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Spider heart-rates and locomotion

Clive Bromhall
Animal Ecology Research Group, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, England

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Summary. 1. A non-invasive, laser/fibre-optic, technique was developed to measure the heart-rates of active unrestrained spiders. The heart-rates of 15 species were measured before, during and after activity.

2. Maximum heart-rate varied between species. A possible association between maximum heart-rate and prey-catching behaviour is proposed. Within a species, body-weight had no significant effect on maximum heart-rate. In *Argyroneta*, mature males had significantly higher maximum heart-rates than mature females.

3. Spiders possessing prosomal tracheae had significantly lower maximum heart-rates than spiders with tracheae limited to the abdomen. The effects of low heart-rates on haemolymph circulation, during locomotion, are discussed.

4. The hearts of all the spiders studied were capable of maintaining pumping during locomotion. Forced fast running was associated with a lowering of the heart-rate: heart-rates decreased at the onset of running and a rise occurred when activity ceased. A rise in heart-rate also occurred as soon as voluntary locomotion ceased.

5. After exercise, recovery of the heart-rate to it's pre-exercise level was faster in *Argyroneta* than in *Trochosa*. It is suggested that gas exchange is more efficient in spiders with prosomal tracheae than in spiders with tracheae limited to the abdomen.

6. In both active and inactive *Dysdera*, it appears that the volume of haemolymph pumped posteriorly by the heart varies, rhythmically in inactive spiders. It is suggested that an increased haemolymph flow posteriorly coincides with a raised pressure gradient into the prosoma which inhibits the heart from pumping haemolymph anteriorly.

Introduction

Locomotion in spiders involves a combination of muscular flexion and hydraulic extension (Ellis 1944; Parry 1957; Parry and Brown 1959). The two main flexion/extension joints of each leg, femur-patella and tibia-metatarsus, lack extensor muscles altogether (Petrunkevitch 1909). Leg extension relies on an internal turgor pressure, the higher the pressure the faster the extension (Parry and Brown 1959). Normal walking requires prosomal pressures in the range of 30–60 mmHg, however, transient pressures over 400 mmHg have been measured (Anderson and Prestwich 1975; Parry and Brown 1959; Stewart and Martin 1974). The pressure required for leg extension is created primarily by a dorso-ventral compression of the prosoma, although the heart and abdominal muscles may be involved (Anderson and Prestwich 1975; Finck 1982; Wilson 1970). Such a hydraulic mechanism for leg extension poses no problems so long as the prosoma and legs are considered as a sealed unit, but this is not the case – the prosoma communicates with the abdomen through the pedicel in which no valves to control fluid movement, have yet been found (Wilson 1965). In addition, the fluid involved in leg extension, the haemolymph, is not inert, but also acts as a transport system and performs a respiratory function. The pedicel and haemolymph provide a vital link between the prosoma and the abdomen which contains the heart, food reserves and, in most spiders, all the respiratory organs. Through the pedicel haemolymph flows forward through the anterior aorta, and back through large sinus'.

It has been suggested that high prosomal pressures, present during maximum effort, prevent the flow of haemolymph into the prosoma, whilst increasing the flow out into the abdomen (Levi and Kirber 1976; Wilson 1967; Wilson and Bullock 1973). The effect would be disastrous for sustained activity if such pressures exist during rapid locomotion, the increased pressures needed for locomotion simultaneously starving the muscles of oxygen and expelling the fluid necessary for leg extension. However, previous studies, using the 'tarantulas' *Dugesiella* (Stewart and Martin 1974) and *Brachypelma* (Anderson and Prestwich 1985), have suggested that, at least in large spiders, the heart can maintain some forward pumping during activity.

The aim of this work was to investigate the effect of activity on the heart, and therefore the circulation, of unrestrained spiders. In choosing species to be used, particular importance was placed on the extent of the respiratory and circulatory systems. Most spiders possess a pair of booklungs and a simple tracheal system, both within the abdomen. However, some species have well-developed tracheae extending into the prosoma and these typically have reduced circulatory systems, the heart being shorter and having a reduced number of ostia (Foelix 1982; Petrunkevitch 1933). Martin and Johansen (1965) go so far as to state that "... with the development of tracheae in the higher spiders the circulatory system lapses back to the less efficient state found in insects." It was postulated that activity would have a greater effect on the hearts of spiders with prosomal tracheae.

Materials and methods

A total of 98 spiders, belonging to 15 species and representing 11 families, were tested; mature females and immatures (of undetermined sex) were used for all genera except *Argyroneta* in which mature males and females were used:

A) Tracheae highly branched and extending into the prosoma:

1. Argyronetidae:	*Argyroneta aquatica* (Clerck)
2. Dysderidae:	*Dysdera erythrina* (Walckenaer)
3. Segestriidae:	*Segestria senoculata* (Linnaeus)
	Segestria florentina (Rossi)

B) Tracheae with little branching (except *Xysticus*) and limited to the abdomen:

4. Agelenidae:	*Tegenaria domestica* (Clerck)
	Tegenaria sp. (unidentified immatures)
	Coelotes terrestris (Wider)
5. Amaurobiidae:	*Amaurobius fenestralis* (Stroem)
	Amaurobius ferox (Walckenaer)
6. Clubionidae:	*Clubiona terrestris* (Westring)
7. Gnaphosidae:	*Drassodes lapidosus* (Walckenaer)
8. Lycosidae:	*Trochosa terricola* (Thorell)
9. Philodromidae:	*Tibellus oblongus* (Walckenaer)
10. Thomisidae:	*Xysticus cristatus* (Clerck)
11. Theridiidae:	*Steatoda bipunctata* (Linnaeus)

A non-invasive technique was used to monitor heart-beat. A 5 mW Helium-Neon laser, with a beam width of 0.8 mm, illuminated the abdomen directly above the heart. Since the amount of light absorbed by the heart changes during the heart-beat cycle, a photodiode measuring the light transmitted through, or reflected from, the abdomen showed the rate of the heart-beat. This technique, however, responds to both heart and pericardial volume changes, variations in the latter being likely to increase or decrease the distance between the heart and the overlying cuticle and thus alter the recorded heart-beat. A change in pericardial volume, which is independent of any heart-volume change, would therefore be expected to cause an irregular-shaped heart-beat trace if lasting for only a part of a heart-beat cycle (single contraction/expansion); alternatively, a pericardial volume change lasting for one or more complete heart-beat cycles would be expected to cause a shift, upwards or downwards, of both the upper and lower levels of the recorded heart-beat trace. Therefore, it is considered that heart-rate, as measured between the peaks of regularly-shaped heart-beat traces, is unlikely to be affected by changes in the pericardial volume; in addition, amplitude changes are only described when there was no coincident change in the shape of the heart-beat trace and when the upper or lower level of the trace remained constant. The photodiode, with a variable operational amplifier, was connected to an oscilloscope and a chart recorder: the light/photo-current response was linear.

In the first type of experiment (Fig. 1 A) the spiders were chased, within a revolving glass 'running chamber', by a ball-bearing held in place by a magnet. After enclosure within the chamber, each spider was left for one hour and then forced to run, as fast as possible, for 90 s: the speed at which the chamber revolved was variable to allow for changes in running speed. Before and immediately after running the spider, the heart-beat was measured; a maximum of five seconds was needed to locate the heart, using a micro-manipulator to move the chamber relative to the laser-beam. Since a high ambient light level obscured the heart-beat signal, the only illumination was a dim D.C. light-bulb. However, a major disadvantage of this experiment was that the heart-beat could not be recorded whilst the spider was moving: indeed, Carrel (1987) points out the general inability of the optical techniques, so far described, to measure the heart-rate in active unrestrained animals and considers that this has limited the widespread use this method.

The second type of experiment (Fig. 1 B–E) enabled the heart-beat to be measured, by reflection, during activity: laser-light was transmitted to, and from, the abdomen by plastic optical-fibres. The fibres, each with a diameter of 0.5 mm, were incorporated into a 'saddle' (Fig. 1 C) which was attached to the abdomen of an anaesthetised (with CO_2) restrained spider with latex glue ("Copydex"). Recordings could be taken from one or two sites (simultaneously) on the abdomen of the spider, this depended on the number of receiving fibres. During the experiment the spider could run, without restraint, on a table-tennis ball floating on a cushion of air (Fig. 1 E). The table-tennis ball was covered with black dots to allow the recording of spider movement: when the ball rotated, the black dots passed a light emitter/sensor, causing a change in sensor output. The whole apparatus operated within a water-bath: the air used to suspend the table-tennis ball was passed through water and a heat-exchanger, thus maintaining a constant 100% humidity and 20 °C around the spider. Heart-beat recordings were taken during periods or rest, voluntary running (always sub-maximal speed), and forced fast running (maximum speed): each spider was forced to run by touching it's legs or abdomen with a fine brush. During voluntary running, observations suggested that the spiderś gait was the same at all running speeds, thus no distinction was made between 'running' and 'walking'. All

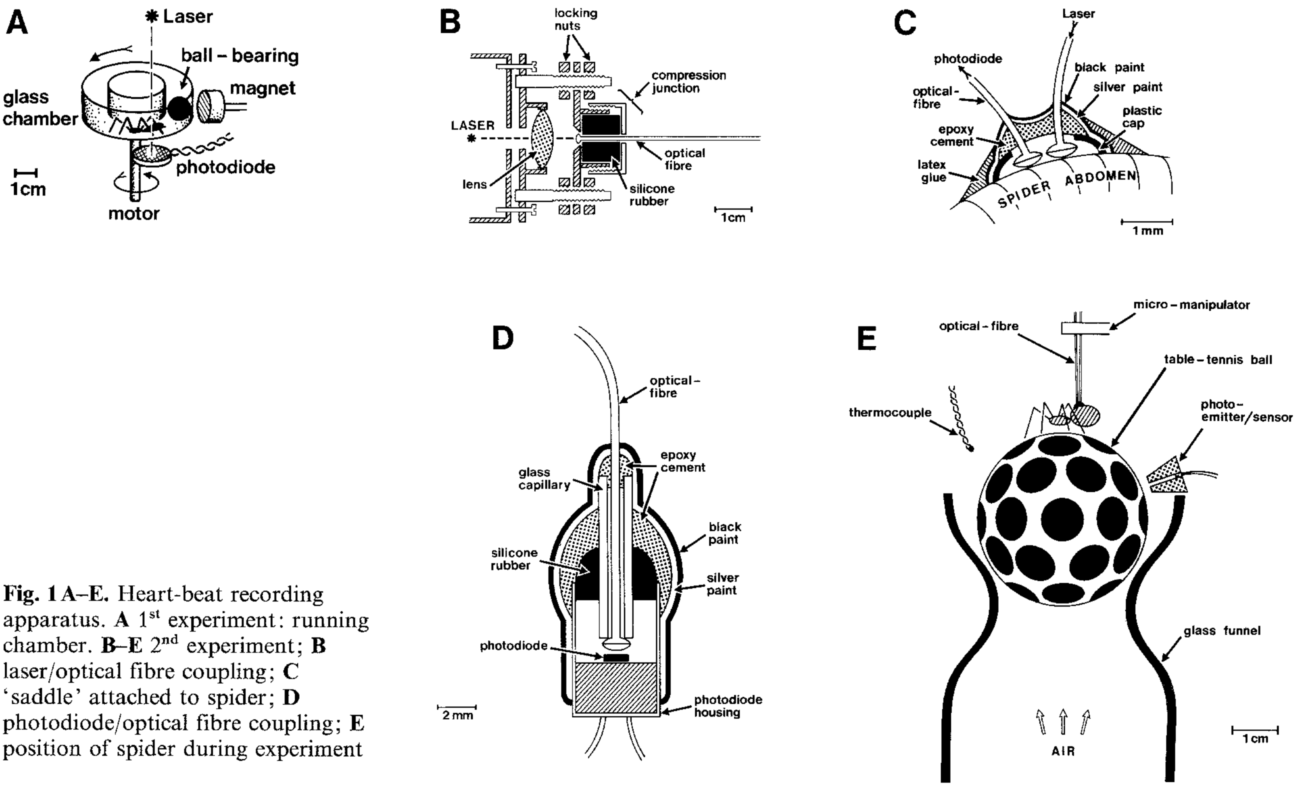


Fig. 1A–E. Heart-beat recording apparatus. **A** 1st experiment: running chamber. **B–E** 2nd experiment; **B** laser/optical fibre coupling; **C** 'saddle' attached to spider; **D** photodiode/optical fibre coupling; **E** position of spider during experiment

experiments were performed at 20 °C, the spiders having previously been housed at this temperature with water ad lib., for one week. One day before the experiment, the spiders were fed ad lib.

Heart-beats, activity and a time-scale were recorded on a chart-recorder. Heart pumping movements were related to the trace on the chart-recorder by observing the spiders under a microscope whilst recording with the laser. The chart was marked when the heart was either fully expanded or contracted. Generally, full expansion coincided with trace peaks and full contraction with troughs. However, in some spiders a small rise in the chart trace occurred at the onset of contraction: this has been explained by Wilson (1967) as a whitening of the muscle fibres as they contract. In the analysis, the mean heart-rates were calculated, in beats per minute (bpm), for each level of activity. Throughout this paper, statistical methods follow Snedecor and Cochran (1967).

In an exploratory investigation, the size of the heart relative to the prosoma was determined in six individuals, of similar weight, belonging to different genera. Longitudinal sections were prepared by standard histological techniques (Drury and Wallington 1967). The cross-sectional areas of the heart and prosoma were measured, along the midline of the spider, using a camera lucida and image analyser.

Results

Maximum heart-rates of different genera

The heart-rates of all the genera investigated are given in Fig. 2. The minimum heart-rates recorded have not been used since different spiders were rarely inactive for similar lengths of time, and recovery-rates after activity varied according to the preceding exercise. However, reproducible upper limits of heart-rate were found to be achievable in the laboratory. The mean maximum heart-rate for genera with prosomal tracheae is 77 bpm (SD ± 16; $n = 3$ genera; mean weight = 98 mg), for genera with tracheae limited to the abdomen, 184 bpm (SD ± 33; $n = 9$ genera; mean weight = 86 mg). With *Argyroneta* and *Trochosa*, the only genera used extensively in both the 'running chamber' and 'saddle' experiments, there were no significant differences between the maximum heart-rates recorded from each type of experiment (two-tailed t-test: $P > 0.5$ for both genera).

Effect of weight and sex on heart-rate

Relationships between weight (M) and maximum heart-rate, for each of six genera tested with $n = 10$ individuals or more, are shown in Fig. 3. There are no significant differences (variance-ratio test) between the slopes of different species ($P > 0.5$), and no significant overall effect of weight (and thus maturity) on heart-rate ($P > 0.1$). However, there was a significant variation between the heart-rates of different genera (one-way ANOVA: $P < 0.001$). The difference between the heart-rates of spiders with and without prosomal tracheae was also

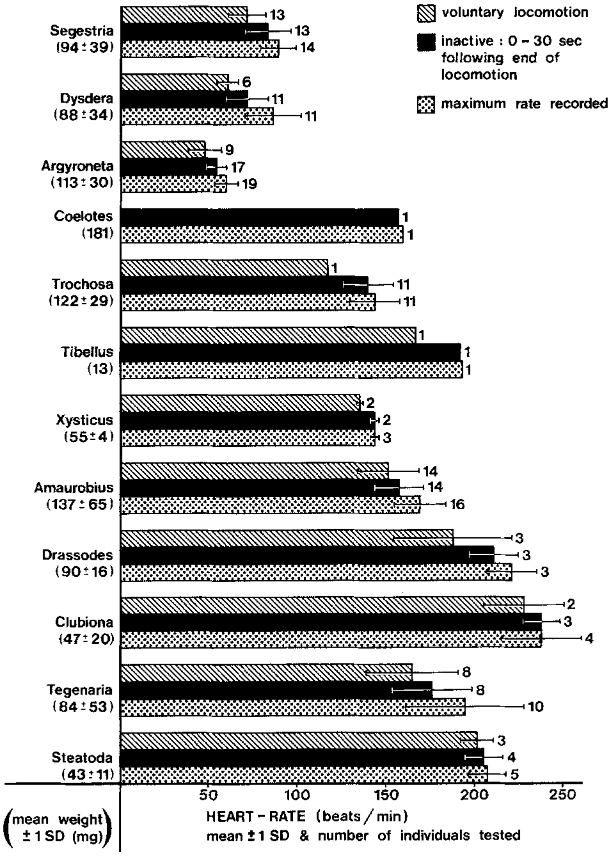


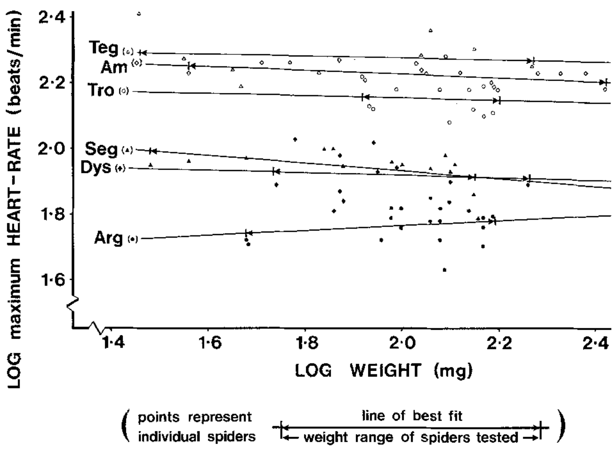
Fig. 2. Heart-rates of all genera tested, during different levels of activity

highly significant (one-way ANOVA: $P<0.001$). In *Argyroneta*, the maximum heart-rates of mature males (mean = 64 bpm, $n=7$ individuals) were significantly higher (single-tailed t-test: $P<0.02$) than the maximum heart-rates of mature females (mean = 56 bpm, $n=12$ individuals).

Heart-function during running

When forced to run, the spiders were all capable of running continuously for 90 s: an initial period of very fast running, lasting 10–20 s, was followed by slower but steady running. A problem commonly encountered was the unwillingness of a spider to stop moving. In all genera, voluntary running regularly persisted for over 15 min; however, all *Dysdera* individuals rarely stopped running, some resting only once or twice over a two-hour recording period.

The hearts of all spiders investigated were capable of maintaining pumping during every observed type of activity. In all genera the mean heart-rate after voluntary running was higher than the mean rate during running. There was no overall change in the heart-rate whilst the spiders were running voluntarily. The rise in heart-rate at the end of voluntary running was higher in *Dysdera* and *Segestria* (15%, SD ± 1, $n=2$ genera) than in the other genera (5%, SD ± 2, $n=9$ genera). Fig. 4 shows heart-rates during the first 20 s of forced fast running: heart-rates were always lower during the first five seconds of forced fast running than before or after running. Heart-rate depression at the onset of running increased with the time since the last forced exercise. In 94% of all the spiders tested, the onset of forced fast running was associated with a reduction in heart-beat amplitude: during the first five seconds of running, the mean fall in amplitude was 28% (SD ± 18, $n=64$) of the amplitude immediately before running. In both *Dysdera* and *Segestria*, an arrest of heart-pumping



	Tegenaria	Amaurobius	Trochosa	Segestria	Dysdera	Argyroneta
gradient	−0·03	−0·05	−0·03	−0·12	−0·04	0·08
r	−0·10	−0·32	−0·08	−0·45	−0·06	0·19
n	10	16	11	14	11	19

Fig. 3. Heart-rate/weight relationships

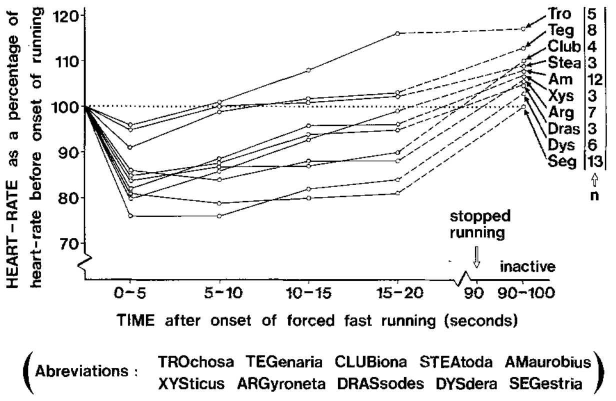


Fig. 4. Effect of forced fast running on heart-rate. For each genus, the mean heart-rates during running are given as a percentage of the mean heart-rate 0–10 s before the onset of running

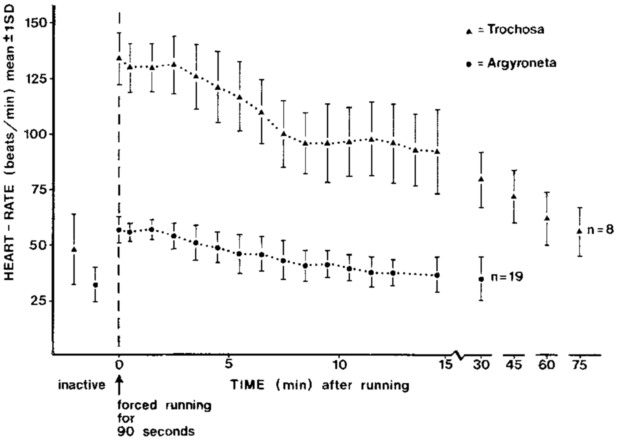


Fig. 5. Heart-rate recovery after forced exercise

often occurred at the onset of forced fast running, the heart remaining fully expanded for up to 5 s.

Resting heart-rates and recovery from exercise

Under the experimental conditions of the running chamber, some spiders, notably all *Dysdera* individuals, remained inactive for little more than a few seconds at any one time. However, members of two genera, *Argyroneta* and *Trochosa*, tended to remain inactive for long periods. With spiders which remained inactive during the hour before enforced running it was therefore possible to record lower 'resting' heart-rates. After forced fast running, recovery rates were recorded (Fig. 5). Spiders which remained active during the recovery period were discounted. *Argyroneta* had significantly lower 'resting' and maximum heart-rates than *Trochosa* (single-tailed Mann-Whitney *U*-test: $P<0.01$ and $P<0.001$, respectively). The ratios of the mean maximum heart-rate to the mean 'rest' rate were: *Argyroneta*, 1.8:1 (56:31 bpm); *Trochosa*, 2.8:1 (133:47 bpm). The highest ratio for any spider was 6:1 (198:32 bpm), for a mature female *Tegenaria domestica* (141 mg); the highest ratio for a spider with prosomal tracheae was 3.8:1 (88:23 bpm), for a mature female *Segestria senoculata* (30 mg). An interesting result involved a single *Clubiona* individual which, after being left undisturbed for 18 h, had a heart-rate of 9 bpm: when the chamber was illuminated, this increased to 88 bpm, and then to 204 bpm after 90 s of running, i.e. a rise of 27 times the lowest rate.

Heart-rate of Dysdera

In all but one genus, the heart pumped regularly, frequency changes occurring gradually over many heart-beats. However, in *Dysdera* large changes in heart-beat duration often occurred from one beat to the next. During inactivity two forms of heart-beat were clearly seen, one typically having a shorter systole time and a smaller amplitude. Both forms were also present during locomotion: the relative proportion of each form depended on the activity level of the spider (Figs. 6 and 7).

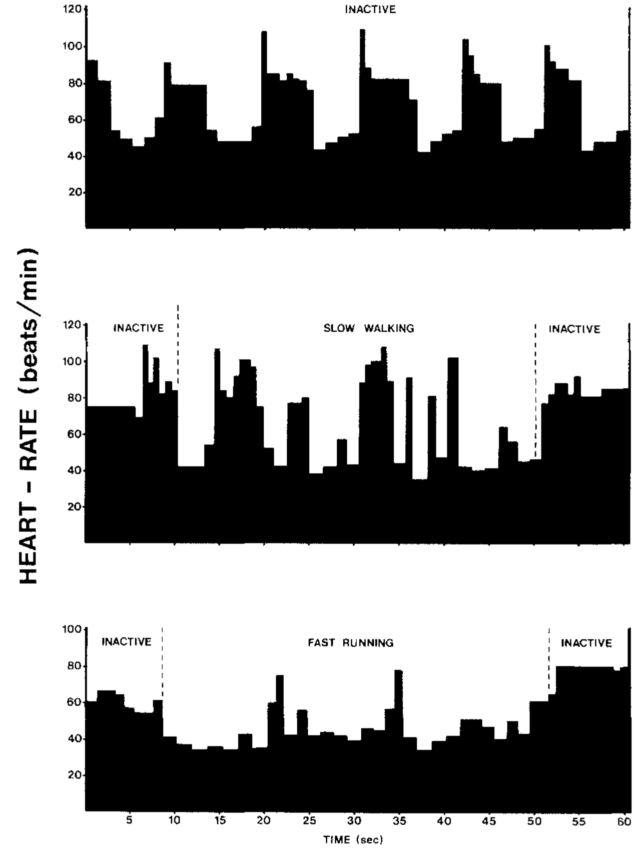


Fig. 6. *Dysdera* heart-rate patterns: examples during different levels of activity

Using two recording fibres, one anterior and one posterior, it was possible to monitor blood flow posterior to the heart as well as contractions of the heart. As the saddle was moved posteriorly on the abdomen, a site was reached after which the two recorded wave-forms were in anti-phase: this is interpreted as the posterior aorta expanding as the heart contracts. In all genera, except *Dysdera*, the posterior aorta pulsated with every heart-contraction; however, in *Dysdera* pulsations occurred only during the form of heart-beat with a short systole (Fig. 7).

Heart-size in different genera

In the analysis of heart-sizes, the cross-sectional area of the heart was calculated as a percentage

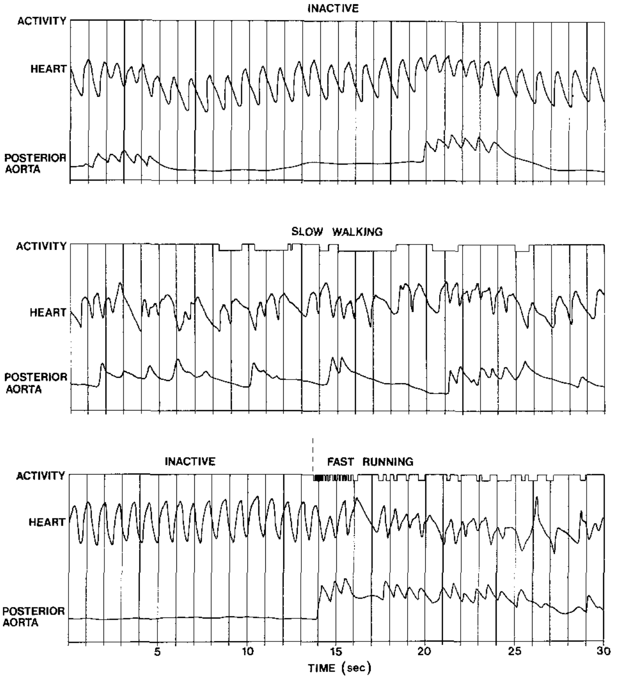


Fig. 7. Simultaneous recording of the heart-rate and posterior aorta pulsations in *Dysdera*: examples during different levels of activity

of the cross-sectional area of the prosoma: *Xysticus* (31 mg), 33%; *Trochosa* (111 mg), 29%; *Argyroneta* (93 mg), 25%; *Amaurobius* (113 mg), 24%; *Dysdera* (52 mg), 15%; *Segestria* (110 mg), 14%.

Discussion

Maximum heart-rate of different genera

Significant variation was found in the maximum heart-rates of different species. The results suggest that, for spider species without prosomal tracheae, a relationship exists between the maximum heart-rate and the prey-catching behaviour. Actively foraging spiders (e.g. *Clubiona* and *Drassodes*) have the highest heart-rates, followed by sit-and-wait web-building spiders (e.g. *Tegenaria* and *Steatoda*), with sit-and-wait spiders which do not use webs for prey-capture having the lowest heart-rates (e.g. *Trochosa* and *Xysticus*). Each pair of examples given above has a significantly different heart-rate from the other two (one-way ANOVA: $P<0.001$). A comparison of the heart-rates of different species may therefore indicate evolutionary adaptations: in this case, it is likely that the higher maximum heart-rates of some spiders allow them to meet the higher energy demands (e.g. higher rates of oxygen consumption and/or faster recovery) of particular types of prey-catching behaviour. Clearly, further experiments are needed to relate heart-rate to oxygen consumption during and after exercise since interspecific variations in heart pumping-volume, respiratory system (surface area and gas-permeability) and haemocyanin concentration would also affect the supply of oxygen to the muscles. Whilst Greenstone and Bennett (1980) and Anderson and Prestwich (1982) both found resting heart-rate to be an unreliable predictor of resting metabolic rate, Carrel (1987) considers that "heart rate and metabolic rate in spiders are generally correlated with each other". Carrel and Heathcote (1976), measuring resting rather than maximum heart-rate, also found higher heart-rates in spiders which use webs to catch prey than in 'hunting' spiders (lycosids) of the same weight. However, the extent to which resting and maximum heart-rates need be linked is debatable: whereas maximum heart-rates are likely to be related to short-term prey-catching behaviour, resting rates may reflect energy requirements over longer periods (perhaps associated with food availability, posture or anabolic processes). Thus, if maximum and resting heart-rates are influenced by separate evolutionary pressures then they would be expected to vary independently.

A further consideration is the possible effects that high heart-rates may have on oxygen uptake. Whilst it is likely that a greater haemolymph flow through the book-lungs usually increases the oxygen uptake, this might not always be the case. Angersbach (1978) found that the heart-rate of *Eurypelma*, during recovery from exercise, was negatively correlated with the P_{O_2} of haemolymph in the heart; he suggests that increased heart-rates allow less time for the oxygenation of haemocyanin in the lungs. It has also been suggested that heart-movements increase oxygen uptake by causing ventilation of the book-lungs (Hill 1977); however, Paul et al. (1987) have shown that, in *Eurypelma*, heart-synchronous ventilation plays no significant role in gas transport.

With those spiders possessing prosomal tracheae, it is unlikely that the heart-rates can be compared in the same way as was possible with spiders without prosomal tracheae. The situation is complicated both by the reduced participation of the circulatory system in respiratory gas exchange, and the large differences in the size of the heart relative to the size of the prosoma. For example, *Argyroneta*, a foraging underwater spider possesses a lower maximum heart-rate but a larger heart-size than *Segestria*, a hole-dwelling spider.

Effect of weight and sex on heart-rate

Within a species, weight (M) was found to have no significant effect on maximum heart-rate (H_{max}). Anderson and Prestwich (1982), using three species with larger size-ranges than those used in the present study, found a small effect of weight on maximum heart-rate (*Lycosa*, $H_{max} \propto M^{-0.07}$; *Filistata*, $H_{max} \propto M^{-0.12}$; *Atypus*, $H_{max} \propto M^{-0.12}$). Similarly, weight appears to have a limited effect on resting heart-rate, Carrel (1987) concluding that "intraspecific variation in spider [resting] heart-rate is weakly related in a negative fashion to body size".

The results of the present study show that maximum heart-rate depends more on species than on weight; that the same applies to the 'resting' heart-rate is suggested by the significant difference between the resting heart-rates of *Argyroneta* and *Trochosa*. Carrel and Heathcote (1976) also found significant interspecific differences in resting heart-rate, large hunting spiders having heart-rates approximately half those of web-weavers of the same size (Carrel 1987) and 'primitive hunters and weavers' having similar heart-rates to theraphosids 100 times their size; consequently, it is surprising that, in the same paper, it is stated that the "resting heart rate of spiders is primarily a function of body size". It therefore appears that heart-rate/weight relationships which include a number of species, of different weights, are of limited value.

In *Argyroneta*, the different maximum heart-rates of mature males and females lends support to warnings of complications arising from using different sexes in species-comparisons (Anderson 1970). However, in addition to possible differences in the activity patterns of the two sexes, it appears that they may also have different energetic capabilities.

Heart-function during locomotion

The ability of the heart to maintain pumping during every observed type of activity has been demonstrated for all the species tested. In all genera except *Dysdera* (see below), similar forms of heart-beat, in terms of the size and shape of the chart-recorder trace, were seen during inactivity and all types of activity; this suggests that pressure gradients high enough to prevent the circulation of haemolymph around the prosoma do not persist during any type of activity. Since this study included a range of spiders with a large variation in the development of the respiratory, and circulatory systems, it is likely that this conclusion can be applied to most, if not all, spider species. Slow and distorted heart-beats, with increased systole times, have been described in active *Heteropoda venatoria* (Wilson 1967); however, abnormal pressures may have existed in the spiders, which were struggling under restraint.

It is often reported that spiders are incabable of sustaining locomotion after a few seconds of rapid running (Bristowe 1958; Bristowe and Millot 1933; Cloudsley-Thompson 1957; Wilson and Bullock 1973). This could be explained on energetic grounds, since spider muscles contain few mitochondria (Linzen and Gallowitz 1975); however, Herreid (1981) calculated that oxygen- and phosphate-stores could last roughly 9 min in a fast-running theraphosid. On the other hand, Wilson and Bullock (1973), working with *Amaurobius*, suggested that an early cessation of activity resulted from the high prosomal pressures present during fast running, which shift the haemolymph from the prosoma into the abdomen and thereby prevent leg-extension. However, all 15 species investigated in this study could maintain forced fast running for at least 90 s. This result, combined with the heart-beat observations during locomotion, suggests that haemolymph is pumped into the prosoma during maximum speed running as well as during voluntary running, thus allowing continued leg extension. During 20 min of 'steady-state' locomotion in a theraphosid, Herreid (1981) calculated that 38% of the total oxygen consumed came from oxygen delivered during running. It is possible that a withdrawal reaction to prodding caused a premature cessation of activity in previous studies.

Locomotion affected the hearts of all the spiders studied to some degree, causing a decreased heart-rate. The rise in heart-rate at the end of voluntary running, regardless of the speed or duration of running, suggests that even slow voluntary walking involves prosomal pressures high enough to impede heart-pumping. In the first five seconds of forced fast running, heart-rates were always lower than before, or after, running: the disruption occurring during forced fast running persisted for longer in the spiders with prosomal tracheae and low heart-rates. In nearly all the spiders tested, forced fast running was also associated with a reduced heart-beat amplitude. Both heart-rate and heart-beat amplitude are known to be neuronally modulated in spiders (Gonzales-Fernandez and Sherman 1984); however, during locomotion, physical effects (such as pressure changes within the prosoma or abdomen) seem more likely to explain the variations in heart-beat amplitude and heart-rate. For example, it is possible that heart-beat amplitude varies with the tension of the cardiac ligaments which join the heart with the cuticle and expand the heart after muscular contraction. An increase in tension, which might occur after a shift of haemolymph into the abdomen, could prevent full contraction by the cardiac muscles. Alternatively, a reduction in tension, perhaps caused by a contraction of the abdominal sub-cutaneous and dorso-ventral muscles (shown to occur during activity by Anderson and Prestwich 1975), could prevent full heart-expansion. Contraction of the abdominal muscles would also increase abdominal pressure and may be advantageous in reducing both the flow of haemolymph out of the prosoma (Anderson and Prestwich 1975) and the disruptive effect of high prosomal pressures on the heart.

Heart-rate of Dysdera

Periodic changes in the pressure differential, between the prosoma and the abdomen, may also explain the alternation between the two forms of heart-beat in *Dysdera*. The simplest explanation of the results is that, when the pressure gradient into the prosoma is too high, the heart fails to pump haemolymph through the anterior aorta. At such times, a greater haemolymph flow posteriorly would cause pulsations in the posterior aorta. Since the pulsations are intermittent in both active and inactive spiders, this phenomenon is not simply an immediate 'side-effect' of locomotion. Rather, it is likely to be an essential part of *Dysdera*'s normal circulation. For example, a periodic rise in the pressure gradient into the prosoma may aid haemolymph circulation by increasing the flow around the abdomen, and by 'flushing' haemolymph from the prosoma. The variation in heart-beat amplitude suggests changes in abdominal volume and cardiac ligament tension. The regularity of the pulsations in other species may be explained by these spiders having stronger hearts than *Dysdera* and/or there being less resistance to haemolymph flow through the posterior aorta. Obviously, further experiments are needed to test the above speculations; these could involve pressure measurements (for techniques see: Stewart and Martin 1974; Wilson and Bullock 1973) as well as blood-flow measurements (for thermographic techniques see: Wasserthal 1980).

Resting heart-rates and the rate of recovery

The faster recovery of *Argyroneta* than *Trochosa* after forced exercise, in terms of the time taken for the heart-rate to return to it's 'resting' level, suggests energetic and behavioural advantages in possessing prosomal tracheae. Not only may prosomal tracheae obviate the necessity for the heart to pump at a highly elevated rate for long periods during recovery, thus saving energy, but may also allow faster gas-exchange, thereby reducing the need for anaerobic metabolism during exercise and hastening recovery. However, no difference was found in the ability of different spiders, with and without prosomal tracheae, to run for long periods, or to resume activity soon after forced running. This may well result from the well-developed ability of spiders to obtain energy via anaerobic pathways (Anderson and Prestwich 1985; Herreid 1981; Linzen and Gallowitz 1975; Prestwich 1983a, b). The levelling of the *Trochosa* curve after 9 min indicates a change in the predominant factor which causes the elevated heart-rate. Carrel (1987) describes similar-shaped curves in spiders recovering from exercise and suggests that the rapid recovery phase indicates neuroendocrine influences, with biochemical recovery (from lactate built up during the exercise) maintaining an elevated heart-rate after the levelling of the curve. However, without further information (such as oxygen consumption data) any explanation remains speculative. Prestwich (1983a, b) investigated anaerobic metabolism in four spider species: his results showed that anaerobic dependence, during maximum activity, was lowest in *Phidippus*, the only spider used which had tracheae extending into the prosoma. Sherman and Pax (1968) measured a heart-rate of 48–138 bpm in *Geolycosa*, a spider with tracheae limited to the abdomen: after only 'several seconds' of forced exercise, the heart-rate took over 25 min to return to it's original level.

Heart-size and haemolymph flow in different genera

Phylogenetic considerations suggest that a highly-branched tracheal system, extending into the prosoma, evolved a number of times amongst spiders (Foelix 1982). Consequently, it is not surprising that other characters, such as heart-size, are not associated with prosomal tracheae. However, it is of relevance that the investigation into heart-size showed that low heart-rates are not necessarily associated with larger heart-size in spiders: indeed, *Dysdera* and *Segestria* with their low heart-rates had considerably smaller hearts, relative to the size of the prosoma, than the other species investigated. The spiders with lower heart-rates must therefore have a slower circulation of haemolymph around their body unless, that is, the total volume of their circulatory system is smaller. Tracheae extending into the prosoma would, at least partially, obviate the need for haemolymph to return to the abdomen for gas exchange, and thus reduce the adverse respiratory consequences otherwise associated with a slow circulatory rate. However, to avoid a total drainage of haemolymph from the prosoma during activity, and thus enable continued locomotion involving leg extension, low heart-rates must be accompanied by a reduced flow of haemolymph out of the prosoma. This could be achieved either by a restriction of the pedicel, perhaps involving the bundles of tracheae, or by a reduced pressure differential between the prosoma and the abdomen, involving a lower prosomal pressure, or higher abdominal pressure. In *Dysdera* and *Segestria*, the frequent arrest of heart-pumping and the persisting depression of the heart-rate during fast running suggest that some form of restriction is present, which causes a high pressure gradient to build-up and then dissipate slowly. It is of interest that *Liphistius* (Bristowe and Millot 1932) and *Atypus* (Petrunkevitch 1933; Anderson and Prestwich 1982), two 'primitive' species of similar weights to the spiders used in this study, have large hearts, relative to body size, and maximum heart-rates of just over 100 bpm. It is therefore possible that maximum heart-rates much above or below 100 bpm are derived states, as are the small hearts of *Dysdera* and *Segestria*.

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