WALKING AND SURFACE FILM LOCOMOTION IN TERRESTRIAL AND SEMI-AQUATIC SPIDERS

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SUMMARY

The walking and surface film locomotion of a terrestrial spider, *Lycosa rabida* Walckenaer, and a semi-aquatic spider, *Dolomedes triton* (Walckenaer), are compared. Stepping patterns during locomotion on a solid substrate resemble an alternating tetrapod in both species. *L. rabida* retains elements of the terrestrial gait when moving on water: propulsive thrusts are concentrated at the tarsi and intra-segmental legs step in alternation. However, protraction/retraction (p/r) values are generally greater and phase values of adjacent ipsilateral legs are lower compared to values for walking animals. *D. triton* shows greater behavioural specialization for aquatic locomotion: propulsive forces are generated along the length of the leg, intrasegmental legs move in synchrony and leg 4 (which is not used for propulsion on water) functions in yaw correction. Changes in p/r value and ipsilateral phase accompanying the transition from a solid substrate to the water surface are similar to those found in *L. rabida*. The fact that coordination within a segment and co-ordination between segments can be altered independently in both proximate and evolutionary time suggests that interleg coupling in spiders is governed by two distinct mechanisms: intrasegmental and intersegmental mechanisms. It is suggested that proximate changes in p/r value and ipsilateral phase in both spiders may be the effect of sensory modulation of similar motor control mechanisms and that certain specializations for aquatic locomotion in *D. triton* (such as yaw corrective movements of leg 4) are derived from elements of the primitive terrestrial motor programme.

INTRODUCTION

Despite the attention arthropod walking has received, there are relatively few studies devoted to the locomotion of spiders. Nevertheless, there are a number of recent studies on a broad taxonomic range of spiders, including mygalomorphs (Wilson, 1967; Seyfarth & Bohnenberger, 1980), wolf spiders (Moffett & Doell, 1980; Ward & Humphreys, 1981), sheet-web spiders (Fröhlich, 1978), jumping spiders (Land, 1972) and crab spiders (Ferdinand, 1981). Bowerman (1975) has examined locomotion in the scorpion. The coordination used by most terrestrial arachnids and insects is similar, despite the difference in leg number. In general, each leg tends to alternate with its contralateral homologue and ipsilateral neighbours

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but moves in near synchrony with diagonally adjacent contralateral legs. In arachnids, the resulting gait is termed an alternating tetrapod, an analogue to the alternating tripod of insects. This stepping pattern provides a stable base of support throughout the locomotor cycle, an important feature of effective terrestrial walking.

Although spiders are best known for their accomplishments as terrestrial predators, certain species within the genus *Dolomedes* (Pisauridae) are among the largest and most adept semi-aquatic arthropods. These spiders may be found at the margins of ponds and streams awaiting prey at the water surface. When *Dolomedes* detects the vibrations of a potential victim, perhaps a struggling insect, the spider moves rapidly over the surface film to capture its prey and then returns to a solid resting place to consume it. Thus, the surface film serves as a ready-made 'web'. Although diving, swimming (McAlister, 1959) and wind-assisted movements (Deshefy, 1981) of *Dolomedes* have been investigated, surface film locomotion, despite clear adaptive significance, has received little study. Ehlers (1939) briefly describes surface film locomotion in several species, including the European fishing spider *Dolomedes fimbriatus*. When on water, *D. fimbriatus* rests with its ventral body surface on the water and legs extended to increase the area in contact with the supporting surface film. During locomotion, the third and then second leg pairs retract in quick succession, often followed by retraction of the first pair. Each leg moves in synchrony with its contralateral homologue. The last pair of legs does not aid in propulsion but appears to function in stabilization. In some respects, rowing in *Dolomedes* is similar to that of its insect counterpart, the water strider (Hemiptera, Gerridae) (Anderson, 1976). However, the aquatic gait, characterized by synchrony of intrasegmental legs and near synchrony of adjacent ipsilateral legs, is quite different from the alternating pattern used by most spiders during terrestrial locomotion.

I have studied the control of spider walking and the evolution of rowing in *Dolomedes* by comparing terrestrial and surface film locomotion in a fishing spider, *Dolomedes triton*, and a wolf spider, *Lycosa rabida* (Lycosidae). *D. triton* is probably the most aquatic of the North American pisaurids (Carico, 1973). This species appears to use the same rowing gait as *D. fimbriatus* when moving on water and uses a gait similar to the alternating tetrapod during locomotion on a solid substrate. *L. rabida* is terrestrial, although many lycosids move over water facultatively (Ehlers, 1939), and is similar to *D. triton* in size and general proportions. The results of this analysis suggest that interleg coordination in spiders is governed by two distinct coupling mechanisms: intrasegmental and intersegmental mechanisms. These coupling units are identified by their independent effects upon coordination and may have served as the sites at which natural selection acted to produce the rowing gait used by *Dolomedes*.

MATERIALS AND METHODS

All spiders used in this study were collected in Athens County, Ohio, USA. *Dolomedes triton* was found at the water surface among emergent vegetation growing

along the margins of lakes and slowly moving streams. Adults of this species were collected from May to September. Adult *Lycosa rabida* were collected during late summer and were usually found well away from bodies of water. In both species, only adult females were used. (Males differ from females in being smaller and having relatively longer legs, factors which would have complicated species comparisons.) The average length of the carapace in females of both species is about 18 mm. Species were housed individually in plastic boxes (7×12×7 cm) at an average temperature of 23 °C.

I filmed individuals of both species as they moved over a dry substrate (two *D. triton,* two *L. rabida*) and across the water surface (four *D. triton,* two *L. rabida*). A large arena was partitioned into a rectangular 0·25×1·0 m runway. The floor consisted of a roughened plastic sheet marked with a 2-cm grid. To obtain sequences of surface film locomotion, I covered the arena floor with water to a depth of about 2 cm. The runway was illuminated by two 500-W slide projectors positioned about 2 m away. Light from the projectors was directed into a mirror which had been mounted above the runway at 45° to the arena floor. I aimed the camera lens at the mirror to capture the reflected dorsal image of the moving spider. Films were taken with a Ciné-8 high speed camera (Visual Instrumentation Corp., Model SP-1) at 100 frames s^{-1} using Kodak 4-X reversal film (ASA 400). Sequences were filmed at an average air temperature of 23 °C and water temperature of 20 °C.

I limited quantitative film analyses to sequences showing three or more complete stepping cycles during which turning did not exceed an angle of 30°. I examined all such sequences frame-by-frame using a stop-action Kodak Ektagraphic film projector. When analysing the stepping cycle of each leg, I considered retraction (the propulsive stroke) to begin when the leg contacted the substrate and then moved backwards. Protraction (the return stroke) began when the leg lifted from the substrate and moved forwards. If for some fraction of a stepping cycle a leg did not move relative to the spider's body, it was included within the preceding phase. In films of walking spiders, these features were fairly easy to recognize, since the tips of the legs were usually stationary with respect to the substrate during retraction. In aquatic locomotion, the legs move relative to the substrate throughout the stepping cycle. Therefore, protraction and retraction could be recognized most readily as movements relative to the spider's body. This was accomplished by projecting the film on a graphics tablet (Tektronix, Inc.; Model 4956) attached to a Tektronix graphic computer (Model 4051) and plotting the positions of the spider's body and tarsi for each frame. I programmed the computer to calculate the angle between each tarsus and the spider's midline for each frame. By comparing the magnitudes of the angles in consecutive frames, I was able to identify phases of the stepping cycle in each leg.

Since stepping is a cyclic process, one can in principle use any point as a reference when comparing coordination in two legs. To simplify analysis and allow comparisons with previous studies, I selected the onset of retraction as the point of reference. The time between the start of retraction in a reference leg and that of

another is termed 'lag'. The phase of the two legs is calculated by dividing lag by the stepping period of the reference leg. Phase values near 0·0 or 1·0 indicate that the legs are stepping in near synchrony and those near 0·5 indicate that the legs are moving in alternation. Circular statistics for analysis of phase, including calculation of mean and standard deviation, follow Batschelet (1965). All other statistical treatments follow Sokal & Rohlf (1981) and all tests were performed at the 0·05 level of significance.

The arrangement of segments in a spider's leg is shown in Fig. 1.

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RESULTS

Posture and general features of movement

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Posture

When standing or moving on a solid surface, both *L. rabida* and *D. triton* adopt a posture typical of many terrestrial arthropods; the body is held close to the substrate suspended from a ring of legs which forms a broad base of support (Fig. 2A). Usually, only the tips of the tarsi bear the spider's weight and convey propulsive forces to the substrate. When on water, the habitually terrestrial *L. rabida* places its ventral body surface on the surface film, but some elements of the terrestrial posture remain (Fig. 2B). The legs still provide some support and propulsive forces are transferred primarily through the tarsi, as indicated by the displacement and frequent penetration of the surface film by the tips of the legs. When on water, *D. triton* also places its sternum against the water surface, but the legs are extended horizontally, thus distributing the body weight over a larger area (Fig. 2C). Propulsive forces may therefore be generated along the length of the leg and not just at the tarsus.
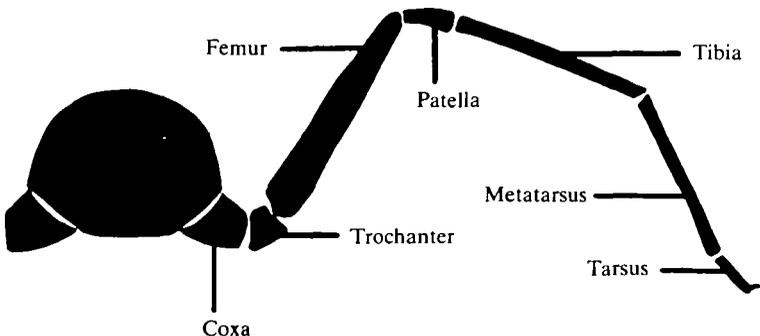

Fig. 1. Diagram showing arrangement of segments in the legs of a typical spider. Movements at the trochanter–femur, femur–patella and tibia–metatarsus joints occur primarily within the plane of the page (flexion–extension), and movements at the body–coxa, coxa–trochanter and patella–tibia joints are largely perpendicular to the page (promotion–remotion). Significant rotational movements also occur at the coxa–trochanter joints. The metatarsus–tarsus joint is flexible in all directions.
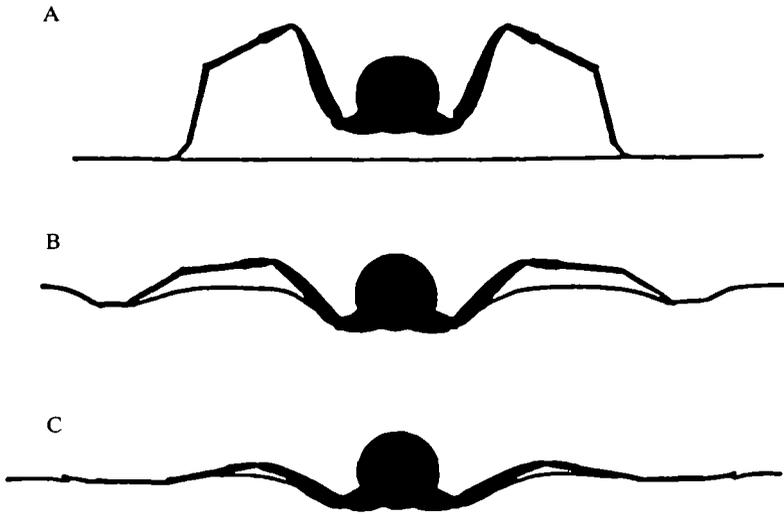
Fig. 2. Schematic cross-sections of spiders showing postures on different substrates. (A) *Dolomedes triton* and *Lycosa rabida* on a solid substrate. (B) *L. rabida* on the water surface. (C) *D. triton* on the water surface.

Locomotion on a solid substrate

During terrestrial locomotion, the leg movements of *L. rabida* and *D. triton* are similar and resemble those described in other spiders (see Ehlers, 1939). The first and fourth pairs of legs work in an essentially vertical plane; leg 1 pulls and leg 4 pushes. The movements of the second and third leg pairs are more complicated, but can be generally described as oar-like, having a large horizontal component.

When walking, both spiders use a gait which is approximately an alternating tetrapod; sets of diagonally adjacent legs (R1–L2–R3–L4 and L1–R2–L3–R4) tend to work in alternation. If one considers stepping of only ipsilateral appendages, retraction typically occurs in the order 4–2–3–1. While *L. rabida* uses leg 1 regularly during the stepping cycle, *D. triton* may go through several cycles in which one or both members of the first leg pair do not contact the substrate and remain extended in front of the animal. *D. triton* also differs from *L. rabida* in frequently dragging the tarsus of leg 4 following full extension. In these respects, terrestrial locomotion in *D. triton* resembles that of the burrowing wolf spider, *Lycosa tarentula* (Ward & Humphreys, 1981).

Locomotion on the water surface

Intraleg movements used by *L. rabida* on water are very similar to those used during walking, although stepping movements of legs 1 and 4 tend to have larger horizontal components (Fig. 3). Interleg coordination differs from that seen during terrestrial locomotion. While each leg continues to alternate with its contralateral homologue, ipsilateral legs assume the metachronal stepping pattern 4–3–2–1. Although this spider can maintain a net linear course when on the water surface, it generates a great deal of turbulence and the body undergoes continuous yaw and roll.

Surface film locomotion in *D. triton* differs from walking and from aquatic locomotion in *L. rabida*. Movements producing retraction in legs 2 and 3 occur largely at the proximal joints. The tibiometatarsal joints (see Fig. 1) remain in an extended position, although some flexion may occur at the end of retraction (Fig. 4). Due to a rotation about the long axis of the coxotrochanteral articulation, the
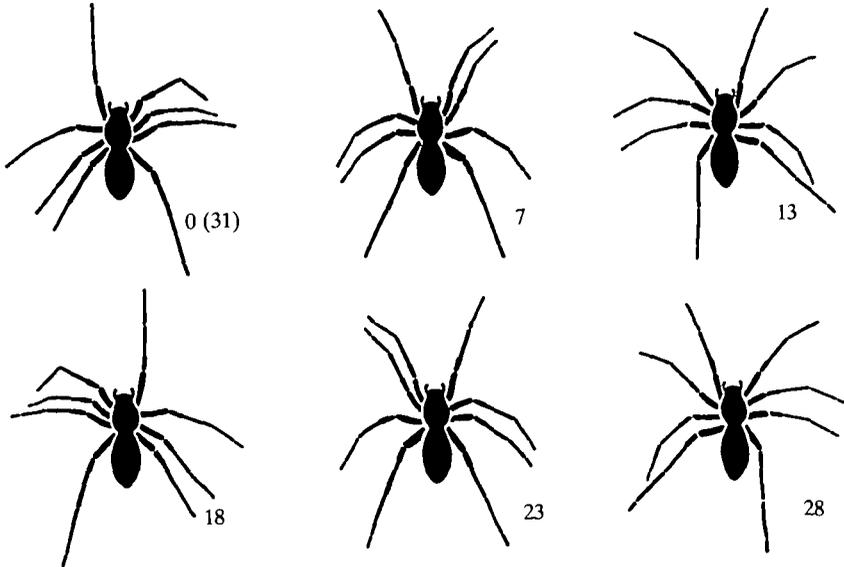

Fig. 3. Kinematics of one stepping cycle during surface film locomotion in *Lycosa rabida* (semi-diagrammatic). Numbers indicate frames upon which drawings are based. Film speed is 100 frames s^{-1}.
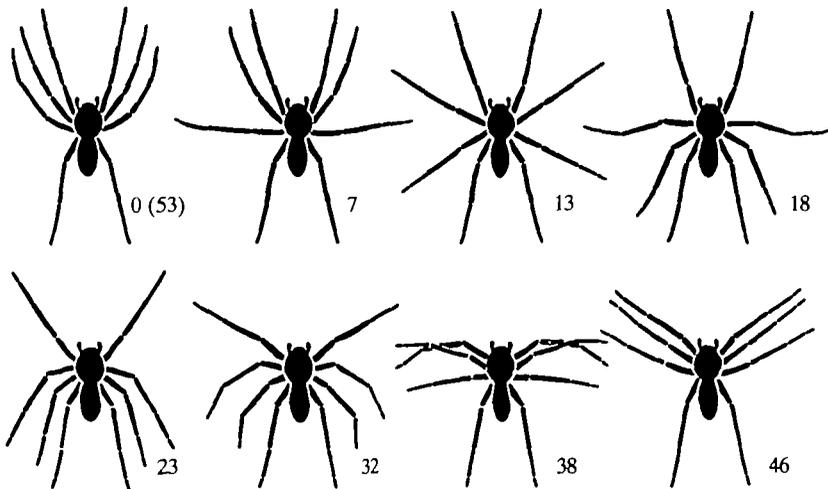

Fig. 4. Kinematics of one stepping cycle during surface film locomotion in *Dolomedes triton*. Numbers indicate frames upon which drawings are based. Film speed is 100 frames s^{-1}.

movements of the distal elements of leg 1 show a greater horizontal component than during terrestrial locomotion. During protraction, legs 1, 2 and 3 are lifted from the water surface. The fourth leg pair does not contribute to propulsion but remains extended behind the spider. Important directional control movements of leg 4 will be discussed below.

Interleg coordination during surface film locomotion in *D. triton* is quite different from that found in walking. As Ehlers (1939) described in *D. fimbriatus*, intrasegmental legs move in synchrony rather than in alternation. This behaviour may minimize the production of asymmetrical forces which generate yaw and roll. Likewise, ipsilateral legs assume the metachronal pattern 3–2–1. The nearly simultaneous retractions of legs 2 and 3 result in a period of rapid acceleration followed by deceleration during their protraction, a situation which seems energetically inefficient.

Directional control during aquatic locomotion in Dolomedes triton

Directional control during rowing in *D. triton* can be divided into two types: turning (rotational movements made in order to establish a new course) and yaw correction (rotational movements made in order to compensate for deviations from an established course). Each form of directional control is associated with a distinctive pattern of leg movements.

Turning involves only the first three leg pairs, the fourth pair rests nearly motionless on the water surface. A left turn is usually initiated by the independent retraction of the third leg on the right side (R3). The rotation of the body resulting from this movement establishes the new direction of travel. Next, L3 and R2 retract simultaneously, followed by the synchronous retraction of L2 and R1. L1 remains extended in front of the spider throughout the turn. A right turn is the mirror image of a left turn. After the turning sequence is completed, the spider returns to the regular rowing pattern.

D. triton rides over the surface film on a layer of air held by many hydrofuge hairs covering the ventral body surface. This arrangement decreases friction with the water, probably reducing drag and thus the energy the animal must expend in moving from place to place. However, low friction increases the potential for unintended rotations (yaw) due to even slight asymmetry in the forces generated during the propulsive strokes. Transverse phase synchrony may have evolved to minimize yaw, but directional control remains an apparent problem.

The most obvious yaw corrective movements used by *D. triton* are rapid 'protractions' of leg 4. The kinematics of these sweeping lateral kicks are similar to those seen in normal protractions of the fourth leg pair during aquatic locomotion in *L. rabida* (Fig. 3). If a corrective rotation to the right is required, R4 is swept rapidly forward, while L4 remains motionless or undergoes slight 'retraction'. Interestingly, these yaw corrective 'protractions' only occur just prior to, or simultaneously with, the protraction of leg 3, the period during which one would expect protraction in leg 4 if it participated in the metachronal sequence seen in the other legs. Legs 1, 2 and 3 may also participate in yaw correction by varying the
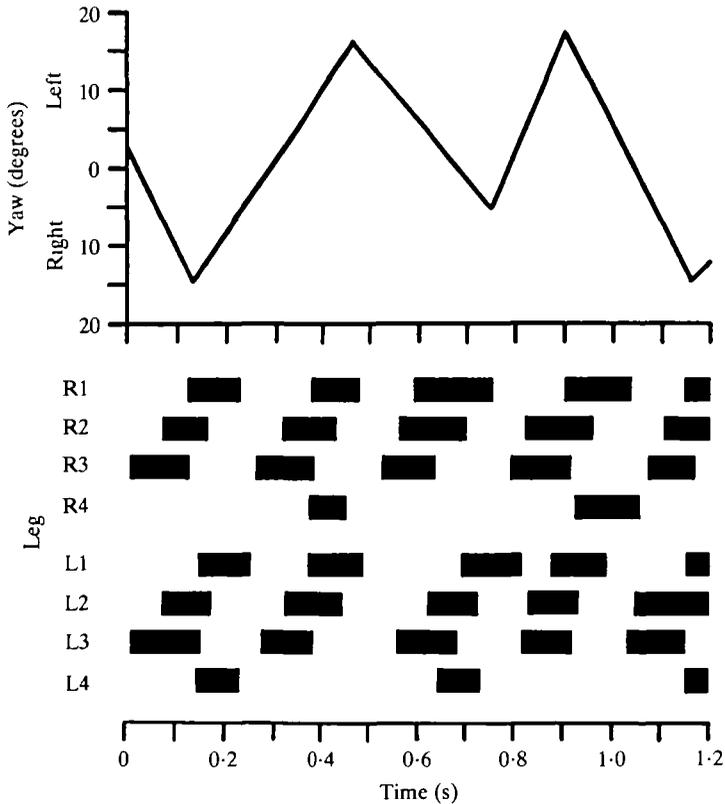
Fig. 5. Diagram depicting yaw corrective behaviour during surface film locomotion in *Dolomedes triton*. The graph shows deviations of the long axis of the body from the direction of travel (yaw). In the gait diagram, the dark bars indicate periods of retraction for legs 1–3 and yaw corrective kicks (protractions) in leg 4. Note the correlation between changes in the orientation of the long axis of the spider's body with the movements of leg 4 and that intrasegmental legs are not moving in strict synchrony. The film used for this analysis was taken at 100 frames s^{-1}.

timing of retraction across the body. This behaviour is especially evident in leg 1. Fig. 5 depicts a sequence of surface film locomotion in *D. triton* during which the spider makes several yaw corrective movements.

During surface film locomotion in *L. rabida,* intended and unintended rotational movements cannot be distinguished. It is interesting to note that leg pairs may move in transverse phase synchrony during rotational movements rather than the usual alternating pattern. The same behaviour has been observed in walking tarantulas (Wilson, 1967).

Intraleg coordination: protraction and retraction

Durations of protraction and retraction for each leg were found to vary linearly with stepping period (Tables 1, 2). During terrestrial locomotion in both species, retraction changes more rapidly with stepping period than does protraction, but this relationship is reversed during aquatic locomotion in *D. triton* and in leg 3 of

Table 1. *Regression parameters for the relationship of protraction (ms, y) and stepping period (s, x)*

Leg	N	Regression equation	r^2	Range (x)
Dolomedes triton (terrestrial)				
1	37	y = 335·63x+9·93	0·452	0·189–0·769
2	57	y = 312·13x+2·40	0·668	0·090–0·714
3	67	y = 211·62x+24·21	0·657	0·130–0·667
4	64	y = 177·09x+22·59	0·490	0·141–0·667
Comparison of slopes 1 2 3 4				
Dolomedes triton (aquatic)				
1	201	y = 783·21x−37·91	0·823	0·141–0·556
2	215	y = 792·10x−64·94	0·834	0·159–0·556
3	213	y = 699·17x−38·44	0·881	0·149–0·526
Comparison of slopes 1 2 3				
Lycosa rabida (terrestrial)				
1	44	y = 481·21x−8·99	0·622	0·179–0·385
2	46	y = 354·13x+18·28	0·500	0·159–0·345
3	50	y = 270·43x+26·60	0·471	0·159–0·345
4	50	y = 339·53x+0·75	0·836	0·159–0·417
Comparison of slopes 1 2 4 3				
Lysoca rabida (aquatic)				
1	83	y = 126·22x+56·88	0·107	0·070–0·714
2	113	y = 422·33x+12·83	0·668	0·110–0·385
3	119	y = 621·94x+23·39	0·882	0·100–0·400
4	82	y = 253·93x+55·01	0·012	0·110–0·417
Comparison of slopes: all differ				

Comparison of slopes were made at the 0·05 level of significance (Sokal & Rohlf, 1981). Legs that are underlined have slopes that are not significantly different.

L. rabida (Fig. 6). The relationships for the other legs in *L. rabida* differ but, in general, retraction is shorter and protraction is longer during aquatic locomotion than during walking at similar stepping periods. Thus, the slope of the p/r ratio (y) *versus* stepping period (x) tends to be negative during terrestrial locomotion and positive during aquatic locomotion.

Interleg coordination: phase relationships

Ipsilateral coordination

In terrestrial locomotion, mean phase values for each combination of adjacent ipsilateral legs approach 0·5 in both *L. rabida* and *D. triton* (Table 3). For surface film locomotion, means are consistently lower for all combinations of neighbouring legs within a species and are very similar between species. Alternate ipsilateral legs (i.e. R1 and R3, etc.) show no clear pattern.

Contralateral coordination

Mean phase values for the first and second leg pairs are not statistically significant in walking *D. triton* (Rayleigh test, $P > 0·05$) (Table 4). Intrasegmental legs tend to

Table 2. *Regression parameters for the relationship of retraction (ms, y) and stepping period (s, x)*

Leg	N	Regression equation	r^2	Range (x)
Dolomedes triton (terrestrial)				
1	37	$y = 664\cdot12x - 10\cdot31$	0·780	0·189–0·769
2	57	$y = 694\cdot15x - 2\cdot90$	0·921	0·090–0·714
3	67	$y = 779\cdot86x - 21\cdot96$	0·960	0·130–0·667
4	64	$y = 817\cdot58x - 21\cdot55$	0·949	0·141–0·667
Comparison of slopes <u>1 2 3 4</u>				
Dolomedes triton (aquatic)				
1	201	$y = 183\cdot99x + 49\cdot16$	0·227	0·141–0·556
2	215	$y = 196\cdot21x + 68\cdot06$	0·287	0·159–0·556
3	213	$y = 295\cdot70x + 39\cdot99$	0·601	0·149–0·526
Comparison of slopes <u>1 2</u> 3				
Lycosa rabida (terrestrial)				
1	44	$y = 501\cdot39x + 12\cdot39$	0·639	0·179–0·385
2	46	$y = 630\cdot99x - 14\cdot75$	0·755	0·159–0·345
3	50	$y = 711\cdot39x - 22\cdot63$	0·862	0·159–0·345
4	50	$y = 658\cdot13x - 0\cdot36$	0·943	0·159–0·417
Comparison of slopes 1 <u>2 4</u> 3				
Lycosa rabida (aquatic)				
1	83	$y = 167\cdot04x + 61\cdot80$	0·182	0·070–0·714
2	113	$y = 563\cdot68x - 10\cdot31$	0·787	0·110–0·385
3	119	$y = 363\cdot83x - 26\cdot08$	0·708	0·100–0·400
4	82	$y = 541\cdot69x - 4\cdot68$	0·575	0·110–0·417
Comparison of slopes 1 <u>2 4</u> 3				

Comparisons were made as in Table 1.

alternate during surface film locomotion in *L. rabida* and during terrestrial locomotion in both species. Means of intrasegmental legs approach 0·0 in *D. triton* during aquatic locomotion, indicating that the members of each leg pair are moving in synchrony.

Phase values for diagonally adjacent contralateral legs are also presented in Table 4. Mean phase values for contralateral legs of segments 2 and 3 are very similar in walking *L. rabida* and both forms of locomotion in *D. triton*, while the values for the same combination of legs during aquatic locomotion in *L. rabida* are much higher. Diagonally adjacent legs of segments 3 and 4 tend to move in near synchrony in walking *D. triton* and during both forms of locomotion in *L. rabida*.

No significant relationship was found between phase and stepping period in any combination of legs.

Statistical measures of variation, such as circular standard deviation, are used to indicate the strength of coordination or coupling between legs; lower values indicate tighter coupling. The results are consistent with the respective habits of the two species. *D. triton* shows less variation for all leg combinations when rowing as compared to walking. *L. rabida* tends to have stronger coordination during
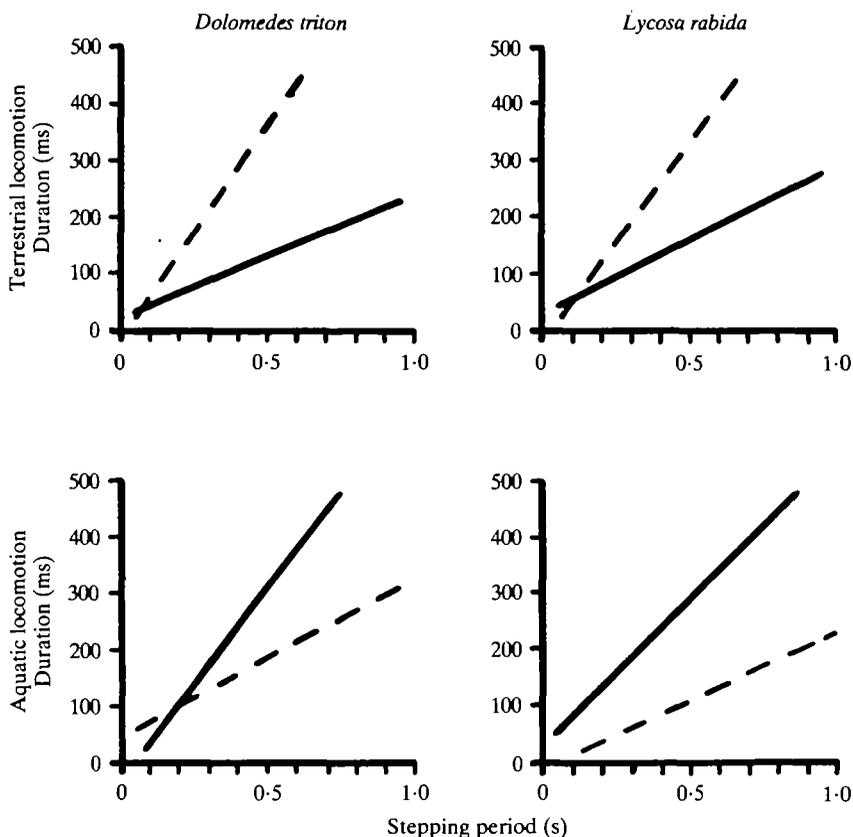
Fig. 6. Regression lines showing relationships of protraction (solid lines) and retraction (dashed lines) of leg 3 with stepping period in *Dolomedes triton* and *Lycosa rabida*. In both species, retraction during terrestrial locomotion changes more rapidly with stepping period than does protraction. These relationships are reversed during aquatic locomotion. See Tables 1 and 2 for regression parameters.

terrestrial locomotion than during surface film movement. When interspecific comparisons are made, leg movements in *D. triton* tend to be more weakly coupled than those of *L. rabida* during terrestrial locomotion. The opposite is found during surface film locomotion.

DISCUSSION

Interleg coupling mechanisms in spiders

Our understanding of the factors underlying coordination in arthropod walking has been aided by modelling the motor control apparatus as a system of interconnected subcomponents. The stepping cycle of each leg is considered to be governed by a single centrally driven oscillator, the timing of which may be altered by changes in sensory input. The relative timing of neighbouring oscillators is determined by a coupling mechanism (Stein, 1977). Such systems have predictive value, but it has yet to be shown whether these subcomponents represent real

Table 3. *Phase relationships of ipsilateral legs of* Dolomedes triton *and* Lycosa rabida *during terrestrial and aquatic locomotion*

		Dolomedes (terrestrial)	Dolomedes (aquatic)	Lycosa (terrestrial)	Lycosa (aquatic)
$_1L_2$	x̄	0·61	0·30	0·65	0·22
	S.D.	0·121	0·075	0·118	0·127
	N	34	206	47	98
$_2L_3$	x̄	0·52	0·16	0·58	0·18
	S.D.	0·131	0·060	0·107	0·117
	N	52	219	46	111
$_3L_4$	x̄	0·46		0·49	0·38
	S.D.	0·082	—	0·045	0·095
	N	64		51	83
$_1L_3$	x̄	0·20	0·53	0·34	0·37
	S.D.	0·172	0·058	0·127	0·112
	N	36	238	43	92
$_2L_4$	x̄	0·99		0·10	0·55
	S.D.	0·156	—	0·106	0·125
	N	49		52	83

Calculations of mean (x̄) and standard deviation (S.D.) follow Batschelet (1965).

entities or are simply a convenient shorthand which captures certain properties of the actual mechanism (Delcomyn, 1985). The results reported here suggest that the subdivision of the motor control apparatus of spiders into separate functional components is justified.

Differences in interleg coordination during walking and surface film locomotion in the habitually terrestrial *Lycosa rabida* suggest that this behaviour is governed by at least two types of coupling mechanisms: *intrasegmental* and *intersegmental* mechanisms. When moving on a solid substrate, this spider uses the alternating tetrapod gait. During movement on the surface film, ipsilateral legs adopt a metachronal pattern of stepping while legs of the same segment continue to alternate as in the walking gait. The independent effects of substrate type on two elements of coordination seem most readily explained by the presence of functionally distinct units within the motor control apparatus of the spider.

Evidence from the comparison of locomotion in *L. rabida* and *D. triton* is also consistent with the notion of subcomponents within the motor control apparatus. These species show the same basic stepping pattern during terrestrial locomotion, implying the existence of similar motor control mechanisms. Although obvious interspecific differences occur during surface film locomotion (e.g. intrasegmental legs move in synchrony in *D. triton*), coordination of adjacent ipsilateral legs is essentially the same. This result suggests that natural selection has favoured the evolution of transverse phase synchrony in the amphibious *D. triton*, leaving the mechanism that controls intersegmental coordination unaltered. Thus, it appears that intra- and intersegmental coordination in spiders can be varied independently in both proximate and evolutionary time, implying that interleg coordination is

regulated by two types of mechanisms which maintain a large degree of functional and genetic autonomy.

If the separation of the motor control apparatus into intra- and intersegmental components is valid, the question arises as to the orientation of the intersegmental mechanism. The typical walking gait of spiders (Fig. 7A) shows two internal patterns which serve as the basis of two qualitative models of pattern generation in walking arthropods. The *alternating tetrapod model* emphasizes the importance of synchronous stepping in sets of diagonally adjacent contralateral legs (R1–L2–R3–L4 and L1–R2–L3–R4) and suggests that intersegmental coupling is arranged diagonally (Fig. 7B). The *metachronal model* (Wilson, 1966) gives emphasis to the wave-like stepping pattern which travels along each side of the arthropod's body. Although this model, in its strictest sense, fails to predict some stepping patterns used by walking mygalomorphs (Wilson, 1967), the assumption that intersegmental coupling is arranged longitudinally (Fig. 7B) is still useful.

The pattern of phase values observed during surface film locomotion in *L. rabida* and *D. triton* is consistent with the assumptions of the metachronal model. Fig. 7C

Table 4. *Phase relationships of contralateral legs of* Dolomedes triton *and* Lycosa rabida *during terrestrial and aquatic locomotion*

		Dolomedes (terrestrial)	Dolomedes (aquatic)	Lycosa (terrestrial)	Lycosa (aquatic)
R1 in L1;	$\bar{x}$	0·50 (NS)	0·07	0·49	0·48
L1 in R1	S.D.	0·193	0·136	0·150	0·107
	N	14	104	23	36
R2 in L2;	$\bar{x}$	0·46 (NS)	0·04	0·56	0·49
L2 in R2	S.D.	0·194	0·079	0·129	0·169
	N	25	110	30	57
R3 in L3;	$\bar{x}$	0·51	0·03	0·54	0·49
L3 in R3	S.D.	0·095	0·054	0·102	0·092
	N	26	83	26	58
R4 in L4;	$\bar{x}$	0·48		0·56	0·50
L4 in R4	S.D.	0·077	—	0·081	0·114
	N	29		28	32
R1 in L2;	$\bar{x}$	0·28	0·31	0·21	0·71
L1 in R2	S.D.	0·184	0·105	0·152	0·156
	N	30	215	43	93
R2 in L3;	$\bar{x}$	0·05	0·16	0·14	0·67
L2 in R3	S.D.	0·173	0·076	0·128	0·141
	N	51	222	42	113
R3 in L4;	$\bar{x}$	0·08		0·99	0·90
L3 in R4	S.D.	0·118	—	0·109	0·121
	N	57		52	83

Calculations of mean ($\bar{x}$) and standard deviation (S.D.) follow Batschelet (1965).

Note that mean intrasegmental phase relationships for the first two pairs of legs in walking *D. triton* are not significant (NS).
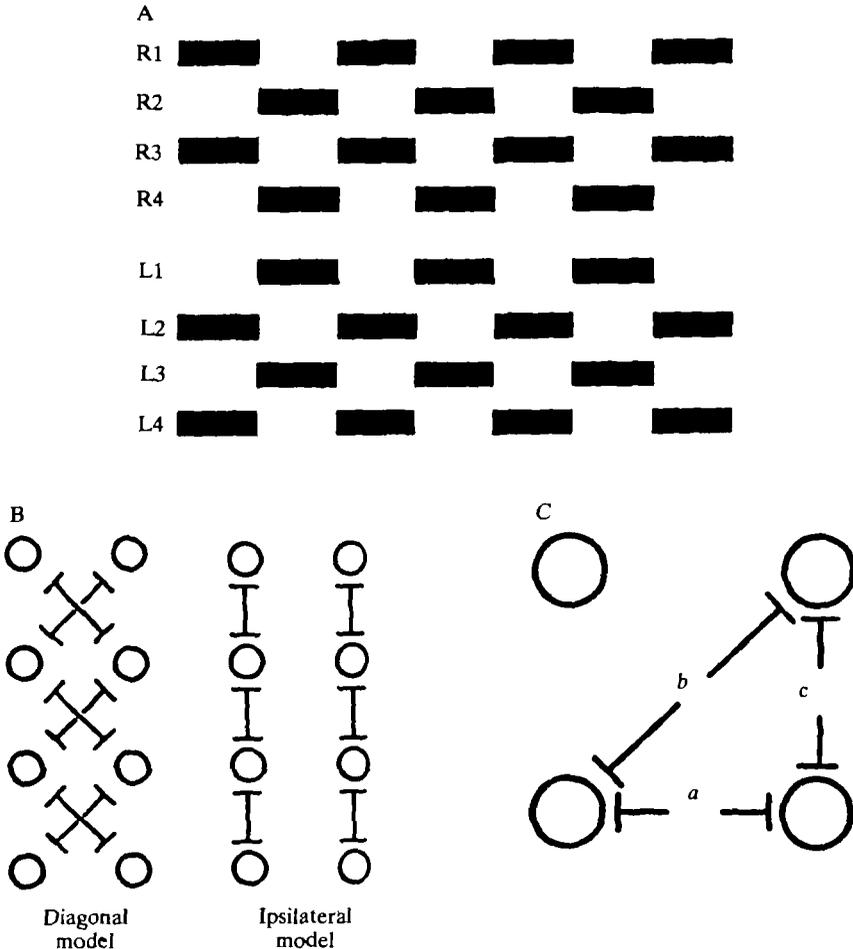
Fig. 7. (A) Gait diagram showing idealistic stepping pattern of spiders. Note that diagonally adjacent contralateral legs step in phase and ipsilateral legs step in a meta-chronal pattern. (B) Diagrams showing direction of intersegmental coupling predicted by the alternating tetrapod (diagonal) model and the metachronal (ipsilateral) model. (C) Diagram showing phase relationships measured for legs of adjacent segments: a is intrasegmental phase, b is diagonal phase and c is ipsilateral phase. The value for a is obtained from the posterior segment because this generally shows less variability in the spiders examined here.

represents the arrangement of the phase relationships between legs of any two adjacent segments, where a represents the intrasegmental phase value, b is the diagonal phase and c is the ipsilateral phase. The variables must show the relationship $a+c=b$ measured on a circular scale. Since intrasegmental legs in *D. triton* move in synchrony (phase $=0\cdot0$), diagonal and ipsilateral phase values must be equivalent and should represent the effects of the intersegmental coupling mechanism alone. Changing intrasegmental phase to $0\cdot5$ (legs moving in alternation) and assuming that intersegmental coordination is governed by an ipsilateral mechanism, the phase values measured in *D. triton* accurately predict those found in

L. rabida. When one assumes a diagonal mechanism and the procedure is repeated, the resulting phase values bear no resemblance to those measured in *L. rabida* (Table 5). That such an exercise can be performed at all points to the great similarity of the motor control mechanisms of the two species and the independent action of the intra- and intersegmental coupling mechanisms. This reasoning also suggests that, while diagonal phase synchrony may be of great functional significance to walking arthropods, one need not evoke a diagonally arranged coupling mechanism to account for this behaviour.

These results have been anticipated by the findings of previous research. Many of the spiders studied thus far show stronger coupling between adjacent ipsilateral legs than between intrasegmental legs (mygalomorphs, Wilson, 1967; Seyfarth & Bohnenberger, 1980; wolf spiders, Moffett & Doell, 1980; jumping spiders, Land, 1972). Seyfarth & Bohnenberger suggest that this indicates two different coupling mechanisms, one intrasegmental and one ipsilateral. Ferdinand (1981) also provides evidence to support the ipsilateral model of intersegmental coordination in his study of unusual stepping patterns in crab spiders.

Changes accompanying the land–water transition: comparisons with other arthropods

In the transition from walking to surface film locomotion, *L. rabida* and *D. triton* show similar changes in coordination: the protraction/retraction ratio (p/r) increases in each leg and lag time between adjacent ipsilateral legs decreases for a given stepping period. Certain aquatic insects, such as nepid water bugs (Wendler, Teuber & Jander, 1985) and gerrid water striders (Bowdan, 1978), display stepping patterns similar to those of spiders when transferred from a solid substrate to water. Altered proprioceptive or exteroceptive input may produce such changes by triggering a shift from one specialized motor programme to another or by altering a single flexible

Table 5. *Comparison of observed phase values from* Dolomedes triton *and* Lycosa rabida *during surface film locomotion and phase values for* L. rabida *predicted by two models of intersegmental coordination*

| | Observed values | | Predicted values for *L. rabida* | |
	D. triton	*L. rabida*	Diagonal model	Ipsilateral model
Segments 1 and 2				
a	0·0	0·5	0·5	0·5
b	0·3	0·7	0·3	0·8
c	0·3	0·2	0·8	0·3
Segments 2 and 3				
a	0·0	0·5	0·5	0·5
b	0·2	0·7	0·2	0·7
c	0·2	0·2	0·7	0·2

Predictions are based on values observed in *D. triton*.
All values are rounded to the nearest 0·1. See text for explanation.

system capable of producing a variety of patterns (Wendler *et al.* 1985). The demonstration of a gait intermediate between walking and swimming in nepid water bugs suggests that the latter mechanism operates in these insects. Sensory cues from strain (load) receptors located on the legs may provide the stimuli which modify motor output in the transition from walking to swimming (Wendler *et al.* 1985).

Gait shifts associated with changes in vertical loading or horizontal loading (resistance to retraction) have received considerable attention (Graham, 1985). Most of these studies concern the effects of increased loads on locomotor behaviour. However, when *L. rabida* and *D. triton* are on water, the legs do not support the entire body weight, and water would not be expected to resist leg movements to the same extent as a solid substrate. Therefore, the effects of reduced loads are probably more important in understanding the coordination used during surface film locomotion. Gait shifts similar to those found in *L. rabida* and *D. triton* have been observed in other arthropods under conditions of reduced load or reduced sensory input. For example, an inverted cockroach shows intrasegmental coordination similar to normal walking but the p/r ratio is higher; bursts from the levator muscles are proportionally longer and depressor activity is significantly reduced in comparison with walking at the same stepping period (Reingold & Camhi, 1977; Sherman, Novotny & Camhi, 1977). Also, if a cockroach is suspended over a low-friction substrate, reduction in horizontal and vertical loading may elicit a metachronal stepping pattern to replace the normal alternating tripod (Spirito & Mushrush, 1979). These changes appear to result from sensory modulation of a single flexible motor control system. Similar changes in p/r ratio and ipsilateral phase occur in lobsters when placed under conditions of reduced load (as when the legs are moving freely in the water) or when the legs are autotomized. However, this change appears to be a sensory-mediated transition from a walking programme to another programme that may be associated with gill ventilation (Pasztor & Clarac, 1983). In contrast to these examples, reduction of horizontal loading in a stick insect moving over a slippery surface does not significantly alter normal interleg co-ordination, while an increase in resistance brings about a metachronal pattern (Epstein & Graham, 1983).

Given this apparent diversity within motor control systems of arthropods, studies dealing with the effects of different substrates on coordination in spiders are needed before any firm conclusion can be made about the role of sensory input in producing the aquatic gaits of *L. rabida* and *D. triton*. Even then, the role of sensory input may differ between species. For instance, it seems unlikely that a terrestrial spider like *L. rabida* would have an alternative motor programme adapted for aquatic loco-motion. I suggest that the coordination displayed by this spider when moving on the water surface is elicited largely (if not solely) by the effects of this novel sensory environment on a flexible motor system adapted for effective locomotion on solid substrates. A single flexible system may also occur in *D. triton* (as in nepid water bugs) but the existence of two distinct motor programmes would not be surprising in this species.

Evolution of locomotion in Dolomedes triton

Behavioural comparisons have provided some insight into how the evolution of the motor control strategy of *Dolomedes* is related to this spider's lifestyle and phylogenetic history. *D. triton* occupies a heterogeneous habitat of emergent vegetation and open water. If a spider is to be successful in this habitat, its behaviour and morphology must be a compromise response to the different physical conditions of solid substrates and the water surface. Its potential for acquiring new behaviour is limited by the adaptability of the motor programme of its terrestrial ancestors; complex patterns of behaviour, like the coordination of legs during locomotion, cannot be expected to arise *de novo*. Therefore, it is not surprising to find evidence for the derivation of the rowing gait from the terrestrial motor programme. *Dolomedes* shows the same ipsilateral coordination when moving on the water surface as its terrestrial relative, *L. rabida*. The timing and kinematics of yaw corrective kicks used by the amphibious spider are like the protractions of the fourth leg pair observed in the terrestrial spider when it is forced to move on water. The two species also show certain similarities in the relative durations of protraction and retraction. Transverse phase synchrony used by *Dolomedes* is undoubtedly an adaptation to aquatic locomotion, but its evolutionary origin is obscure. If surface film locomotion had been examined without reference to a terrestrial species, all features of rowing in *Dolomedes* might have been assumed to be adaptations for aquatic movement, rather than a complex of primitive and specialized features.

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