LOCOMOTION IN BURROWING AND VAGRANT WOLF SPIDERS (LYCOSIDAE)

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SUMMARY

Locomotion in the vagrant wolf spider *Trochosa ruricola* is compared to that in the burrow dwelling wolf spider *Lycosa tarentula* (Araneae: Lycosidae). *L. tarentula* takes relatively shorter steps than *T. ruricola*. At high speeds *T. ruricola* approximates an alternating tetrapod gait but this does not occur in *L. tarentula*. Phase lag differs between species and varies marginally with speed except for ipsilateral phase lags in *L. tarentula* which are erratic if they include leg 1. In both species the protraction/retraction ratio is directly related to both running speed and stepping frequency, but the relationship is more marked in *L. tarentula*. The protraction/retraction ratio is more variable in leg 1 and varies between legs along the body but by a greater amount in *L. tarentula*. In these spiders, in contrast to the situation in many insects, both the duration of protraction and retraction show marked inverse relationships to stepping frequency. The power stroke (retraction) occupies a variable proportion of the stepping cycle, which is not the case in other spiders, and this proportion is lower than for other spiders.

It is suggested that the first pair of legs is used more for sensory than for locomotory purpose and that this is more marked in the burrow dwelling species, *L. tarentula*.

INTRODUCTION

The characteristic gaits determined from studies of arthropod locomotion fall into two basic models; the metachronal wave and the alternating tripod gait (Wilson, 1966; Graham, 1972; Pearson & Iles, 1973). The former predominates in the non-insect uniramid groups (Manton, 1973) and is epitomised in the gait of millipedes. The alternating tripod gait is seen in insects (Hughes, 1952) and is essentially similar to the alternating tetrapod gait of octopodal arthropods since both are based on the alternation of ipsilateral and contralateral legs. Arthropod locomotion has been studied extensively to examine evolutionary relationships (Manton, 1953, 1973) and intensively to elucidate the underlying neural control of locomotion. The latter workers have concentrated on insects (reviews by Wilson, 1967; Bowerman, 1977), although crustacea (Burrows & Hoyle, 1973; Barnes, 1975; MacMillan, 1975; Ayres

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& Davis, 1977) and arachnids (Bowerman, 1975 a; Wilson, 1967; Land, 1972) have been examined.

Amongst octopods the alternating tetrapod gait predominates (scorpions – Bowerman, 1975 a; Root & Bowerman, 1978; spiders – Wilson, 1967) although in fiddler crabs aspects of both alternating and metachronal gaits were present (Barnes, 1975). Stepping patterns may vary within individuals to compensate for irregular surfaces (Pearson & Iles, 1973), inclines (Spirito & Mushrush, 1979) and missing legs (spiders – Wilson, 1967; scorpions – Bowerman, 1975 b; cockroach – Delcomyn, 1971 b). Additionally steps may be missing from the stepping cycle of grasshoppers (Graham, 1978) and the stepping cycle may change between instars (stick insects – Graham, 1972). Stereotyped burying behaviour is present in a *Sicarus* spider (Reiskind, 1969).

Such variation suggests that gaits may be adapted to the life style of closely related species and this report compares the stepping pattern of vagrant and burrowing wolf spiders.

MATERIALS AND METHODS

Two species of wolf spiders were investigated. *Trochosa ruricola* (DeGeer, 1778) is typically vagrant in habit and the spiders move over the substrate at night but, like many lycosids, are probably sit and wait predators relying on prey movement for initial contact. They were collected from peat workings on Shapwick Heath, Somerset. *Lycosa tarentula* (Linné, 1758) lives in burrows and spends most of the day at the mouth of the burrow awaiting prey contact and thermoregulating behaviourally (Humphreys, unpublished) like many burrow inhabiting lycosids (Humphreys, 1978). They were collected from old talc workings at Arnissa in northern Greece. This should not be confused with the new world tarantulas which are mygalomorph rather than araeneomorph spiders.

A 'Hycam' rotating prism camera was used for filming at between 250 and 400 frames per sec, f.p.s. (interval between frames 4–2·5 ms). A neon light inside the camera placed time marks on the film at 10 ms intervals. Double perforated Kodak 4 X negative film was used and rated at 400 ASA for hand processing in D 76 developer.

The spiders were run in an arena from a holding area across a grid beneath the camera lens and illuminated through heat filters by two 150 W slide projectors located 1 m away on either side of the arena. This provided hard shadows of the spiders legs to give a precise indication of lift-off and touch-down. To encourage straight runs with *T. ruricola* the lights were placed perpendicular to the direction of movement and the spiders ran to the darkened receiving area in more than half the runs. *L. tarentula* tended to run towards the light so for runs with this species the lights were rotated by 90° so that the projectors shone along rather than across the expected path of the spider. All filming was done at laboratory temperatures of about 23 °C.

Terminology

The terminology used in the literature to describe stepping patterns is confused. Burns (1973) uses the term 'stepping period' to describe the same thing that Wilson

1967) calls 'interval' and Graham (1977) calls simply 'period'. These studies all use the time from lift-off to lift-off to define period. To avoid confusion, the terms used in this paper are defined below.

Protraction (p)	leg raised and moved forward.
Retraction (r)	leg down, moved backward.
Period (τ)	the time taken (ms) for one leg to complete a stepping cycle. For this paper it was measured from touch down to touch down. Any other phase could have been used but this cycle could be most precisely determined.[*]
Lag (l)	the time difference (ms) between touch down for different specified legs ([*]see above).
Phase lag (Φ)	lag/period.
p/r ratio	duration of protraction/duration of retraction.
Stepping frequency (ν)	the number of steps/s.
Leg numbering	legs are number in sequence from 1 (front legs) to 4 (hind legs) and the left (L) and right (R) sides distinguished where appropriate.

Analysis

Two methods are commonly used to represent stepping patterns. The first records the position of the tarsal segments relative to the body (Hughes, 1952; Manton, 1953) whilst the second records whether the legs are on or off the ground (Wilson, 1967). The latter method was adopted here as it is better suited to quantitative analysis.

Stepping patterns were drawn from frame by frame analysis ($\simeq$ 4000 frames) using a stop motion projector and the time corrected every ten frames to correct for the varying film speed through the camera. The movement of a single leg was followed through an entire run before further legs were analysed to prevent bias. In both species the hind legs dragged for part of the stepping cycle. The drag was recorded on the stepping patterns but for quantitative analysis the drag was taken to be a constituent part of protraction as a dragged leg cannot provide propulsion. Ground speeds were calculated from the movement of the spiders across the grid using the time marks on the film. Frame numbers were converted to time from the start of a run before quantitative analysis.

Analysis is presented only for juvenile and mature female spiders. Successful runs were defined as those in which the spider ran at constant speed and turned less than 30° in one field of view of the camera (9 cm for *T. ruricola* and 20 cm for *L. tarentula*). Data are presented for 27 successful runs for *T. ruricola* and 17 for *L. tarentula* obtained from three individuals of each species, although for one of the individuals of each species only one run was successful. Because more than one stepping cycle per run was analysed, the number of data used in analysis was higher, varying with the parameter analysed up to $N = 85$.
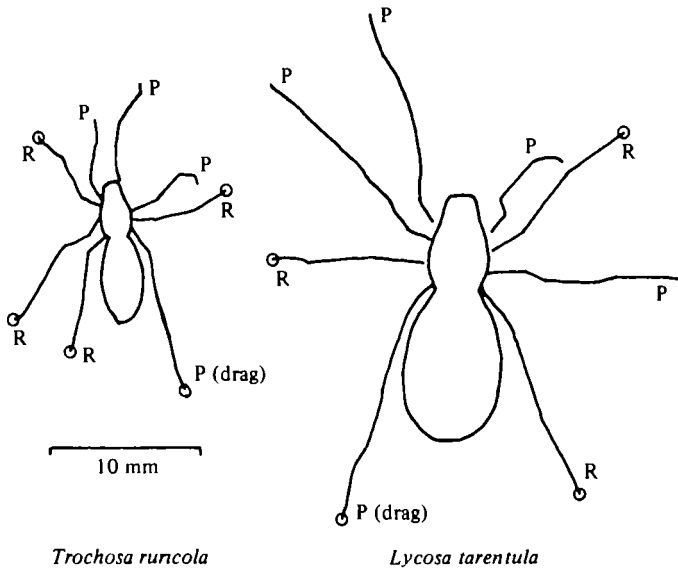
Fig. 1. Typical leg arrangements during running, traced from film.
P = protraction, R = retraction.

Statistical treatment

In biology the application of statistics for circular distributions is widely employed in studies of animal orientation but is equally applicable to the analysis of periodic fluctuations. Their application to locomotory rhythms was first suggested by Graham (1977) and they are used here. Mean direction and angular standard deviation were determined from standard algorithms (Batschelet, 1965; Mardia, 1972). The Rayleigh Test and the Two Sample Test were used for tests of significance and the critical values read from the tables of Watson and Williams (in Mardia, 1972).

Mardia (1972) suggests that if the range of values considered does not exceed $\pi/2$ radians (0·25 phase lag units) then the data may be treated as for linear normal distributions. Since in this study the range of values exceeds $\pi/2$ radians the circular normal distribution has been applied throughout.

To aid continuity probability values only are presented in the text for some statistical tests. Least-squares regressions were tested for significant slopes by t test and their slopes compared by analysis of variance and a posteriori STP. Multiple comparison of means was conducted a priori using least significant difference and a posteriori by least significant range following analysis of variance. All tests followed Sokal & Rohlf (1969).

RESULTS

Leg movements and size

Leg movements appear similar in both species. The movements of legs 1 and 2 are similar (Fig. 1); the leg is lifted, extended in front of the spider, touched down and then flexed to provide the propulsive force. Flexion in leg 1 brings the tarsal segments almost under the cephalothorax while leg 2 touches down further to the
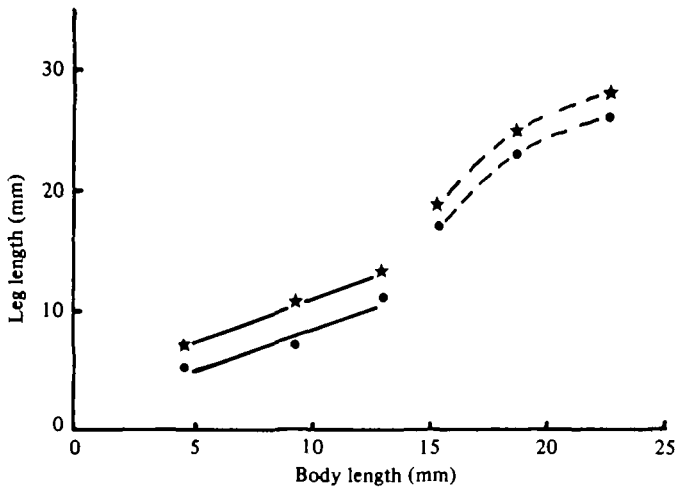
Fig. 2. The relationship between body length and the lengths of leg 1 (●) and leg 4 (★) in *T. ruricola* (———) and *L. tarentula* (—).
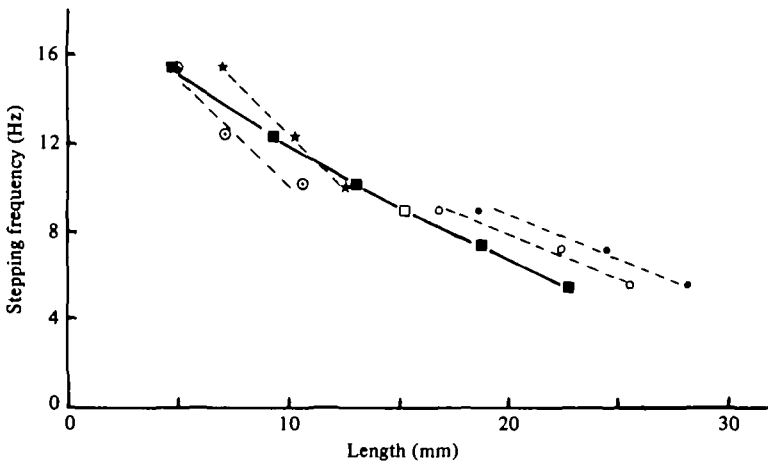

Fig. 3. The relationship between stepping frequency (Hz) at a speed of 0·2 m s⁻¹ and body (■, □), leg 1 (⊕, ○) and leg 4 (★, ●) lengths in *T. ruricola* and *L. tarentula*. The three smaller individuals are *T. ruricola* and the larger three *L. tarentula*. □, Estimated from the common slope of the lines in Fig. 9.

side and flexion brings the tarsal segments level with the front of the abdomen. Leg 3 is swept backward whilst held straight, with the coxa to tarsal distance remaining relatively constant, although some twisting occurs. In leg 4 propulsion results from extension of the leg. While running, both species move their body from side to side, but the significance of this would require analysis of forces exerted on the substrate, using photoelastic substrate transduction (Harris, 1978).

In *T. ruricola* the legs become proportionately shorter as body length increases (allometric mean slope = 0·78, Fig. 2) while in *L. tarentula* leg lengths increase relative to body length (allometric mean slope = 1·76, Fig. 2). In both species, at a given speed (0·2 m s⁻¹), stepping frequency is inversely related to both body and leg
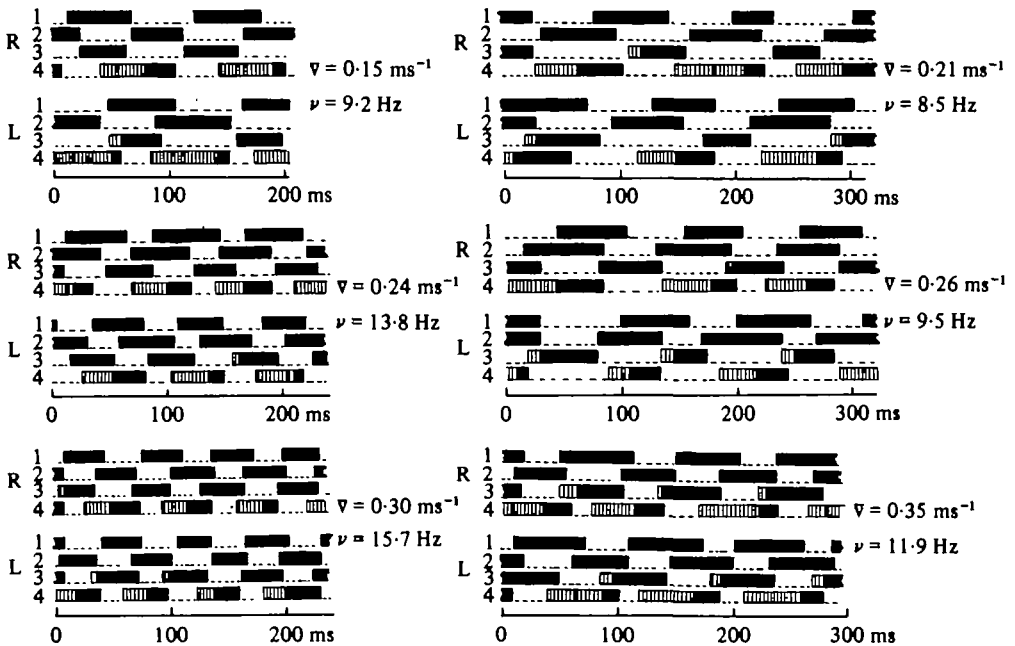
Fig. 4. Stepping pattern diagrams at the stepping frequencies (ν) and velocities ($\bar{v}$) indicated. Solid bars denote protraction and hatched bars indicate leg drag. Diagrams on the left are for *T. ruricola* and on the right for *L. tarentula*. $\bar{v}$ and ν increase down the page for both species.

length (Fig. 3). For either species body length is a good predictor of stepping frequency (Fig. 3) but stepping frequency decreases more rapidly with increasing leg length in *T. ruricola* than in *L. tarentula* (Fig. 3).

Stepping pattern

Stepping pattern diagrams (Fig. 4) for a range of speeds ($\bar{v}$) show that the period (γ) decreases and the stepping frequency (ν) increases as the speed increases and that the larger and longer legged *L. tarentula* has a longer period for a given speed. In *T. ruricola* the gait becomes close to an alternating tetrapod gait at higher speeds but in *L. tarentula* a true alternating tetrapod gait is not achieved even at the highest speeds filmed. The stepping pattern is highly variable so visual inspection is of little value and quantitative analysis was made using the stepping pattern diagrams.

Phase lag (Φ)

Both species show contralateral phase lag distributions closely grouped around the mean (i.e. 0·5, the value expected from an alternating tetrapod gait; Fig. 5). Contralateral phase lags are greater in *L. tarentula* than *T. ruricola* for R1:L1 and R4:L4 (two-sample test; $P \approx 0.05$). Phase lag distributions for adjacent ipsilateral leg pairs (Fig. 6) fall into two main groups; those including leg 1 and those not including leg 1. Phase lags including leg 1 have greater spread especially in *L. tarentula* where the distributions of phase lags R1:R2 and R1:R4 are random ($P > 0.05$, Rayleigh test). The non-random phase lags have different means ($P < 0.05$, two
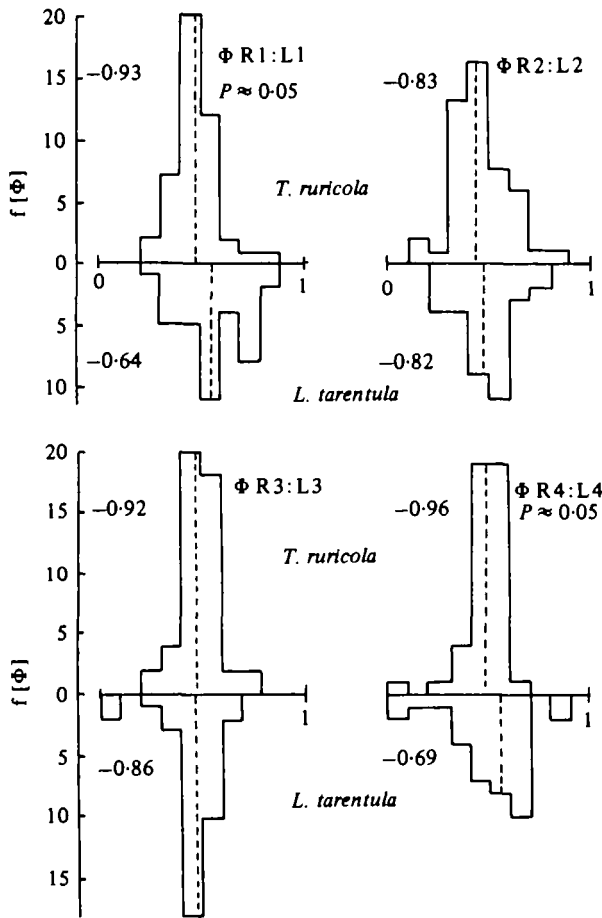
Fig. 5. Phase-lag (Φ) distributions for contralateral leg pairs. In each diagram the upper distribution represents *T. ruricola* and the lower distribution *L. tarentula*. R1:L1 indicates that the first right and left legs are compared. Probability values are given if the distributions differ significantly between species. Broken lines present the circular mean and the number in light type is the index of phase coupling (see text) which has limits of −1·0 and +1·0.

sample test) for the two species. Phase lags not including leg 1 have distributions closely grouped around the mean which for both species is close to 0·5 as expected from an alternating tetrapod gait.

Phase lag distributions for alternate ipsilateral leg pairs (Fig. 7) also fall into two groups again determined by whether or not the comparison includes leg 1. As before there is greater spread in phase lag including leg 1, particularly in *L. tarentula*, with phase lag R1:R3 being random ($P > 0.05$; Rayleigh test). The mean phase lag R1:R3 and L1:L3 differ between the species ($P < 0.05$, Two Sample Test). The mean phase lags for *L. tarentula* were close to 0·5 whilst those for *T. ruricola* were close to 0, the value expected for an alternating gait. Phase-lag distributions for comparisons not including leg 1 showed no difference between the two species and did not differ from zero.

The possibility that phase lag might change with speed was investigated by grouping
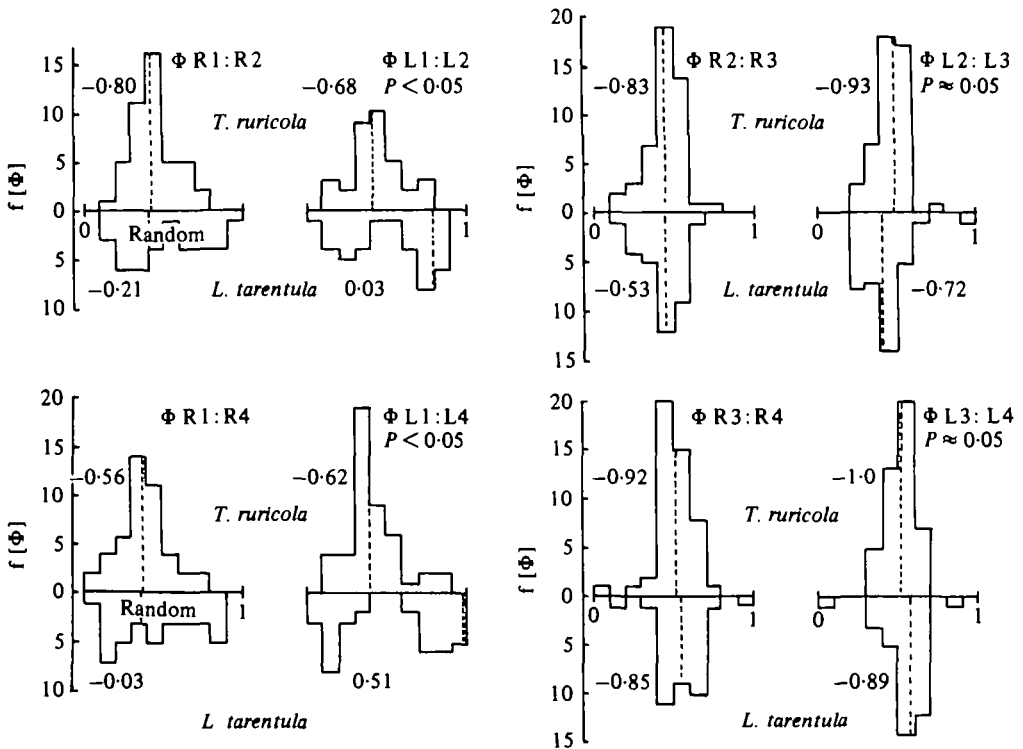
Fig. 6. Phase-lag (Φ) distributions for adjacent and adjacent-but-two ipsilateral leg pairs in both species of spider. Conventions follow those in Fig. 5.

the data into classes of 0·05 m s^{-1} (average speed over a filming run). Of the 16 comparisons, phase lag varied significantly at least at one speed in 10 and 6 cases in *L. tarentula* and *T. ruricola* respectively (Least significant range, α = 0·05). In all but one case (R2:R3 in *L. tarentula*) the significant variation of phase lag with speed occurs in comparisons including either leg 1, leg 4 or both. It will be seen from a number of other measurements that leg 1 is less closely coordinated than the other legs. Measurements on leg 4 are often ambiguous due to the high degree of leg dragging being included, for functional reasons, as part of protraction. Representative plots are shown in Fig. 8 for ipsilateral phase lags as these are more likely to show a change in phase lag with speed. The figure for ΦR2:R3 is typical of those found for contralateral phase lag whether or not leg 1 was involved. For the ipsilateral comparisons shown in Fig. 8 R2:R3 is typical of phase lags not including leg 1. Ipsilateral phase lags including leg 1 (R1:R2, R1:R4, R1:R3) show erratic changes with speed in *L. tarentula* and only slight changes in *T. ruricola*.

Comparison of the phase lag between species over a range of speeds shows that the mean phase lag differs (P < 0·05) in 33% of cases (N = 80) of which 70% of the differences occur in comparisons including leg 1. The same trend is true when the data are not divided into speed classes.

The degree of phase locking between different leg pairs is summarised using the index from Land (1972, p. 23). This index, which has limits of − 1·0 and + 1·0, ◢
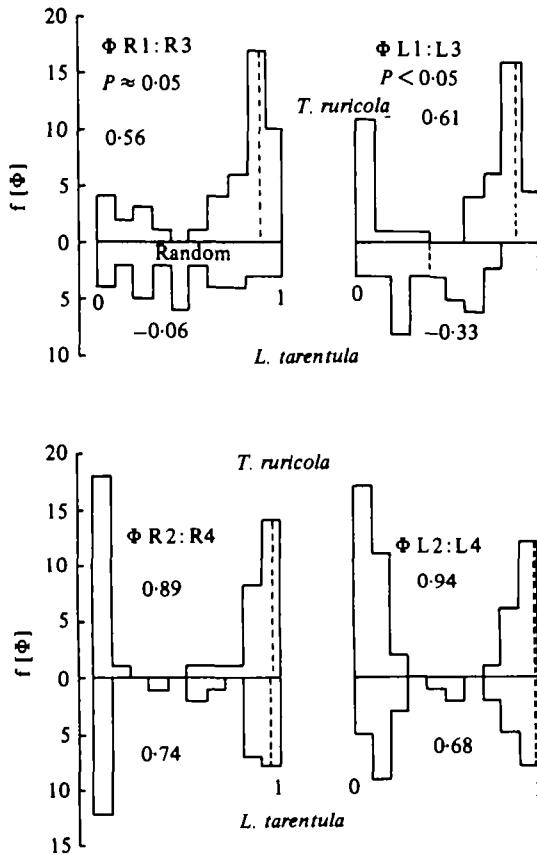
Fig. 7. Phase lag (Φ) distributions for adjacent-but-one ipsilateral leg pairs in both species of spider. Conventions follow those in Fig. 5.

negative when the legs step out of phase and positive when in phase with the magnitude indicating the strength of this tendency. The values are shown on each graph in Figs. 5–7 and the mean values for different leg comparisons in Table 1, where they are compared with other values for spiders from the literature. Although the degree of similarity varies according to the leg pairs considered, *T. ruricola* always has index values closer to the limits than *L. tarentula* (sign test; $P < 0.001$) showing its overall greater degree of phase locking. The overall degree of similarity (final matrix in Table 1) shows that phase locking differs more within a family of spiders (Lycosidae) than between the suborders represented by the mygalomorph and the salticid. While *T. ruricola* shows phase locking similar to the mygalomorph, *L. tarentula* differs markedly despite the latter having the more mygalomorph type of life style.

The relationship between speed ($\bar{v}$) and stepping frequency (ν)

This relationship is shown in Fig. 9 for individuals of both species. The change in stepping frequency with size (Fig. 4) suggests that the vertical displacement of ▮e graphs in Fig. 9 is primarily due to size differences between the spiders. Larger
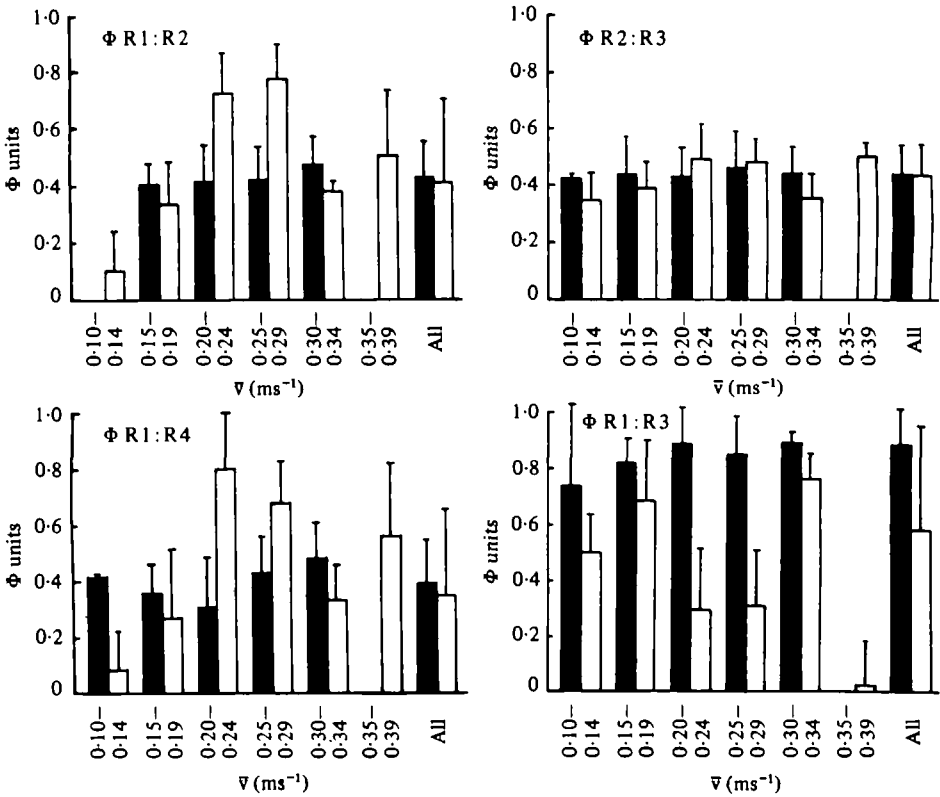
Fig. 8. Examples of mean phase lag (Φ) divided into classes of average speed ($\bar{v}$, m s⁻¹) for ipsilateral legs. Solid bars represent the values for *T. ruricola* and open bars those for *L. tarentula*. Vertical lines represent one angular standard deviation above the mean.

spiders have longer legs so for a given speed they have a lower stepping frequency. The lines in Fig. 9 are not parallel ($P < 0.01$). The slope for spider 2 differs from all others ($P < 0.01$) but the slopes for spiders 3, 4 and 6 do not differ ($P > 0.05$).

The relationship between protraction/retraction ratio (p/r) and both stepping frequency (v) and average speed ($\bar{v}$)

The correlation coefficients between p/r and both $\bar{v}$ and v are shown in Table 2. The data for *L. tarentula* show more significant correlations than those for *T. ruricola* ($P = 0.042$, Fisher's Exact Test) despite having fewer data points ($N = 14$–18, c.f. $N = 35$).

The data are more grouped and consistent for the relationship between p/r and $\bar{v}$ but in both relationships the data for leg 1 are markedly less grouped than those for the other legs. In both relationships the slopes of the best fit lines are, within legs, always greater for *L. tarentula* and the difference between the slopes is more marked for the relationship between p/r and v. For all legs the mean slope describing the relationship between p/r and $\bar{v}$ is greater for *L. tarentula* ($P < 0.005$) but the greater variability for the relationship between p/r and $\bar{v}$ makes the mean slopes for all legs not different between the species ($P > 0.05$).

Table 1. *Comparison of the mean index for phase locking* (limits $-1.0 + 1.0$) *between different leg groupings in* L. tarentula *and* T. ruricola *and the same index for the jumping spider* Metaphidippus harfordi (*Land, 1972*) *and the mygalomorph spider* Dugesiella hentzi (*Wilson, 1967, in Land, 1972*).

(Below are given matrices for the rank order of the difference between species (1 is most similar) for the three different leg comparisons, the mean absolute differences and their rank order in parentheses. TR, *Trochosa ruricola*; LT, *Lycosa tarentula*; MH, *Metaphidippus harfordi*; DH, *Dugesiella hentzi*.)

	T. ruricola	*L. tarentula*	*M. harfordi*	*D. hentzi*
Adjacent legs	−0·86	−0·53	−0·53	−0·89
Opposite legs	−0·90	−0·75	−0·25	−0·49
Next-but-one legs	0·75	0·26	0·42	0·61

Adjacent legs

	TR	LT	MH
LT	3·5	—	—
MH	3·5	1	—
DH	2	5·5	5·5

Opposite legs

	TR	LT	MH
LT	1	—	—
MH	6	5	—
DH	4	3	2

Adjacent-but-one legs

	TR	LT	MH
LT	6	—	—
MH	4	2	—
DH	1	5	3

Mean absolute difference of index (rank order)

	TR	LT	MH
LT	0·32 (4·5)	—	—
MH	0·44 (6)	0·22 (2)	—
DH	0·19 (1)	0·32 (4·5)	0·26 (3)

When considering the p/r ratio at a given speed ($\approx$ 0·2 m s^{-1}; range 0·200–0·212 m s^{-1}) p/r varies along the body in both species. In *L. tarentula* the p/r ratio of leg 1 = 2 > 3 < 4 ($P < 0.01$) with respective mean p/r ratios of 1·13, 1·14, 0·63 and 1·57. The same analysis for *T. ruricola* showed p/r leg 1 = 2 = 3 < 4 ($P < 0.01$) with mean p/r respectively of 1·23, 1·27, 1·15 and 1·95. The relative movement of the legs clearly differs along the body but analysis by other methods (those of Hughes, 1952, and Manton, 1953) would be needed to further elucidate these relationships.

The duration of protraction and retraction at different stepping frequencies

In *T. ruricola* the duration of both p and r are inversely related to stepping frequency (Table 2; $P < 0.01$ except r4 where $P < 0.05$). Further analysis of these regressions (*a posteriori* STP; Sokal & Rohlf, 1969) shows that the slopes of these relationships differ between legs for both p and r but that different legs are involved (Table 3). In addition the durations of p and r vary with stepping frequency, by the same slope in legs 1 and 2 ($P > 0.05$) but by different slopes in legs 3 and 4 ($P < 0.001$ and $P < 0.01$ respectively).

In *L. tarentula* the duration of retraction in all legs is inversely related to stepping frequency but this is only true for protraction in leg 2 (Table 3). As was the case in *T. ruricola* the slopes for the relationship between duration of retraction and stepping frequency differ between legs (Table 3). The only possible comparison between the slopes for p and r shows that the slopes for leg 2 are equal ($P > 0.25$).

The slopes of the relationships between duration of retraction and stepping frequency differ between species for legs 1, 3 and 4 ($P < 0.025$, $P < 0.001$ and
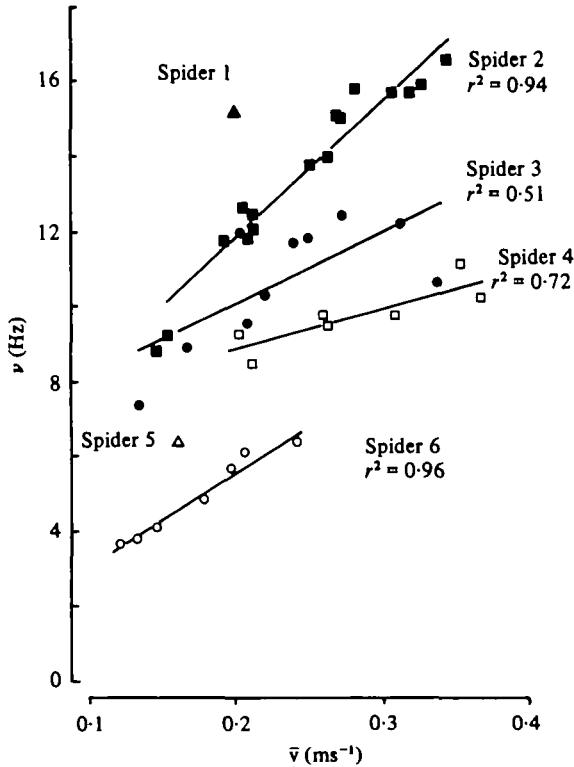
Fig. 9. The relationships between average speed ($\bar{v}$, m s^{-1}) and stepping frequency (ν, Hz). Open symbols, *L. tarentula*; filled symbols, *T. ruricola*. Spiders are numbered in order of increasing size.

Table 2. *Correlation coefficients* (r) *for the relationship between* p/r *ratio and both average speed* ($\bar{v}$) *and stepping frequency* (ν)

		T. ruricola		L. tarentula	
		Spider 2	Spider 3	Spider 4	Spider 6
		r_s	r_s	r_s	r_s
$\bar{v}$	R1	0·003	−0·165	0·629*	−0·120
	R2	−0·042	0·306	0·329	0·766*
	R3	0·547*	0·483	0·853*	0·680*
	R4	0·291	0·364	0·579*	0·542*
	L1	0·375*	0·277	0·349	−0·123
	L2	0·227	0·670*	0·065	0·243
	L3	0·514*	0·413	0·696*	0·775*
	L4	−0·094	0·325	0·582*	0·760*
		r_s	r_s	r_s	r_s
ν	R1	0·051	0·207	0·550*	−0·181
	R2	0·104	0·287	0·228	0·664*
	R3	0·467*	0·635*	0·825*	0·594*
	R4	0·207	0·246	0·594*	0·547*
	L1	0·339*	0·215	0·092	0·018
	L2	0·326*	0·380	0·257	0·144
	L3	0·413*	0·418	0·450*	0·730*
	L4	−0·097	0·067	0·379	0·747*

* $P < 0.05$.

Table 3. *Regression statistics describing the relationships between stepping frequency* (x, Hz) *and the duration* (y, ms) *of both protraction and retraction in two species of wolf spiders*

(The lines beneath the numbers 1–4 include legs with slopes, as defined by the regressions, which are not different at P = 0·05 (tested by *a posteriori* STP; Sokal & Rohlf, 1969, p. 457).)

	Legs	Regression equation	r^2	N	P
		Lycosa tarentula			
Protraction	1	$y = 34·5 + 2·33x$	0·17	14	> 0·05 N.S.
	2	$y = 103·9 - 4·44x$	0·63	15	< 0·01
	3	$y = 31·4 + 2·07x$	0·17	14	> 0·05 N.S.
	4	$y = 69·0 - 0·35x$	0·07	13	> 0·05 N.S.
Retraction	1	$y = 124·7 - 7·91x$	0·72	16	< 0·01
	2	$y = 101·8 - 5·57x$	0·57	14	< 0·01
	3	$y = 176·5 - 12·2x$	0·86	15	< 0·01
	4	$y = 99·6 - 6·29x$	0·36	15	< 0·05

Legs with common slopes: 2 4 1 3

		Trochosa ruricola			
Protraction	1	$y = 89·8 - 3·32x$	0·65	16	< 0·01
	2	$y = 86·1 - 3·12x$	0·62	13	< 0·01
	3	$y = 51·4 - 0·92x$	0·42	17	< 0·01
	4	$y = 94·1 - 3·28x$	0·74	14	< 0·01

Legs with common slopes: 3 2 4 1

Retraction	1	$y = 88·4 - 4·04x$	0·70	14	< 0·01
	2	$y = 76·1 - 3·32x$	0·78	15	< 0·01
	3	$y = 105·2 - 5·13x$	0·88	15	< 0·01
	4	$y = 40·6 - 1·25x$	0·33	16	< 0·05

Legs with common slopes: 4 1 3 2

$P < 0·025$ respectively). In leg 2 the slopes of the relationships do not differ either for retraction or protraction ($P > 0·05$ and $P > 0·25$ respectively).

The relationship between the proportion of the stepping cycle spent in retraction [the power stroke; $r/(p+r)$] at different stepping frequencies was examined by superimposing the regression lines in Table 3 and by adjusting them to the mean value of p and r so that the slopes were considered without regard to the intercepts. In both species the proportion of the stepping cycle spent in retraction (y) increased directly with stepping frequency (x) (*L. tarentula*, $y = 3·94x + 18·5$; $P < 0·001$; *T. ruricola*, $y = 1·12x + 43·7$, $P < 0·05$) but the slope was considerably greater in *L. tarentula* ($P < 0·005$).

DISCUSSION

Although *L. tarentula* is a larger spider than *T. ruricola* the stepping frequency at a given speed has the same relationship with body length in both species. However, the same relationship plotted against leg length suggests a marked discontinuity (Fig. 3), such that *L. tarentula*, despite its relatively longer legs, steps at a higher frequency for a given size and speed than *T. ruricola*; that is it takes shorter steps. This is consistent with their respectively burrowing and vagrant habits.

At higher speeds *T. ruricola* comes close to an alternating tetrapod gait but this

does not occur in *L. tarentula*. Comparison of the phase lags shows that they va█ marginally with speed in both species but that ipsilateral phase lags including leg 1 are erratic in *L. tarentula*, that they differ significantly between species, and that in both species leg 1 is less closely coordinated than the other legs (Wilcoxon's signed rank test $P < 0.05$ in both species: mean absolute phase lock index $\pm$ S.E.M. for ipsilateral leg comparisons including leg 1 – *T. ruricola* = 0.64 ± 0.04, *L. tarentula* = 0.20 ± 0.08; not including leg 1 – *T. ruricola* 0.92 ± 0.02, *L. tarentula* 0.74 ± 0.05).

The protraction/retraction ratio is directly related to running speed and stepping frequency in both species but both relationships increase more rapidly with speed in *L. tarentula*. The ratio is more variable in leg 1 than in the other legs and it varies between legs along the body in both species but this tendency is more marked in *L. tarentula*.

The two species differ in their relationships between the duration of both protraction and retraction and the stepping frequency. In *T. ruricola*, both p and r are inversely related to stepping frequency, unlike in many insects where the duration of p is much less sensitive to stepping frequency (Burns, 1973; Harris & Ghiradella, 1980) and are thus more similar to *L. tarentula*. This inverse relationship between the duration of protraction and stepping frequency may result from the inclusion of leg-drag as part of protraction but this interpretation is functionally realistic. Whereas the jumping spider (Land, 1972) and mygalomorph (Wilson, 1967)˙ engaged in retraction (power stroke) for about 70% of the stepping cycle irrespective of the rate of stepping, in both *L. tarentula* and *T. ruricola* retraction as a proportion of the stepping cycle increased directly with stepping frequency but neither species reached the 70% reported for the other species [mean and range of $r/(p+r)$: *L. tarentula* 0.56 (0.47–0.66); *T. ruricola* 0.58 (0.54–0.62)].

Some of the differences between the parameters measured here and those in other studies may result from the lower filming speeds used in most other studies, particularly p/r ratios as they are very sensitive to filming speed. The effects of filming speed on interpretation of gait is considered elsewhere (Ward & Humphreys, 1981) where it is shown that the maximum sampling error in this study is about 3%.

The main interspecific difference is the lower ipsilateral coordination of leg 1 in *L. tarentula*, which suggests that this species relies mainly on the hind three pairs of legs for support and propulsion during locomotion. A gait which used only three leg pairs would be similar to the alternating tripod gait of insects. This gait has contralateral and adjacent ipsilateral phase lag close to 0.5 and alternate ipsilateral phase lag close to zero. The mean contralateral and adjacent ipsilateral phase lag for the three hind-leg pairs are close to 0.5 in both species. This suggests that both species are adapted to use leg 1 for purposes other than support. Figs 5 and 6 support this by showing that legs 2, 3 and 4 alternate with a phase lag of 0.5 but that leg 1 has a variable phase lag during runs. The markedly lower coordination of leg 1 in *L. tarentula* indicates that this species uses this pair of legs more for non locomotory purposes, possibly sensory, than does *T. ruricola* but in both species support and propulsion are provided mainly by the hind three pairs of legs.

The above interpretation is similar to that proposed by Burns (1973) in hi█ comparison of locusts and grasshoppers. Locusts have short antennae which a█

sed in flight but do not function as tactile receptors while walking so this function is taken over by the prothoracic legs. The long antennae of grasshoppers are used during walking so the prothoracic legs are not required for sensory input. He considered that these functional differences could account for the different gait characteristics of the prothoracic legs in the locust. Using force-print analysis Harris & Ghiradella (1980) concluded that the prothoracic legs of the cricket *Acheta domesticus* were more involved in balancing or searching than in propulsion.

Hexapody has been reported amongst the arachnids in amblypygids (Manton, 1973) where leg 1 is greatly elongated and has a sensory function, being able to swing and feel all around the animal. Locomotory function is thus restricted to the three hind pairs of legs. The sensitive antennae characteristic of insects are not present in arachnids so a multipurpose front leg including a major sensory component would seem a practical adaptation for the arachnids. In lycosids agonistic behaviour often includes stereotyped movement of the front legs. Front leg waving forms an important part of the precopulatory display in *Lycosa rabida* and during foreleg waving the female may take several steps (Rovner, 1968). Anterior legs provide initial contact during prey capture and adhesive hairs are localized on them (Rovner, 1978). Spiders detect web vibrations using the lyriform organs on their legs (Walcott, 1969) and with such sensory input they can orientate towards their prey (Barth & Seyfarth, 1971).

The tarantula (*Dugesiella hentzi*) shows a wide range of gaits and, although alternating patterns dominate, coordination across the body is poor (Wilson, 1967). Reexamination of his data for normal animals shows modal values for adjacent ipsilateral phase lag close to 0·375, the value expected for an animal using eight legs for locomotion but which has only three legs on the ground at any moment. Wilson's data do not suggest any differences between the coordination of leg 1 and the other legs but they do show such a difference for the pedipalps. This suggests that the pedipalps, which are much longer than in the lycosids, may perform the same (sensory?) function as the first leg pair in *L. tarentula*.

Comparison of the data reported here with those of Manton (1973) shows several areas of disagreement. This is probably due to the inadequate sampling speeds used by Manton (Ward & Humphreys, 1981). The p/r ratios she quoted for the low speeds in *T. ruricola* seem in general agreement with extrapolations of values obtained here. However, the maximum p/r she quotes is 0·87; the lack of values greater than 1·0 suggests that the filming speed was too low and 32 f.p.s. is clearly too slow to determine accurately p/r ratios (Ward & Humphreys, 1981).

Manton reported phase lags close to 0·5 but did not consider phase lag differences between different legs. Phase lag varied marginally but significantly with speed in both *T. ruricola* and *L. tarentula* except when the phase lag included leg 1, in which cases the change with speed was both considerable and erratic for ipsilateral legs of *L. tarentula*. These observations are not consistent with other data for spiders (Wilson, 1967) or cockroaches (Delcomyn, 1971a) where no change in phase lag was detected with varying stepping frequency.

Hexapody has been reported in some arachnid groups (Pedipalpi and Solifugae) from observation of limb use rather than film analysis (Manton, 1973) and can now be extended to the lycosidae. The different degrees of hexapody seen in the two

species of lycosids suggest that the mechanism for generating gaits is highly adaptabl⬛ and this is supported by the ease with which spiders compensate for limb loss (Wilson, 1967).

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