

## Sexual selection and the energetics of copulatory courtship in the Sierra dome spider, *Linyphia litigiosa*

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**Abstract.** Mating in the Sierra dome spider, *Linyphia litigiosa* (Linyphiidae) begins with 2–6 h of aspermic copulatory courtship, termed pre-insemination phase copulation. Male intromission rate, that is, the speed of repeated genitalic insertions, withdrawals and re-insertions, and body mass are related to fertilization success via cryptic female choice (i.e. female preferences are expressed in their sperm use patterns; Watson 1991b, *Anim. Behav.*, **41**, 343–360). Carbon dioxide (CO<sub>2</sub>) respirometry indicated that pre-insemination phase copulation is energetically demanding. Male intromission rate and body mass (which are uncorrelated traits) each were positively associated with different subsets of six complementary measures of metabolic competence made during copulatory courtship; (1) efficiency; (2, 3) maximum metabolic rate and scope; (4, 5) rate and linearity of metabolic increase; (6) the consistency of metabolic output during sustained courtship. Composite ranks of males based on the six metabolic and the two overt phenotypic measures of quality were positively correlated. Body mass and intromission rate also were associated with two aspects of male fighting ability, strength and aggressiveness (i.e. willingness to escalate when at a modest size disadvantage), respectively. Fighting is important for defence of webs, prey and mates. Thus metabolic competence, a fundamental and possibly heritable component of viability, is favoured by sexual selection; this may help to yield offspring that fare better under both natural and sexual selection.

Central to the controversy concerning the nature of the sexual selection process (see Kirkpatrick & Ryan 1991) is the connection between criteria used by females to make sexual discriminations and substantive aspects of male fitness that may be passed to offspring (Balmford & Read 1991). Sexual selection studies frequently identify overt phenotypic traits of males that proximately relate to sexual success, such as body size, courtship performance or elaborate ornamentation (Halliday 1983; Harvey & Bradbury 1991). Some studies have found that selective mating by females increases female reproductive success through the production of more vigorous offspring (Partridge 1980; Simmons 1987; Schantz et al. 1989; Norris 1993). Male expression of traits that are favoured by females and female selection criteria that enhance offspring viability or fertility may be currently 'adaptive', but such an interpretation is fraught with ambiguity (Symons 1992). To analyse male sexual traits and female choice mechanisms as 'adaptations', that is, as having

been designed by selection as phenotypic solutions to specific fitness-related problems, it is important to understand their functional design (Thornhill 1990; Williams 1992, pp. 38–41; Reeve & Sherman 1993).

One scheme for investigating functional design is to relate secondary sexual traits and sexually discriminating behaviour to the strength of primary biological processes in adults and their offspring. If a secondary sexual trait reveals variability in a basic aspect of male viability and is heritable, then the evolution of the trait may have been influenced by a good-genes sexual selection process (Balmford & Read 1991). When variation in sexual morphology and behaviour are connected to the functionality of physiological systems that play a causal role in mediating viability, fitness interpretation of sexual signals can be based on biological first-principles, enabling inferences about individual phenotypic quality and a more satisfying connection of the sexual selection system to the basic biology of the organism. Three

systems whose functionality are likely to have direct impacts on viability in both sexes are those underlying immunologic, morphogenetic and, the subject of this research, metabolic competence.

Inter-sexual courtship often includes behaviour, before or during copulation (Dewsbury 1988), that could constitute displays of metabolic competence (Bennett & Houck 1983; Verrell 1985; Watt et al. 1986; Halliday 1987; Eberhard 1991; Nicoletto 1993). The reliability of inter-sexual tests of metabolic competence will depend on whether energetic courtship pushes at least some males to their physiological limits (Ryan 1985). If females can assess the metabolic competence of males by the vigour of their courtship, adaptive mate choice may become established for males of relatively high viability (Charlesworth 1987; Lande 1987, page 89; Maynard-Smith 1987).

Courtship behaviour may serve to close the distance between the sexes (attractant courtship) or to influence the female to choose the courting male to father her offspring (persuasive courtship). There are few studies that quantify inter-individual variation in the energetics of persuasive courtship and none, to our knowledge, that continuously monitor variation in individual performance throughout sustained one-on-one inter-sexual interactions. Cumulative energy use during potentially persuasive sexual behaviour has been studied in salamanders (Bennett & Houck 1983), opisthobranch molluscs (Carefoot 1989), sage grouse (Vehrencamp et al. 1989) and treefrogs (Klump & Gerhardt 1987). High-resolution flow-through respirometry now has made it practical to study even moment-to-moment variation in the physiological performance of small arthropods, whose sexual behaviour can proceed normally in a respirometric vessel (e.g. Lighton & Feener 1989).

Here we report on individual variation in six complementary measures of male metabolic competence (see Table 1) taken during pre- insemination phase copulation (i.e. aspermic copulatory courtship) in the Sierra dome spider, *Linyphia litigiosa* (Keyserling: Linyphiidae). Using these measures we first assess the potential of observed patterns of cryptic female choice (sensu Thornhill 1983) among secondary mates, based on female preferences for greater male body mass and more vigorous copulatory performance (see Watson 1991b), to yield sires of relatively high metabolic competence. We indirectly relate metabolic competence to fighting ability, which

not only determines a male's ability to become a female's first mate (Watson 1990) and principal sire of her offspring (Watson 1991a), but is also important in the acquisition and defence of web sites and prey for both sexes (P. J. Watson, unpublished data).

### Natural History

Sierra dome spiders are one of the largest of the dome-web-building linyphiids, with adult males generally ranging from 5.0 to 7.5 mm in body length and females from 5.0 to 8.5 mm. Sexual size dimorphism is small compared with most groups of spiders, but males have longer legs, larger fangs and thicker cuticle on their prosoma and chelicerae than females; this along with their more aggressive behaviour makes them superior to females in combat. The species is common, although patchily distributed, from Montana south to Utah, and west to the Pacific coast, especially in mountainous areas near fresh water. Small dipterans are the staple prey.

Sierra dome spiders have an annual life cycle. All adults die by mid-autumn and only spiderlings, still within the natal cocoon, overwinter. At my study site in northwestern Montana, spiderlings emerge in March and breeding lasts from July to late August. During this time females maintain and gradually enlarge their semi-permanent webs, but males are nomadic. Males spend their adult life wandering in search of female webs, which they enter freely to forage, gain refuge from predators and guard or court the resident female (males are dominant in virtually all inter-sexual encounters, but cannot force copulation; see Watson 1993). By September nearly all males have been killed in encounters with predators (birds, wasps, other spiders) or in fights with rival conspecifics over possession of females and their webs.

### Mating System

In *L. litigiosa*, males engage in a scramble-competition polygyny mating strategy, combined with multi-day guarding of particular females of high reproductive value (i.e. soon-to-mature penultimate females). Females are sequentially polyandrous. The first male to mate with a given female fertilizes, on average, 60–70% of her eggs. First mates are determined during a 2- to 5-day series of intensive male-male fights immediately

**Table 1.** Standard scores and ranks of eight male Sierra dome spiders for six aspects of metabolic competence and two overt sexually selected phenotypic traits

Fitness	Male							
	A	B	C	D	F	G	H	I
<b>Metabolic competence</b>								
Efficiency*	0.21 (4)	1.16 (1)	-0.07 (5)	-0.76 (6)	—	0.67 (2)	-1.80 (7)	0.60 (3)
Maximum metabolic rate†	-1.80 (8)	0.67 (3)	0.08 (6)	0.57 (4)	0.75 (2)	0.15 (5)	0.86 (1)	-1.28 (7)
Maximum scope‡	-1.71 (8)	0.34 (4)	0.36 (3)	1.62 (1)	0.75 (2)	-0.33 (5)	-0.59 (7)	-0.44 (6)
Slope§	-0.96 (8)	1.93 (1)	-0.75 (6)	-0.39 (5)	-0.89 (7)	0.71 (2)	0.55 (3)	-0.20 (4)
Linearity**	-1.86 (8)	1.50 (1)	-0.64 (7)	0.41 (3.5)	-0.48 (6)	0.41 (3.5)	0.11 (5)	0.55 (2)
Consistency††	0.54 (5)	-1.61 (1)	-0.44 (3)	-0.08 (4)	-1.12 (2)	0.72 (6.5)	1.27 (8)	0.72 (6.5)
Composite	8	1	6	3	2	4	7	5
<b>Overt phenotype</b>								
Intromission rate‡‡	-1.30 (7)	1.15 (1)	-1.01 (6)	0.58 (3)	—	0.29 (4)	1.01 (2)	-0.72 (5)
Body mass (mg)	-0.39 (6)	1.37 (1)	-0.21 (5)	0.72 (3)	0.23 (4)	0.96 (2)	-2.01 (8)	-0.63 (7)
Composite rank	8	1	7	2.5	4	2.5	5	6

Measures of metabolic competence are based on respirometric data collected during pre-insemination phase copulation. Original data were converted to standard scores (i.e.  $X=0$ ,  $SD=1$ ). Negative values denote below average scores. Numbers in parentheses show an individual's rank within each measure (1=highest, 8=lowest). Composite ranks for the metabolic and overt measurement categories are based on means of the single measure ranks within each category.

\*Mean residual from linear regression of metabolic rate ( $\mu\text{W/mg}$ ) versus intromission rate (see Fig. 3a).

†Maximum metabolic rate averaged over any 1-min period.

‡Factor by which maximum metabolic rate rose above resting metabolic rate.

§Slope of metabolic rate versus time during first major increase of metabolic rate.

\*\*Coefficient of determination (i.e.  $r^2$ ) associated with the slope.

††Standard deviation in metabolic rate after the asymptote of the first increase in metabolic rate.

‡‡Maximum observed number of successful genitalic couplings per min.

preceding a female's sexual maturation (Watson 1990). Vigorous males with relatively high body mass are more likely to win these competitions (Watson 1990).

It is not until 4–8 weeks after a female's first mating that she produces her first brood of eggs. During this period most females (85%,  $N=267$ ) accept one to three secondary matings, and multiple paternity within broods is common (Watson 1991a). Re-mating is partly a foraging strategy (Watson 1993), but non-random sperm utilization may yield indirect benefits as well. Male body mass and intromission rate (see below) during copulatory courtship are known to be positively associated with relative fertilization success among the secondary mates of females, and the

sexual selection mechanism appears to be active female choice (Watson 1991b).

### Pre-insemination Phase Copulation

Sperm are absent from the male copulatory organs (paired secondary sexual organs, called the palpi, consisting of modified tarsal segments of the pedipalps) at the beginning of all matings in *L. litigiosa*. Pre-insemination phase copulation lasts 2–6 h ( $\mu=2.6$  h,  $SD=1.1$ ;  $N=102$ ). The male then withdraws to the periphery of the web, constructs a sperm platform, inducts fresh ejaculate into his palpi and returns to inseminate the female. Although both pre-insemination and insemination phase copulation are inactive for

females, copulation appears arduous for males, particularly during the pre-insemination phase when they seemingly try to execute repeated cycles of genitalic coupling and uncoupling as rapidly as possible.

During pre-insemination phase copulation, each intromission lasts 1–2 s and is associated with full inflation of a large hydraulic muscle in the palpus, the haematodoca. Uncoupling of the genitalia follows deflation of the haematodoca. After uncoupling, the male grooms the palpus and may rest for 1–60 s or more (typically 2–5 s) before attempting the next intromission either with the same or the opposite palpus. Blest & Pomeroy (1978) provide a detailed explanation of linyphiid genital mechanics.

Males vary in the peak rate at which they execute cycles of genitalic coupling (i.e. intromission) and uncoupling during pre-insemination phase copulation ( $\mu=6.3$  per min,  $SD=1.8$ , range=2–10,  $N=112$ ). Males also make variable numbers of unsuccessful coupling attempts ( $\mu=1.2$  per min,  $SD=3.8$ , range=0–28,  $N=94$ ), termed flubs, for each full intromission that they achieve. Flubs consist of the male positioning the palpus over the female's epigynum in the usual way, followed by brief partial expansion of the palpus where the haematodoca inflates to about 10% of its capacity. Many flubs may be made in rapid succession before the male stops to groom the palpus and renew his attempts at intromission. As pre-insemination phase copulation proceeds, many males reduce their flub-to-intromission ratio to nearly zero, while the performance of some males gets worse.

Some sexual signalling systems in which females prefer more costly displays are interpretable in terms of passive attraction to more detectable signals, a selection process that may be viewed as male–male competition (Parker 1983; Gerhardt 1991). Pre-insemination phase copulation clearly serves no attractant function; when it begins, the female is already in contact with the male. It also serves no mate-guarding function, because copulation ceases and fighting begins whenever a new male arrives at a web harbouring a copulating pair. It does not represent a passive female choice mechanism based on sperm displacement by males, because males seem unable to displace sperm without being allowed to do so by the female (Watson 1991b). Copulatory courtship in *L. litigiosa* functions to influence female choice.

## METHODS

### Spiders

Females used in our studies were collected from 15 to 24 July 1992 at the Flathead Lake Biological Station, Polson, Montana, U.S.A. We allowed them to build webs in individual plastic cages (240 cm<sup>3</sup> volume) kept at ambient temperature and humidity. We regularly watered and fed the females fresh natural prey, and allowed them to mature in captivity to provide a stock of virgin females. We collected males from the same site on 2–3 August 1992 and housed them similarly. We transported the spiders to the laboratory in these same cages, and fed them cultured *Drosophila pseudoobscura* and deionized water.

We transported all spiders to Arizona State University (Tempe, Arizona) under favourable conditions of temperature (18–25°C) and relative humidity (70–95%) during 4–7 August. We performed respirometric measurements from 8 to 13 August; this period falls well within the study population's natural breeding season (July–August). All spiders consumed at least two fresh prey within 24 h of the respirometric measurements, and appeared to behave normally. The similarity in the diets of males used in the study serves to minimize inter-individual variation in metabolic capacities that might arise due to short-term nutritional effects.

### Respirometry

We made all respirometric determinations with a Sable Systems TR2 flow-through respirometry system (Sable Systems, Salt Lake City, Utah). We used a mass flow controller to maintain flow rates of 100 ml/min through the respirometry chamber (50 cm<sup>3</sup> inverted erlenmeyer flask). We monitored temperature continuously throughout all runs with a resolution of 0.01°C, using a thermocouple taped to the flask's surface. Temperature ranged from 28.1 to 30.6°C during the recordings ( $\mu=29.2$ ,  $SD=0.6$ ) and showed no relationship to intromission rates, flub rates, energy efficiency, or metabolic scope (all  $P_s>0.133$ ). The respirometer flask was illuminated by a 40-W halogen lamp placed 25 cm away. We measured resting rates of carbon dioxide emission ( $\dot{V}CO_2$ , in litres per h) while the spiders were completely inactive and located on their webs in the same respirometer

chambers that we used for the courtship energetics studies.

Each respirometric run proceeded in a stereotyped way. First, we placed a virgin female spider in a respirometer flask overnight, during which time she constructed a sheet web typical of the species. The following morning, we attached the flask to the respirometry system and recorded her rate of carbon dioxide emission ( $\dot{V}CO_2$ ) for about 10 min. We observed the female continuously, and entered behavioural codes into the respirometric record at the computer keyboard that allowed us to discard readings raised by female locomotor or grooming activity.

After determining  $\dot{V}CO_2$  for the female alone, we paused the recording and added a male spider to the same flask. After about 5 min, required to stabilize  $\dot{V}CO_2$  readings, we re-started the recording. Copulation often began within 30 min. We counted intromission rates, that is, the number of successful genitalic couplings, as well as the number of failed coupling attempts, or flubs (see above), over a 3-min period; we made between one and eight counts per male, including at least one count near the time of the male's peak copulatory performance. During the recordings, we continuously entered behavioural codes at the computer keyboard denoting locomotor behaviour, breaks in copulation, and other variations in the activity of the pair that might affect metabolic rate. These codes were stored in synchrony with the respirometric data. During all phases of copulation, the female usually remained quiescent. Toward the end of most recordings, after copulation, there were prolonged periods during which both sexes were immobile. In three cases we removed the male immediately after completion of copulation and again recorded female  $\dot{V}CO_2$  to check for unanticipated effects of copulation on female metabolic rate. In the other cases we allowed the pair to rest together in the flask after copulation in order to verify that their combined resting  $\dot{V}CO_2$  matched their resting rates as determined individually. We measured male resting  $\dot{V}CO_2$  with the male alone in a respirometry flask within 2 days of his mating. We determined female and male body mass to the nearest 0.1 mg 1–2 h before or after the recorded mating (body weights do not change during copulation; P. J. Watson, unpublished data). We quantified the body mass dependence of  $\dot{V}CO_2$  and standard metabolic rate data from males ( $N=9$ ) and

females ( $N=9$ ) by least-squares power regression using ANCOVA categorized by sex.

Prior to final analysis: (1) we baseline-corrected and converted the recordings to  $\dot{V}CO_2$  in ml/h, (2) we subtracted male and female resting  $\dot{V}CO_2$  from the recordings, (3) we converted the  $\dot{V}CO_2$  records to metabolic rate in  $\mu W$ ; this conversion was based on measures of the respiratory quotient of active and inactive males and females and use of the resulting Joule- $CO_2$  equivalence coefficients; males and females had respiratory quotients of 0.80 and 0.70, respectively. We converted the  $\dot{V}CO_2$  values used in statistical analyses to equivalents at a constant temperature of 30°C assuming a  $Q_{10}$  of 2.0. We removed the time-lag between behavioural coding and the respirometric data by correcting the data to reduce the effect of distortions caused by respirometer volume and flow rates (Lighton 1991).

### Measures of Metabolic Competence

Several complementary ways of assessing metabolic competence are possible when active individuals are subjected to continuous respirometric measurement. We calculated the energetic efficiency of courtship, the slope and linearity of metabolic increase upon commencement of courtship, the maximum metabolic rate and scope demonstrated by the male, and the consistency of metabolic rate during sustained performance of copulatory courtship (see Table I). Of the six measures we employed, only slope and linearity were significantly correlated ( $\rho_p=0.809$ ,  $P=0.0133 \pm 0.0038$ ), although maximum scope and maximum metabolic rate were marginally correlated ( $\rho_p=0.689$ ,  $P=0.0657 \pm 0.0084$ ). We assume that individuals scoring better across these measures possess greater metabolic competence.

### Male-Male Fights

To determine indirectly how male metabolic competence relates to fighting performance, we collected field data on associations between body mass, intromission rate and fighting ability. We performed experiments relating intromission rate and body mass to fighting ability in 1989 and 1991. We found males in the midst of pre-insemination phase copulation by scanning vegetation. We observed each of these males until it was clear that they had attained a stable

intromission rate. We then determined their intromission rate over a 3-min period, after which we captured each male. Males captured on a given day were weighed to the nearest 0.1 mg. Those closest in body mass were chosen to fight on the following day (mean difference in mass among all 59 pairs was 9.1%,  $SD=7.6$ , median=6.5%; there was a weight disparity of less than 20% in 90% of all pairs and the maximum disparity was 32.4%). To help separate the effects of body mass and copulatory performance I usually paired contestants so that the individual with the residual weight advantage had a lower intromission rate than his lighter adversary (mean difference in pre-insemination phase intromission rate among all pairs was 2.5%,  $SD=49.0$ , median=15.8%; the lighter male had the higher intromission rate in 73% of all fights). There was no systematic quantitative relationship between the degree of weight disadvantage and intromission rate advantage.

After spending the night housed individually, we marked each male for easy identification by applying a tiny dab of fast-drying enamel paint to the tibial segment of the left or right hindmost leg. We then introduced the males, one at a time and 15–30 min apart, onto a high-quality web harbouring a sexually receptive female. We determined their order of introduction by coin flip. We continuously observed their fighting behaviour until one male exited the web or was killed; we scored this male as the loser of the fight. We staged 59 fights, all involving different males, and calculated a non-subjective index of male aggressiveness for each fight as follows:  $\text{Aggressiveness} = (\% \text{ difference in mass} \times \text{fight duration} \times \text{level of escalation})$ , where level of escalation was 1, 2 or 3, denoting non-contact display, pedipalp wrestling, and biting/grappling, respectively. These levels of escalation represent highly discreet, easily distinguished stages of fighting (see Watson 1990 and Rovner 1968 for detailed descriptions of linyphiid fighting behaviour). We used the per cent difference in mass in the calculation of aggressiveness, because fighting ability is known for many spiders, including *L. litigiosa*, to be correlated with size or weight (Austad 1983). All else being equal, we rated individuals that fought opponents only slightly larger than themselves as less aggressive than those that fought opponents that were substantially larger. The observer of the fights was not blind to which contestant was lighter in body

mass or had the higher intromission rate, but because the aggressiveness measure is based on objective criteria, biased data are unlikely to be a problem in this study.

### Data Analyses

We summarized data relevant to the six measures of metabolic competence (Table 1) from the overall respirometric records using Sable Systems Datan V software. We performed statistical analyses using SYSTAT (Wilkinson 1990) and LOGIT (Steinberg 1985). We used weighted delete-one jackknife regression to compensate for non-normal or non-homogeneous residuals with Free-Stat (Mitchell-Olds 1989). We calculated 'exact' significance levels with 99% confidence intervals for small sample correlation tests using StatXact (Mehta & Patel 1992).

## RESULTS

### Standard and Resting Metabolic Rates

Standard metabolic rate was scaled to male and female body mass (at 30°C) according to the following equations

$$\text{male: } \mu W = 5.047 \times (\text{mass})^{0.842}$$

$$\text{female: } \mu W = 3.560 \times (\text{mass})^{0.842}$$

Resting metabolic rates ranged from 1.35 to 5.15  $\mu W/mg$  between individuals. Male resting metabolic rates averaged 1.6 times higher than those of females ( $\bar{X} \pm SD = 3.7 \pm 0.83 \mu W/mg$  and  $\bar{X} \pm SD = 2.3 \pm 0.57 \mu W/mg$ , respectively;  $P = 0.0008$ ). Female resting metabolic rate did not vary significantly before versus immediately after copulation (Jonckheere-Terpstra=1.091,  $N=3$  females,  $P=0.40 \pm 0.20$ ), supporting our assumption that the rise in a pair's combined metabolic rate during copulation was attributable to male activity.

Weight-adjusted measures of resting metabolic rate are sometimes used to measure physiological efficiency. Although male resting metabolic rates were not significantly associated with any of the six measures of male metabolic competence that we made during copulatory courtship, the two strongest relationships between resting metabolic rate and the respirometric measures taken in copula (see Table 1) did consist of a

positive association with efficiency ( $\rho_p=0.703$ ,  $P=0.0885 \pm 0.0095$ ) and a negative association with the consistency of energy output ( $\rho_p=-0.658$ ,  $P=0.1174 \pm 0.0110$ , respectively). Moreover, weight-adjusted male resting metabolic rate was strongly negatively associated with male body mass ( $\rho_p=-0.858$ ,  $P=0.0037 \pm 0.0052$ ), but not pre-insemination phase intromission rate ( $\rho_p=0.153$ ,  $P=0.83 \pm 0.06$ ).

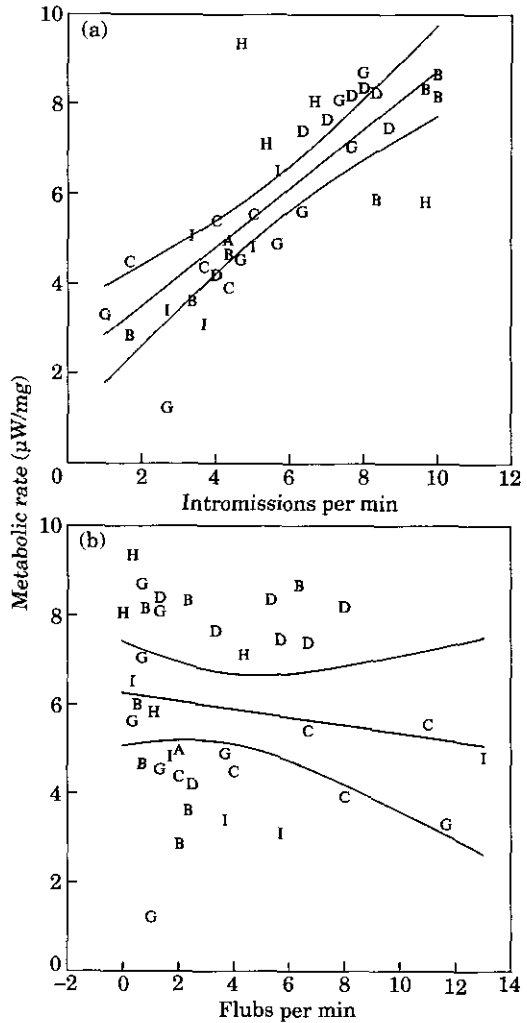
**Metabolic Performance during Copulation**

*Overall energetics*

Male energy output rose, on average, by  $75.4 \mu\text{W}$  ( $\text{SD}=25.5$ ,  $N=8$ ) above resting metabolic rate during pre-insemination phase copulation; this corresponds to an average metabolic scope of 2.68 ( $\text{SD}=0.70$ ; range=1.18–4.48 times resting metabolic rate). Average total male energy output during pre-insemination phase copulation was  $119.7 \mu\text{W}$  ( $\text{SD}=34.0$ ), significantly higher than that during resting metabolic rate (paired  $t=7.74$ ,  $df=7$ ,  $P=0.0001$ ).

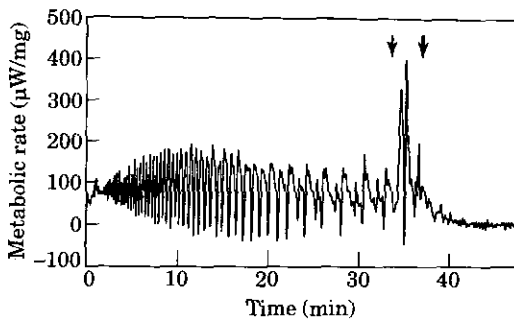
There was a positive relationship between male intromission rate and energy output during pre-insemination phase copulation (Fig. 1a;  $\rho_p=0.79$ ,  $N=37$ ,  $P=6 \times 10^{-9}$ ). In contrast, there was no relationship between flub rate and energy output (Fig. 1b;  $\rho_p=0.13$ ,  $N=37$ ,  $P=0.430$ ). Because counts of intromission and flub rates were made simultaneously, the data leave little doubt that the association between male intromission rate and energy output reflects the costs of successful intromission per se, that is, of coupling and locking the genitalia while fully inflating the haematodoca. Further support for this conclusion came from the temporal cross-correlation between single intromissions and metabolic rate peaks during insemination phase copulation ( $r=0.99$  at lag=0,  $\text{SE}=0.18$ ,  $N=31$  from three different matings,  $P<0.0001$ : detrended time series analysis).  $\text{CO}_2$  peaks associated with single intromissions are resolvable during the insemination phase, because each intromission lasts much longer than in the pre-insemination phase (Fig. 2).

The relationship between energy use during pre-insemination and insemination phase copulation was inconsistent: in two of the six matings where we recorded both phases, output during the pre-insemination phase averaged 22 and  $50 \mu\text{W}$  higher than in the insemination phase. In the remaining four matings we detected little



**Figure 1.** Energy output versus copulatory performance. Between one and seven records for each of seven males are plotted ( $N=37$ ). Individual males are denoted by letter. Linear regression with 95% confidence intervals is shown. (a) Metabolic rate versus the rate of intromissions. (b) Metabolic rate versus the rate of unsuccessful intromission attempts (i.e. flubs).

difference: pre-insemination phase metabolic rate ranged from  $4.8 \mu\text{W}$  above to  $5.5 \mu\text{W}$  below that during the insemination phase. Overall, pre-insemination phase metabolic rates averaged  $11.7 \mu\text{W}$  higher than during insemination phase ( $\text{SD}=21.1$ ,  $N=6$ ), but this difference was not significant (paired  $t=1.36$ ,  $P=0.233$ ). Comparing metabolic rates during all nine bouts of pre-insemination phase copulation recorded during



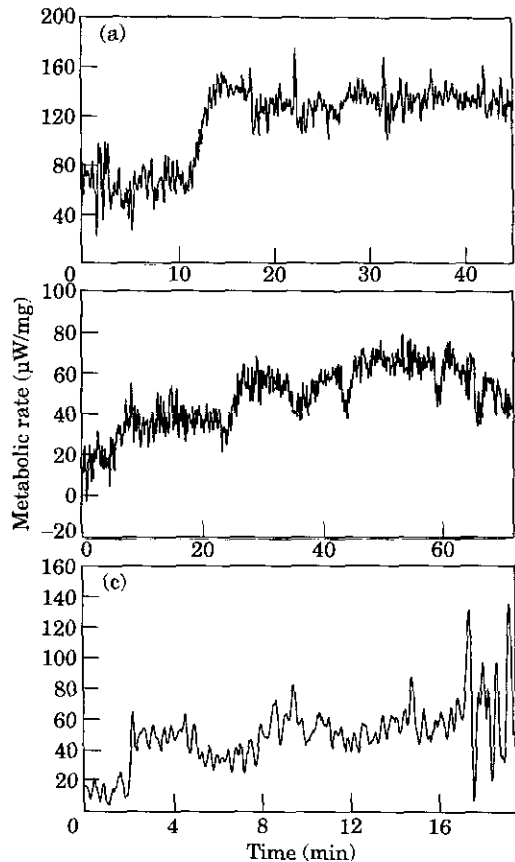
**Figure 2.** Net energy output during insemination phase copulation (male F). Insemination phase copulation commences at the beginning of the trace. Oscillations in metabolic rate correspond to single intromissions, each lasting about 40 s. Left arrow marks cessation of copulation, followed by a short period of male and female locomotion. Right arrow denotes cessation of activity followed by return to joint male-female resting metabolic rates. Rates shown are exclusive of resting metabolic rates. Readings of less than zero are artefacts due to an algorithm used to adjust for temporal lag in the respirometry system.

the study (involving eight males and nine females; median output =  $6.04 \mu\text{W}/\text{mg}$ ) and all six bouts of insemination phase copulation (five males and six females; median output =  $4.32 \mu\text{W}/\text{mg}$ ) also revealed no significant difference (Jonckheere-Terpstra =  $-1.65$ ,  $P=0.114 \pm 0.026$ ).

#### Individual variation

The respirometric records of the three males (out of the eight included in the study) that achieved the highest, middle, and lowest composite ranks for metabolic competence are shown in Fig. 3. There was a strong correlation between the composite ranks of male metabolic competence incorporating the six respirometric measures we made during copulatory courtship, and the composite ranks based on the two phenotypic traits known to be associated with male fertilization success: pre-insemination phase intromission rate and body mass ( $r_s=0.85$ ,  $N=8$ ,  $P=0.001 \pm 0.006$ ; Table I). Previous studies have shown that body mass and intromission rate themselves are uncorrelated ( $\rho_p=0.02$ ,  $N=112$ ,  $P=0.872$ ).

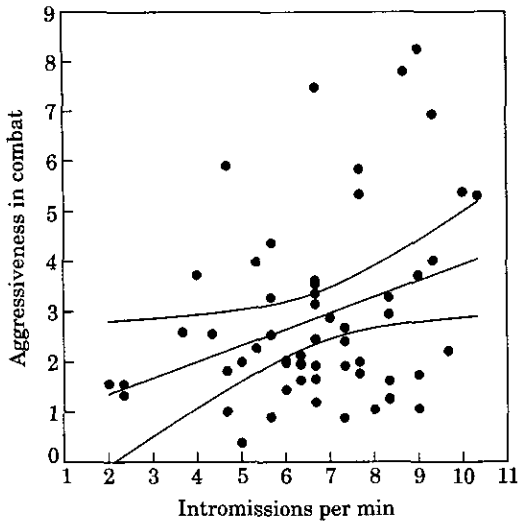
Five of the six respirometric measures were at least marginally correlated either with pre-insemination phase intromission rate (maximum



**Figure 3.** Energy output during pre-insemination phase copulation versus time for the three males that achieved the highest, middle and lowest composite metabolic ranks (see Table I). Male and female resting metabolic rates have been subtracted from the records. (a) Male B featuring steep, linear rise in metabolic rate after about 10 min of copulation, followed by a level plateau lasting ca 27 min before the pre-insemination phase ended. (b) Male I, showing more modest rise in metabolic rate and faltering energy output in the plateau region. (c) Male A, showing little rise in metabolic rate. Although the female remained receptive, male A ceased copulating relatively early and died 18 h thereafter.

metabolic rate:  $\rho_p=0.84$ ,  $P=0.014 \pm 0.004$ ; slope:  $\rho_p=0.81$ ,  $P=0.027 \pm 0.005$ ; linearity:  $\rho_p=0.77$ ,  $P=0.025 \pm 0.005$ ) or body mass (efficiency:  $\rho_p=0.70$ ,  $P=0.079 \pm 0.007$ ; consistency:  $\rho_p=0.75$ ,  $P=0.038 \pm 0.006$ ). Only maximum scope was not significantly correlated with either phenotypic trait (both  $P_s > 0.214$ ).





**Figure 4.** Male aggressiveness in combat versus maximum observed intromission rate during pre-insemination phase copulation. Data are for males that were at a modest weight disadvantage in male-male fights over sexually receptive females ( $N=59$  fights between different pairs of males). The staged fights and naturally occurring copulations all were observed in the field. Linear regression with 95% confidence intervals is shown.

#### Male Copulatory Performance and Aggressiveness

Of the 59 fights, 44% escalated to the wrestling phase and 18% to biting and grappling. The remaining 38% engaged in well-defined non-contact display for a minimum of 15 s (median = 106 s). The median duration of all fights was 116 s and the maximum duration 525 s (not including occasional breaks or temporary retreats by one male). The probability that the lighter weight contestant won the fight was not affected by his being introduced first ( $\chi^2=0.813$ ,  $df=1$ ,  $N=56$ ,  $P=0.367$ ), or by temperature ( $\chi^2=1.085$ ,  $df=1$ ,  $N=50$ ,  $P=0.298$ ). Aggressiveness scores also were not affected by order of introduction ( $F=2.307$ ,  $N=56$ ,  $P=0.135$ ) or temperature ( $\rho_p=0.131$ ,  $N=57$ ,  $P=0.331$ ).

Introumission rates were positively associated with male aggressiveness in male-male combat (Fig. 4;  $\rho_p=0.33$ ,  $N=59$ ,  $P=0.007$ ), a measure of how intensely and persistently a male is willing to fight when at a modest weight disadvantage (i.e. <15% difference in weight between the contestants). There was no such pattern among the heavier contestants of each fighting pair ( $\rho_p=0.05$ ,

$N=55$ ,  $P=0.830$ ), suggesting that fight intensity is usually limited by the aggressiveness of the lighter contestant.

Male body mass was not a predictor of aggressiveness for either the lighter or heavier contestant (all  $P_s>0.099$ ). However, mass was a predictor of the probability of winning a fight. The probability that the lighter contestant would win was negatively related to the weight difference between the contestants ( $\chi^2=7.75$ ,  $df=1$ ,  $P=0.005$ ). Introumission rates were negatively associated with the probability of winning a fight in lighter contestants ( $\chi^2=4.62$ ,  $df=1$ ,  $P=0.032$ ), but contestants with higher introumission rates were at a weight disadvantage in 73% of the fights (see Methods).

## DISCUSSION

The results of this study suggest a good-genes rationale for the sexual preference of female Sierra dome spiders for males that are vigorous copulators and high in body mass; expression of these preferences result in males of greater metabolic competence siring more of the female's offspring. Variation in metabolic competence may often be heritable, because so many elements of an individual's metabolic machinery would be capable of limiting overall metabolic capacity if maladapted and hence not quantitatively matched in capacity to related elements (Diamond & Hammond 1992). Thus, mutation bias is likely to reintroduce genotypes into the population each generation that yield males with relatively low metabolic capacities (see Iwasa et al. 1991; Pomiankowski et al. 1991). In the only study to demonstrate active female choice directly for a favourable genotype (Watt et al. 1986), the principal effect of the favoured alleles for phosphoglucose isomerase was to enhance metabolic competence as manifested in flight capacity. The *Colias* butterfly in that study has sustained, one-on-one in-flight courtship, a parallel to the sustained copulatory courtship of the Sierra dome spider. Furthermore, it is known that physiological efficiency often increases with protein heterozygosity (Mitton & Grant 1984; Mitton 1993) and quantitative modelling has demonstrated mechanisms that can yield correlations between individual heterozygosities of parents and their offspring (Mitton et al. 1993). Genetically based variation in physiological efficiency may affect key

components of viability besides the amount of energy available for growth and energetic behaviour (see Watt 1986). For example, Mitton (1993) shows that individual killifish, *Fundulus heteroclitus*, that are heterozygous at the lactate dehydrogenase locus have greater developmental homeostasis than homozygotes.

Intromission rates cannot reliably be used to predict fight outcome in this study. The residual weight advantage enjoyed by the male with the lower intromission rate in 73% of all fighting matches evidently was more important in determining fight outcome than the disadvantage represented by the lower intromission rate. However, based on the results of this study we anticipate that further research will show that the weight-adjusted measures of metabolic competence related to pre-insemination phase intromission rate (i.e. maximum metabolic rate, slope and linearity; see Table I) will be positively associated with both aggressiveness and fight outcome.

Our results hint that while body mass is associated with a male's endurance (i.e. efficiency and consistency; see Table I), intromission rate may reveal how quickly and decisively a male can mobilize energy. Thus male copulatory performance may offer females physiological information and a predictor of fighting ability complementary to that provided by body mass.

On average, body mass differences of as little as 5–10% apparently predict fight outcome better than differences in copulatory performance of 10–20%. However, males facing a modest weight disadvantage can produce upsets: 26 of 59 (44.6%) in this study did so. The ability to suddenly convert energy into arduous muscular activity, which may be revealed by the slope and linearity of metabolic increase upon commencement of pre-insemination phase copulation, should be very important in fights that escalate beyond the non-contact display phase and into the wrestling phase. In such fights the displaying males suddenly interlock pedipalps and immediately begin straining to push their opponent up and through the finely woven silk sheet that makes up the dome portion of the web (the males are hanging from the under surface of the dome while fighting). The male that is pushed through usually retreats. If male decision-making during fights is informed by self-assessment, the ability to rapidly mobilize energy may modulate a male's willingness to fight a slightly larger opponent, especially because the

probability that the fight will escalate to the wrestling phase is positively associated with the closeness of the match between the contestants by weight (P. J. Watson, unpublished observations). Males of high aggressiveness may fight more often against moderately heavier opponents and occasionally overwhelm them with sudden, highly energetic onslaughts. Such fights occur with substantial frequency (P. J. Watson, unpublished observations).

Three factors may determine the relationship between metabolic rate and performance during pre-insemination phase copulation in individual males: (1) perfection of the morphological development of the palpi, because the male and female genitalia appear to have a 'lock and key' fit, (2) functionality of the nervous system, because precise alignment of the genitalia is necessary before each intromission, and (3) metabolic competence, because the ability to maintain high intromission rates demands substantial, efficient and stable energy use. Maximum scopes measured in this study during copulatory courtship (Table I) corresponded closely to those attained in several spider species during forced locomotor activity. Studies involving forced movement have yielded metabolic rates ranging from 2.0 to 10.4 times that of resting metabolic rates in various spiders (Miyashita 1969; Seymour & Vinegar 1973; Humphries 1977; McQueen 1980; Prestwich 1983; Lighton & Gillespie 1989). But, unlike copulatory activity in *L. litigiosa* these rates usually are sustained only for several minutes at the most. Furthermore, the majority of the increased metabolic rates in our male spiders was caused by the musculature associated with operation of the palpi, whereas in locomotion a much larger absolute mass of musculature is presumably involved. This suggests that high intromission rates during the copulatory courtship of *L. litigiosa* makes severe metabolic demands on the musculature associated with palpus expansion.

The level of energy expenditure required of males to perform well in pre-insemination phase copulation is likely to reveal to females a basic aspect of male viability: metabolic competence. In addition to the role copulatory courtship plays in female choice, females often take advantage of the male's pre-occupation during pre-insemination phase copulation by capturing prey. Intensive

male kleptoparasitism usually prevents female foraging during non-copulatory phases of pairings (Watson 1993). Thus, pre-insemination phase copulation seems designed to provide an integrated solution to two different fitness-related problems, one nutritional and the other to do with choosing high-quality sires.

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### REFERENCES

- Austad, S. N. 1983. A game theoretical interpretation of male combat in the bowl and doily spider, *Frontinella pyramitela*. *Anim. Behav.*, **31**, 59–73.
- Balmford, A. & Read, A. F. 1991. Testing alternative models of sexual selection through female choice. *Trends Ecol. Evol.*, **6**, 274–276.
- Bennett, A. F. & Houck, L. D. 1983. The energetic cost of courtship and aggression in a plethodontid salamander. *Ecology*, **64**, 979–983.
- Blest, A. D. & Pomeroy, G. 1978. The sexual behaviour and genital mechanics of three species of *Mynoglenes* (Araneae: Linyphiidae). *J. Zool. Soc., Lond.*, **185**, 319–340.
- Carefoot, T. H. 1989. A comparison of time/energy budgeting in two species of tropical sea hares *Aplysia*. *J. exp. mar. Biol. Ecol.*, **131**, 267–282.
- Charlesworth, B. 1987. The heritability of fitness. In: *Sexual Selection: Testing the Alternatives* (Ed. by J. W. Bradbury & M. B. Andersson), pp. 21–40. New York: John Wiley.
- Dewsbury, D. A. 1988. Copulatory behavior as courtship communication. *Ethology*, **79**, 218–234.
- Diamond, J. & Hammond, K. 1992. The matches, achieved by natural selection, between biological capacities and their natural loads. *Experientia*, **48**, 551–557.
- Eberhard, W. G. 1991. Copulatory courtship and cryptic female choice in insects. *Biol. Rev.*, **66**, 1–31.
- Gerhardt, H. C. 1991. Female mate choice in treefrogs: static and dynamic acoustic criteria. *Anim. Behav.*, **42**, 615–635.
- Halliday, T. R. 1983. The study of mate choice. In: *Mate Choice* (Ed. by P. Bateson), pp. 3–32. Cambridge: Cambridge University Press.
- Halliday, T. R. 1987. Physiological constraints on sexual selection. In: *Sexual Selection: Testing the Alternatives* (Ed. by J. W. Bradbury & M. B. Andersson), pp. 265–277. New York: John Wiley.
- Harvey, P. H. & Bradbury, J. W. 1991. Sexual selection. In: *Behavioral Ecology*, 3rd edn (Ed. by J. R. Krebs & N. B. Davies), pp. 203–233. Oxford: Blackwell.
- Humphries, W. F. 1977. Respiration studies on *Geolycosa godeffrayi* (Araneae: Lycosidae) and their relationship to field estimates of metabolic heat loss. *Comp. Biochem. Physiol.*, **57A**, 255–263.
- Iwasa, Y., Pomiankowski, A. & Nee, S. 1991. The evolution of costly mate preferences. II. The 'handicap' principle. *Evolution*, **45**, 1431–1442.
- Kirkpatrick, M. & Ryan, M. J. 1991. The evolution of mating preferences and the paradox of the lek. *Nature, Lond.*, **350**, 33–38.
- Klump, G. M. & Gerhardt, H. C. 1987. Use of non-arbitrary acoustic criteria in mate choice by female gray treefrogs. *Nature, Lond.*, **326**, 286–288.
- Lande, R. 1987. Genetic correlations between the sexes in the evolution of sexual dimorphism and mating preferences. In: *Sexual Selection: Testing the Alternatives* (Ed. by J. W. Bradbury & M. B. Andersson), pp. 83–94. New York: John Wiley.
- Lighton, J. R. B. 1991. Insects: Measurements. In: *Concise Encyclopedia of Biological and Biomedical Measurement Systems*. (Ed. by P. A. Payne), pp. 201–208. New York: Pergamon Press.
- Lighton, J. R. B. & Feener, D. H., Jr. 1989. A comparison of energetics and ventilation of desert ants during voluntary and forced locomotion. *Nature, Lond.*, **342**, 174–175.
- Lighton, J. R. B. & Gillespie, R. G. 1989. The energetics of mimicry: the cost of pedestrian transport in a formicine ant and its mimic, a clubionid spider. *Physiol. Entomol.*, **14**, 173–177.
- McQueen, D. J. 1980. Active respiration rates for the burrowing wolf spider *Geolycosa domifex*. *Can. J. Zool.*, **58**, 1066–1074.
- Maynard-Smith, J. 1987. Sexual selection: a classification of models. In: *Sexual Selection: Testing the Alternatives* (Ed. by J. W. Bradbury & M. B. Andersson), pp. 9–20. New York: John Wiley.
- Mehta, C. & Patel, N. 1992. *StatXact for SYSTAT*. Version 1.0. Cambridge, Massachusetts: CYTEL Software Corporation.
- Mitchell-Olds, T. 1989. *Free-Stat*. Version 1.1. Missoula, Montana: University of Montana.
- Mitton, J. B. 1993. Theory and data pertinent to the relationship between heterozygosity and fitness. In: *The Natural History of Inbreeding and Outbreeding* (Ed. by N. Thornhill), pp. 17–41. Chicago: University of Chicago Press.
- Mitton, J. B. 1993. Enzyme heterozygosity, metabolism, and developmental stability. *Genetica*, **89**, 47–65.
- Mitton, J. B. & Grant, M. C. 1984. Associations among protein heterozygosity, growth rate, and developmental homeostasis. *A. Rev. Ecol. Syst.*, **15**, 479–499.
- Mitton, J. B., Schuster, W. S. F., Cothran, E. G. & De Fries, J. C. 1993. The correlation between individual heterozygosity of parents and their offspring. *Heredity*, **71**, 59–63.

- Miyashita, K. 1969. Effects of locomotory activity, temperature, and hunger on the respiration rate of *Lycosa t-insignita* (Boes. et Str.) (Araneae: Lycosidae). *Appl. Entomol. Zool.*, **4**, 105–113.
- Nicoletto, P. F. 1993. Female response to condition-dependent ornaments in the guppy, *Poecilia reticulata*. *Anim. Behav.*, **46**, 441–450.
- Norris, K. 1993. Heritable variation in a plumage indicator of viability in male great tits *Parus major*. *Nature, Lond.*, **362**, 537–539.
- Parker, G. 1983. Mate quality and mating decisions. In: *Mate Choice* (Ed. by P. Bateson), pp. 141–166. New York: Cambridge University Press.
- Partridge, L. 1980. Mate choice increases a component of offspring fitness in fruit flies. *Nature, Lond.*, **283**, 290–291.
- Pomiankowski, A., Iwasa, Y. & Nee, S. 1991. The evolution of costly mate preferences. I. Fisher and biased mutation. *Evolution*, **45**, 1422–1430.
- Prestwich, K. N. 1983. The roles of aerobic and anaerobic metabolism in active spiders. *Physiol. Zool.*, **56**, 122–132.
- Reeve, H. K. & Sherman, P. W. 1993. Adaptation and the goals of evolutionary research. *Q. Rev. Biol.*, **68**, 1–32.
- Rovner, J. S. 1968. Territoriality in the sheet-web spider *Linyphia triangularis* (Clerck) (Araneae, Linyphiidae). *Z. Tierpsychol.*, **25**, 232–242.
- Ryan, M. J. 1985. *The Tungara Frog*. Chicago: University of Chicago Press.
- Schantz, T. V., Göransson, G., Andersson, G., Fröberg, I., Grahn, M., Helgée, A. & Wittzell, H. 1989. Female choice selects for a viability-based male trait in pheasants. *Nature, Lond.*, **337**, 166–169.
- Seymour, R. S. & Vinegar, A. 1973. Thermal relation, water loss, and oxygen consumption of a North American tarantula. *Comp. Biochem. Physiol.*, **44A**, 83–96.
- Simmons, L. W. 1987. Female choice contributes to offspring fitness in the field cricket, *Gryllus bimaculatus* (De Geer). *Behav. Ecol. Sociobiol.*, **21**, 313–321.
- Steinberg, D. 1985. *LOGIT: A Supplementary Module for SYSTAT*. Version 1.12. San Diego, California: Salford Systems.
- Symons, D. 1992. On the use and misuse of Darwinism in the study of human behavior. In: *The Adapted Mind* (Ed. by J. H. Barkow, L. Cosmides & J. Tooby), pp. 137–162. New York: Oxford University Press.
- Thornhill, R. 1983. Cryptic female choice and its implications in the scorpionfly *Harpobittacus nigriceps*. *Am. Nat.*, **122**, 765–788.
- Thornhill, R. 1990. The study of adaptation. In: *Interpretation and Explanation in the Study of Behavior, Vol. II* (Ed. by M. Bekoff & D. Jamison), pp. 31–62. Boulder, Colorado: Westview Press.
- Vehrencamp, S. L., Bradbury, J. W. & Gibson, R. M. 1989. The energetic cost of display in male sage grouse. *Anim. Behav.*, **38**, 885–896.
- Verrell, P. A. 1985. Is there an energetic cost to sex? Activity, courtship mode and breathing in the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). *Monit. zool. ital. (N.S.)*, **19**, 121–127.
- Watson, P. J. 1990. Female-enhanced male competition determines the first mate and principal sire in the spider *Linyphia litigiosa* (Linyphiidae). *Behav. Ecol. Sociobiol.*, **26**, 77–90.
- Watson, P. J. 1991a. Multiple paternity and first mate sperm precedence in the sierra dome spider, *Linyphia litigiosa*. *Anim. Behav.*, **41**, 135–148.
- Watson, P. J. 1991b. Multiple paternity as genetic bet-hedging in female sierra dome spiders (*Linyphia litigiosa*: Linyphiidae). *Anim. Behav.*, **41**, 343–360.
- Watson, P. J. 1993. Forging advantage of polyandry for female sierra dome spiders (*Linyphia litigiosa*: Linyphiidae) and assessment of alternative direct benefit hypotheses. *Am. Nat.*, **141**, 440–465.
- Watt, W. B. 1986. Power and efficiency as indexes of fitness in metabolic organization. *Am. Nat.*, **127**, 629–653.
- Watt, W. B., Carter, P. A. & Donohue, K. 1986. Females' choice of 'good genotypes' as mates is promoted by an insect mating system. *Science*, **233**, 1187–1190.
- Wilkinson, L. 1990. *SYSTAT: The System for Statistics*. Version 5.0. Evanston, Illinois: SYSTAT Inc.
- Williams, G. C. 1992. *Natural Selection: Domains, Levels and Challenges*. Oxford: Oxford University Press.