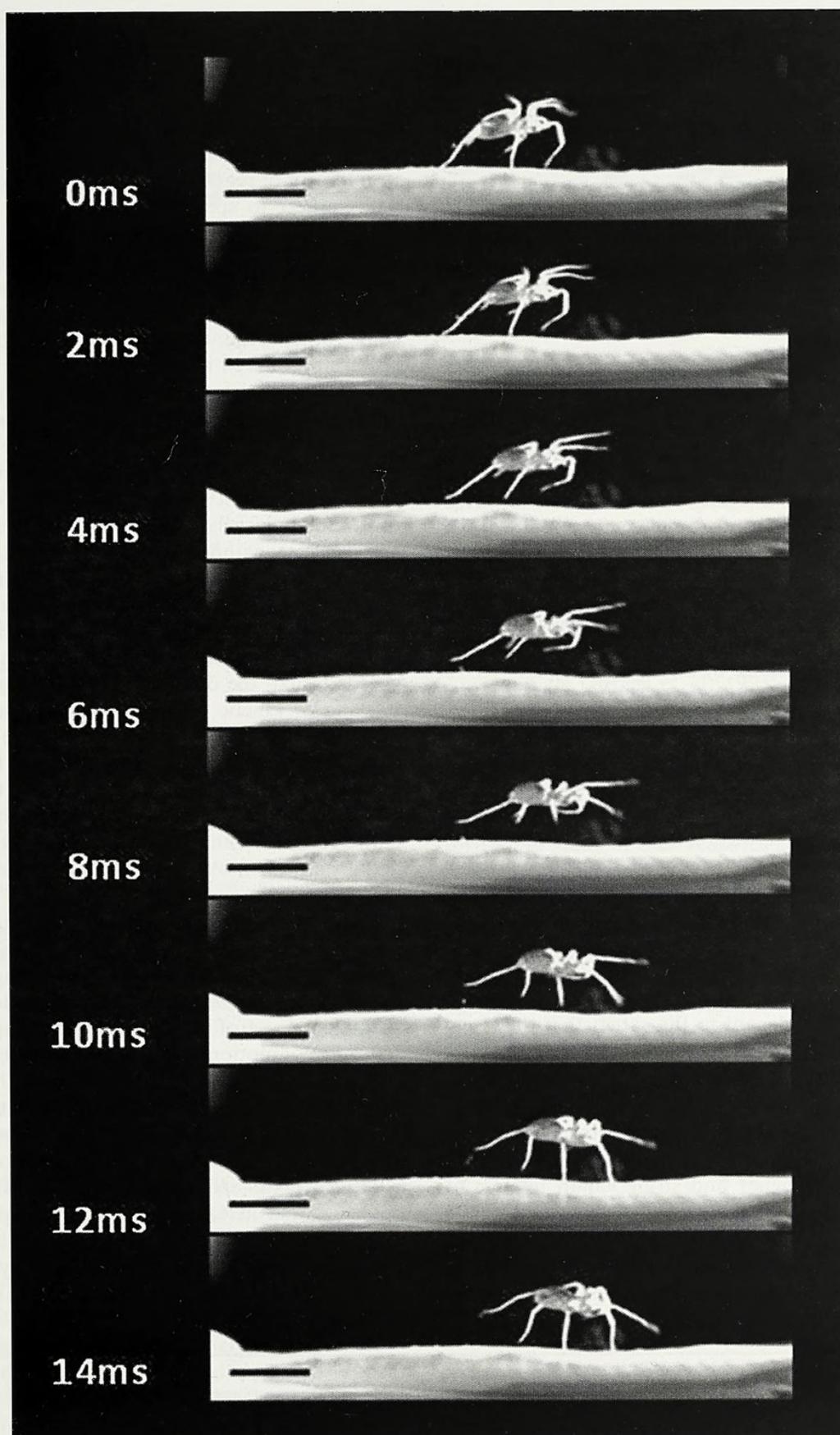


Figure 1.—Sequence of frames (alternating frames filmed at 1000 f/s) showing aerial phase achieved by a specimen of *Hololena curta*.

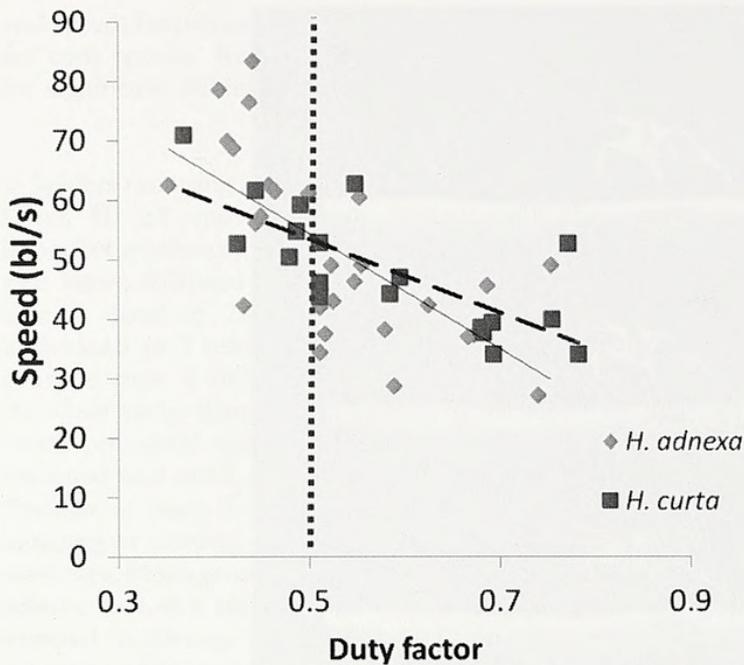


Figure 2.—Negative linear relationships between speed (normalized by body size) and duty factor for two species of grass-spider (*Hololena adnexa* = solid line, *Hololena curta* = hatched line). Points with duty factors of less than 0.5 (left of dotted line) represent runs where an aerial phase was indicated by the kinematic data.

appears that any reduction in variation at increasing speeds is proportional to the reduction in the duty factor and length of stance phase at increasing speeds.

**Gait transitions.**—There are several ways to characterize animal gaits, but it is not always simple to determine with certainty whether a movement is a walk, a run, or some intermediate gait (see Hutchinson et al 2003; Ahn et al. 2004). One rather obvious method, dating back to the early days of motion photography (e.g., Muybridge 1887), is the shift from a gait where at least one leg is in contact with the ground, to one where all legs are in swing phase—the shift to aerial phase. Aerial phases are relevant to the extent that they may represent a shift in or contribute to speed, energy efficiency, or stability.

The aerial phase is rare in arthropods (Blickhan et al. 1993), but a version of it is seen in the *Hololena* spiders characterized here. Other methods of categorizing running gait rely on changes in the stride frequency and stride length relative to speed. Blickhan & Full (1987) showed that while running, the ghost crab has two running regimes: a slow run for which stride frequency increases linearly with speed while stride

length remains stable, and a fast run for which speed increases are associated with increases in stride length. This study, by contrast, showed increases in both stride length and stride frequency contributing to increase speed linearly across a range of speeds, including those for which the spiders show aerial phases. This means that obvious shifts (changes in slope or intercept of regression lines) in gait regime are not apparent with respect to speed. These data may also represent these spiders running in a narrow subset of the range of speeds possible for them. A treadmill experiment at speeds chosen by the experimenter could reveal frequency and stride-length transitions analogous to those characterized in ghost crabs, or some other type of transition at extremes of the speed spectrum not seen in this data set.

These analyses did not include force measurements or tracking of the animals' center of mass in three dimensions, so any discussion of the dynamics of stable running, which have been used in many studies to combine kinematics and kinetics (Blickhan & Full 1987; Blickhan et al. 1993; Full & Tu 1990), must remain largely speculative. However, the existence of the aerial phase without any obvious gait transitions suggests strongly that the animals must be dynamically stable, rather than statically stable, while executing a steady forward run (Ting et al. 1994). Without obvious transition points, we make the conservative assumption that throughout the range of speeds tested, the dynamics contributing to stability, such as phasing of kinetic and potential energies, remain the same. The smooth transition to the aerial phase with respect to speed and other gait parameters suggests that the gait being used is consistent. The shift is thus minor, and the consistency likely contributes to the dynamic stability of the animals during the entire range of runs studied, including those with the visible aerial phase, but also, and perhaps more importantly, during slower runs.

Without associated physiological data such as  $V_{O_2}$  measurements (Anderson & Prestwich 1982, 1986), this study cannot address the question of changes in physiological efficiency of movement with transition to an aerial phase, or the spiders' use of dynamically stable locomotion across the full range of motion, but it does open the possibilities of future work in these areas. A reasonable hypothesis, given the linear appearance of the present data, is that if there is a transition in terms of physiological efficiency, it may occur below the range of speeds studied here.

**Other taxa.**—Although the Agelenidae, including the spiders tested here, are noted for being fast runners among the spiders (Bristowe 1968), with so few kinematic data available, there certainly are other likely untested candidates

Table 1.—Statistical relationships between speed and gait parameters in *Hololena* species.

Regression — Species	<i>n</i>	$r^2$	Slope	Y-intercept	<i>P</i>
Speed / duty factor — <i>H. adnexa</i>	28	0.45	-96.88	102.82	< 0.0001
Speed / duty factor — <i>H. curta</i>	19	0.57	-61.89	84.45	0.0002
Speed / stride length — <i>H. adnexa</i>	28	0.53	26.19	-5.32	< 0.0001
Speed / stride length — <i>H. curta</i>	19	0.39	17.39	9.92	0.004
Speed / frequency — <i>H. adnexa</i>	28	0.64	2.60	-8.40	< 0.0001
Speed / frequency — <i>H. curta</i>	18	0.13	1.20	20.52	0.15 (n.s.)
Speed / synchrony — <i>H. adnexa</i>	27	0.13	30.96	42.75	0.06 (n.s.)
Speed / synchrony — <i>H. curta</i>	19	0.04	-16.18	53.41	0.43 (n.s.)

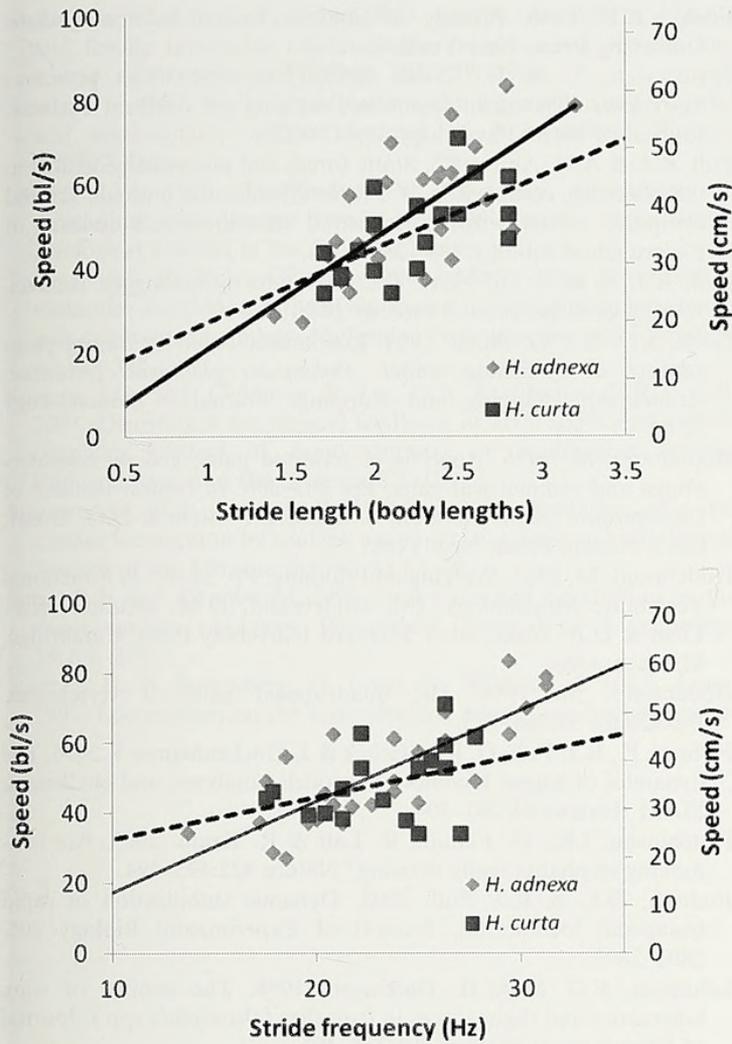


Figure 3.—Top panel: scatterplot and regressions for speed vs. stride length (relative to body length). *Hololena adnexa* runs are represented by diamonds and solid regression line; *Hololena curta* runs represented by squares and hatched regression line. Bottom panel: scatterplot and regressions for stride frequency (Hz) versus speed, with markers using the same conventions as top panel. Secondary axes show raw speeds estimated using the mean carapace plus abdomen length of 7.3 mm.

for the fastest spider. The large range of spider morphologies and running strategies makes these taxa a rich area for study. Spiders with laterigrade (sideways) leg orientations or gaits, such as those in the Thomisidae, Sparassidae and Selenopidae would provide interesting comparisons to both the spiders with more standard leg orientations and to the sideways-running ghost crabs (*Ocypode quadrata*), which are the best-characterized and fastest of eight-legged running animals (Blickhan & Full 1987; Blickhan et al. 1993). Other spiders and arachnids, particularly cursorial hunters such as Lycosidae (wolf spiders) and the Solifugae (wind-scorpions) appear to achieve extremely high speeds, though they have never been rigorously measured and documented. Spiders such as orb-web-weavers that forage in vertically oriented webs may also provide a useful counterpoint to these successful runners, as may the heavier, slower-moving Theraphosidae, or tarantulas (Wilson 1967).

From an evolutionary and comparative viewpoint, arachnids represent the terrestrial branch of a lineage, the

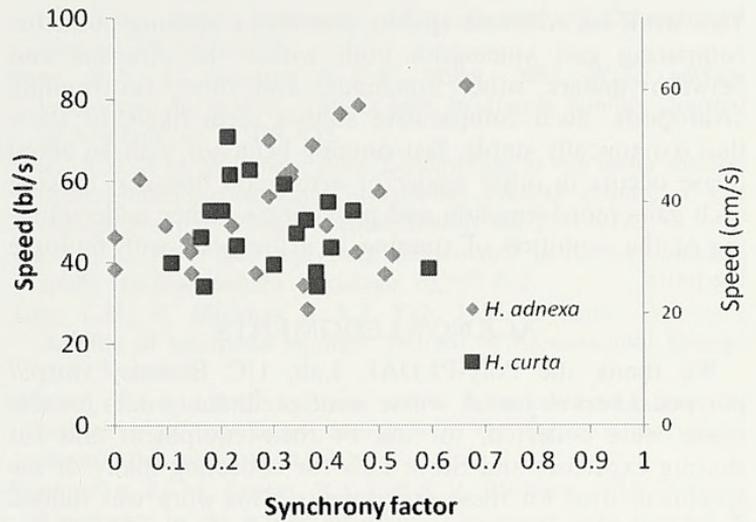


Figure 4.—Scatterplots of synchrony factor (normalized fraction of stride overlap between legs in the same tetrapod, see text) versus speed for *Hololena adnexa* (diamonds) and *Hololena curta* (squares). Regression lines (not shown) are not statistically significant at  $P < 0.05$ .

chelicerates, which diverged from the rest of the arthropods in the ocean at least 550 million years ago, approximately 100 million years before the invasion of terrestrial environments by any animals (Briggs et al. 1993). Thus, similar adaptations specific to terrestrial running behavior that have occurred in both insects and spiders can be considered the result of convergent evolution.

The family Agelenidae (consisting of over 1000 species if Coelotinae are included in the family, following Miller et al. 2010) and many of their relatives have a lifestyle dependent on foraging on irregular substrates such as shrubs and grasses (Roth & Brame 1972; Spagna & Gillespie 2008) and have a high vulnerability to predation and parasitism (Tanaka 1992). Therefore, the ability to escape quickly via a dynamically stable run requiring minimal nervous feedback (Spagna et al. 2007) is an adaptive hypothesis that should be further tested.

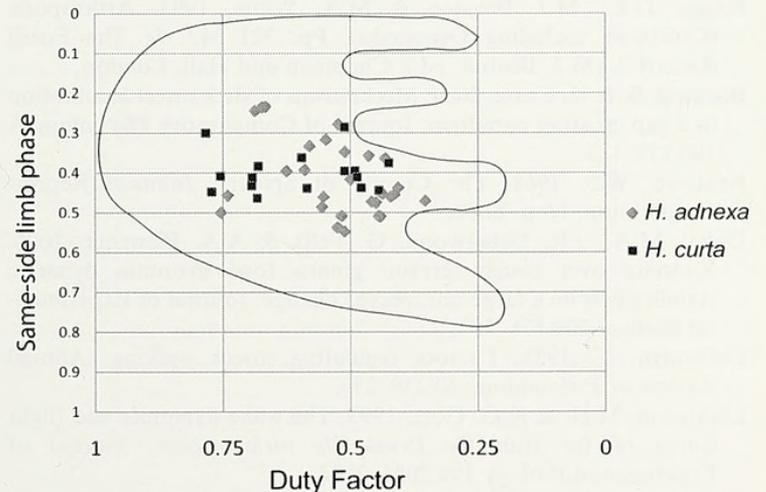


Figure 5.—Hildebrand plot of gait parameters (duty factor and same-side limb phase) used to determine animal gaits. Majority of points fall in range of medium to fast trotting gaits (third 'finger' from the top). Outline represents range of gaits of 156 genera of four-legged animals (Hildebrand 1989).

This work on *Hololena* spiders provides a starting point for comparing gait kinematics both within the Araneae and between spiders, other arachnids, and other fast-running arthropods. Such comparative studies seem likely to show that dynamically stable, fast-running behavior with an aerial phase occurs in other spider or arthropod lineages, making such gaits more common and providing a richer understanding of the evolution of running in arthropods with multiple leg-pairs.

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#### LITERATURE CITED

- Ahn, A.N., E. Furrow & A.A. Biewener. 2004. Walking and running in the red-legged running frog, *Kassina maculata*. *Journal of Experimental Biology* 207:399–410.
- Alexander, R.M. 1988. *Elastic Mechanisms in Animal Movement*. Cambridge University Press, Cambridge, UK.
- Alexander, R.M. 2003. *Principles of Animal Locomotion*. Cambridge University Press, Cambridge, UK.
- Anderson, J.F. & K.N. Prestwich. 1975. The fluid pressure pumps of spiders (Chelicerata, Araneae). *Zeitschrift für Morphologie der Tiere* 81:257–277.
- Anderson, J.F. & K.N. Prestwich. 1982. Respiratory gas exchange in spiders. *Physiological Zoology* 55:72–90.
- Anderson, J.F. & K.N. Prestwich. 1985. The physiology of exercise at maximum aerobic capacity of a theraphosid (tarantula) spider, *Brachypelma smithi* (F.O. Pickard-Cambridge). *Journal of Comparative Physiology B* 155:529–539.
- Blickhan, R. & R.J. Full. 1987. Locomotion energetics of the ghost crab II. Mechanics of the centre of mass during walking and running. *Journal of Experimental Biology* 130:155–174.
- Blickhan, R., R.J. Full & L. Ting. 1993. Exoskeletal strain: evidence for a trot-gallop transition in rapidly running ghost crabs. *Journal of Experimental Biology* 179:301–321.
- Briggs, D.E., M.J. Weedon & M.A. White. 1993. Arthropoda (Crustacea excluding Ostracoda). Pp. 321–342. *In* *The Fossil Record 2*. (M.J. Benton, ed.). Chapman and Hall, London.
- Blaesing, B. & K. Cruse. 2004. Mechanisms of stick insect locomotion in a gap crossing paradigm. *Journal of Comparative Physiology A* 190:173–183.
- Bristowe, W.S. 1968. *The Comity of Spiders*. Johnson Reprint Corporation, New York.
- Daley, M.A., J.R. Usherwood, G. Felix & A.A. Biewener. 2006. Running over rough terrain: guinea fowl maintain dynamic stability despite a large unexpected change. *Journal of Experimental Biology* 209:171–187.
- Delcomyn, F. 1985. Factors regulating insect walking. *Annual Review of Entomology* 30:239–256.
- Dickinson, M.H. & K.G. Gotz. 1993. The wake dynamics and flight forces of the fruit fly *Drosophila melanogaster*. *Journal of Experimental Biology* 199:2085–2104.
- Dickinson, M.H., C.T. Farley, R.J. Full, M.A.R. Koehl, R. Kram & S. Lehman. 2000. How animals move: an integrative view. *Science* 288:100.
- Ferris, D.P., M. Louie & C.T. Farley. 1998. Running in the real world: adjusting leg stiffness for different surfaces. *Proceedings of the Royal Society of London B* 265:989–994.
- Foelix, R.F. 1996. *Biology of Spiders*. Second edition. Oxford University Press, New York.
- Frantsevich, L. & H. Cruse. 1997. The stick insect, *Obrimus asperimus* (Phasmida, Bacillidae) walking on different surfaces. *Journal of Insect Physiology* 43:447–455.
- Full, R.J. & A.N. Ahn. 1995. Static forces and moments generated in the insect leg: comparison of a three-dimensional musculo-skeletal computer model with experimental measurements. *Journal of Experimental Biology* 198:1285–1298.
- Full, R.J. & M.S. Tu. 1990. The mechanics of six-legged runners. *Journal of Experimental Biology* 148:129–146.
- Gorb, S.N. & F.G. Barth. 1994. Locomotor behavior during prey-capture of a fishing spider, *Dolomedes plantarius* (Araneae: Araneidae): galloping and stopping. *Journal of Arachnology* 22:89–93.
- Hildebrand, M. 1976. Analysis of tetrapod gaits: general considerations and symmetrical gaits. Pp. 203–206. *In* *Neural Control of Locomotion*. (R.M. Herman, S. Grillner, P. Stein & D.G. Stuart, eds.). Plenum Press, New York.
- Hildebrand, M. 1985. Walking and running. Pp. 38–57. *In* *Functional Vertebrate Morphology*. (M. Hildebrand, D.M. Bramble, K.F. Liem & D.B. Wake, eds.). Harvard University Press, Cambridge, Massachusetts.
- Hildebrand, M. 1989. The quadrupedal gaits of vertebrates. *BioScience* 39:766–775.
- Holmes, P., R.J. Full, D. Koditschek & J. Guckenheimer J. 2006. The dynamics of legged locomotion: models, analyses, and challenges. *SIAM Reviews* 48:207–304.
- Hutchinson, J.R., D. Famini, R. Lair & R. Kram. 2003. Are fast-moving elephants really running? *Nature* 422:493–494.
- Jindrich, D.L. & R.J. Full. 2002. Dynamic stabilization of rapid hexapedal locomotion. *Journal of Experimental Biology* 205:2803–2823.
- Lehmann, F.O. & M.H. Dickinson. 1998. The control of wing kinematics and flight forces in fruit flies (*Drosophila* spp.). *Journal of Experimental Biology* 201:385–401.
- Lighton, J.R.B. & R.G. Gillespie. 1989. The energetics of mimicry: the cost of pedestrian transport in a formicine ant and its mimic, a clubionid spider. *Physiological Entomology* 14:173–177.
- Miller, J.A., A. Carmichael, M.J. Ramirez, J.C. Spagna, C.R. Haddad, M. Rezac, J. Johannesen, J. Král, X-P. Wang & C.E. Griswold. Phylogeny of entelegyne spiders: affinities of the family Penestomidae (NEW RANK), generic phylogeny of Eresidae, and asymmetric rates of change in spinning organ evolution (Araneae, Araneoidea, Entelegynae). *Molecular Phylogenetics and Evolution* 55:786–804.
- Muybridge, E. 1887. *Animal Locomotion*. University of Pennsylvania, Philadelphia, Pennsylvania.
- Nachtigall, W. 1980. Mechanics of swimming in water-beetles. *Society for Experimental Biology Seminar Series* 5:107–124.
- Naftilan, S.A. 1999. Transmission of vibrations in funnel and sheet spider webs. *International Journal of Biological Macromolecules* 24:289–293.
- Opell, B.D. 1994. Increased stickiness of prey capture threads accompanying web reduction in the spider family Uloboridae. *Functional Ecology* 8:85–90.
- Opell, B.D. 1996. Functional similarities of spider webs with diverse architectures. *American Naturalist* 148:629–648.
- Parry, D.A. & R.H.J. Brown. 1959. The hydraulic mechanism of the spider leg. *Journal of Experimental Biology* 36:423–433.
- Roth, V.D. & P.L. Brame. 1972. Nearctic genera of the spider family Agelenidae (Arachnida, Araneida). *American Museum Novitates* 2505:1–52.
- Sensenig, A.T. & J.W. Shultz. 2003. Mechanics of cuticular elastic energy storage in leg joints lacking extensor muscles in arachnids. *Journal of Experimental Biology* 206:771–784.

- Shillington, C. & C.C. Peterson. 2002. Energy metabolism of male and female tarantulas (*Aphonopelma anax*) during locomotion. *Journal of Experimental Biology* 205:2909–2914.
- Shultz, J.W. 1987. Walking and surface film locomotion in terrestrial and semi-aquatic spiders. *Journal of Experimental Biology* 128:427–444.
- Shultz, J.W. 1989. Morphology of locomotor appendages in Arachnida: evolutionary trends and phylogenetic implications. *Zoological Journal of the Linnean Society* 97:1–56.
- Spagna, J.C. & R.G. Gillespie. 2008. More data, fewer shifts: molecular insights into the evolution of the spinning apparatus in non-orb-weaving spiders. *Molecular Phylogenetics and Evolution* 46:347–368.
- Spagna, J.C., D.I. Goldman, P. Lin, D.E. Koditschek & R.J. Full. 2007. Distributed mechanical feedback in arthropods and robots simplifies control of rapid running on challenging terrain. *Bioinspiration and Biomimetics* 2:9–18.
- Stratton, G., R.B. Suter & P.R. Miller. 2004. Evolution of water surface locomotion by spiders: a comparative approach. *Biological Journal of the Linnean Society* 81:63–78.
- Suter, R.B. & J. Grunewald. 2000. Spider size and locomotion on the water surface (Araneae, Pisauridae). *Journal of Arachnology* 28:201–210.
- Suter, R.B., S. Rosenberg, H. Loeb, H. Wildman & J.H.J. Long. 1997. Locomotion on the water surface: propulsive mechanisms of the fisher spider *Dolomedes triton*. *Journal of Experimental Biology* 200:2523–2538.
- Suter, R.B., G. Stratton & P.R. Miller. 2003. Water surface locomotion by spiders: distinct gaits in diverse families. *Journal of Arachnology* 31:428–432.
- Suter, R.B. & H. Wildman. 1999. Locomotion on the water surface: hydrodynamic constraints on rowing velocity require a gait change. *Journal of Experimental Biology* 202:2771–2785.
- Tanaka, K. 1992. Size-dependent survivorship in the web-building spider *Agelena limbata*. *Oecologia* 90:597–602.
- Ting, L.H., R. Blickhan & R.J. Full. 1994. Dynamic and static stability in hexapedal runners. *Journal of Experimental Biology* 197:251–269.
- Watson, P. & J.R.B. Lighton. 1994. Sexual selection and the energetics of copulatory courtship in the Sierra dome spider. *Animal Behaviour* 48:615–626.
- Weihmann, T., M. Karner, R.J. Full & R. Blickhan. 2010. Jumping kinematics in the wandering spider *Cupiennius salei*. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology* 196:421–438.
- Wilson, D.M. 1967. Stepping patterns in tarantula spiders. *Journal of Experimental Biology* 47:133–151.

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