Energetic costs of size and sexual signalling in a wolf spider

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A prerequisite for honest handicaps is that there are significant condition-dependent costs in the expression of sexual traits. In the wolf spider *Hygrolycosa rubrofasciata* (Ohlert), sexual signalling (drumming) is costly in terms of increased mortality. Here we investigated whether this mortality may be caused by increased energy expenditure. During sexual signalling, metabolic rate was 22 times higher than at rest and four times higher than when males were actively moving. Metabolic rate per unit mass was positively related to absolute body mass during sexual signalling but not during other activities. This positive relationship is novel to any studies of metabolic rates. Indeed, it seems that the largest males can drum only 12 times per minute before reaching the maximum sustainable metabolic rate, whereas the smallest males may drum up to 39 times per minute. However, there is no relationship between body mass and drumming rate, indicating that larger males are able to compensate for the higher cost of drumming. There was a quadratic relationship between relative abdomen mass and overall body mass, which may provide a partial explanation for the increased energy expenditure of largest males while drumming. Altogether, our results indicate that sexual signalling is highly energetically demanding, which may be the main reason for the honesty of signalling in this species. In addition, the energetic costs are surprisingly strongly size dependent, which may compensate any disadvantage of small male size.

Keywords: costs of sexual traits; CO_2 production; *Hygrolycosa rubrofasciata*; indicator mechanism; sexual selection

1. INTRODUCTION

The two currently favoured theories of sexual selection—the Fisherian self-reinforcing theory (Fisher 1958; Lande 1981; Pomiankowski *et al.* 1991) and the indicator mechanisms theory (Zahavi 1975, 1977; Grafen 1990*a*,*b*; Iwasa *et al.* 1991)—both assume costs of male secondary sexual traits. However, these two theories differ in respect to how they consider the male ability to bear the costs. In Fisherian self-reinforcing theory, males are not expected to vary in their ability to bear costs and thus male condition is not considered to influence the expression of the sexual trait. Instead, the ability to bear costs differentially depending on male condition is the crux of the indicator mechanism models, and male condition is assumed to be positively related to the expression of the sexual trait.

Costs associated with the expression of male sexual traits may take many forms, even if ultimately such costs lead to increased risk of mortality. In general, costs can be divided into direct costs (e.g. predation and parasitism) and physiological costs (e.g. energetic costs).

Direct costs increase the risk of mortality directly in proportion to the expression of the trait. Increased risk of predation or parasitism resulting from a conspicuous sexual trait has been demonstrated to exist with a variety of sexually signalling organisms (see Burk 1982; Thornhill & Alcock 1983; Sakaluk 1990; Kotiaho *et al.* 1998*a*). For example, in the neotropical frog *Physalemus pustulosus*, calling males suffer heavy predation by bats, which home in on the male calls (Ryan *et al.* 1981, 1982). The field cricket *Gryllus integer* is parasitized by tachinid flies, and calling males of the species are subject to much higher risk of parasitism than non-calling males or females (Cade 1975, 1979).

Physiological costs are often difficult to demonstrate, as males are expected to optimize their level of signalling in each situation. This is the general problem of studying trade-offs in any life-history trait that has so frequently been addressed when studying female reproductive effort (see Roff 1992; Stearns 1992). It is well established that sexual displays are highly energetically demanding (see Halliday 1987; Ryan 1988; Andersson 1994). For example, in the grey tree frog *Hyla versicolor*, estimated energy consumption during calling is about 21 times the basal metabolic rate (Taigen & Wells 1985), and in several stridulating tree-cricket species, song raises their metabolic rate 6–16 times above the resting metabolic rate (Prestwich & Walker 1981). Despite the evidence that

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sexual displays are energetically demanding, there are only very few studies that have verified costs to have detrimental fitness consequences (Møller 1989; Møller & deLope 1994; Mappes *et al*. 1996).

Large body size has often been found to be advantageous in sexual selection (for review, see Andersson (1994)). Larger males are either directly selected by females or have an advantage in male–male competition. However, a large body size may also incur additional costs. For example, in the red-winged blackbird *Agelaius phoeniceus*, large body size is advantageous in male–male competition, but larger males spend more time foraging and have less time for displaying and defending their territory (Searcy 1979; Eckert & Weatherhead 1987). As in most other animals, spiders demonstrate an increase in energy consumption with increasing body mass (e.g. Kleiber 1932; Hemmingsen 1960; Andersson 1970; Greenstone & Bennett 1980; Nielsen & Baroni-Urbani 1990; Lighton & Fielden 1995). However, it is essential to examine in detail how the energy demand for sexual signalling is related to body mass; the question is whether males of different body mass need to pay different energetic costs per unit mass.

In the wolf spider *Hygrolycosa rubrofasciata* (Ohlert) (Lycosidae), males court females by drumming dry leaves with their abdomen. One drumming consists of *ca*. 30–40 separate pulses and lasts *ca*. 1 s (Kronestedt 1984, 1996). The drumming is clearly audible from several metres and it has been demonstrated to be a target of female choice (Kotiaho *et al*. 1996, 1998*a*; Parri *et al*. 1997). However, presence of a female or female silk is not necessary to induce the drumming. Body mass of the males varies greatly from *ca*. 13–30 mg (body length of males is *ca*. 5–6 mm. (Kronestedt 1984, 1996)). Even though larger males are able to repel smaller males in fights (Kotiaho *et al*. 1997), there is no mating advantage for larger males (Kotiaho *et al*. 1996). However, larger males benefit from their size by being able to search for females more actively than smaller males (Kotiaho *et al*. 1998*b*). Under physical stress, larger males also have a slight survival advantage compared with smaller males (Mappes *et al*. 1996), and there is a positive correlation between male drumming activity and male survival (Kotiaho *et al*. 1996, 1998*b*; Kotiaho 1998). However, males that were experimentally induced to increase their drumming rate suffered increased mortality (Mappes *et al*. 1996), indicating that drumming incurs significant costs for males.

In this paper we report the results of a series of metabolic rate and morphological measurements on the wolf spider *H. rubrofasciata*. Our first objective was to determine the mechanisms by which increased sexual signalling may cause increased mortality. The second objective was to determine the effect of body mass on metabolic rate and to compare the energetic expenditure of sexual signalling to the energetic expenditure of other activities. We explored these issues by measuring the CO_2 production during resting, moving, sexual signalling and during maximal exertion. Results from these measurements innovated our third objective: to determine the mechanisms by which larger males had higher energy expenditure during drumming. This was examined through measurements on male morphology.

2. MATERIALS AND METHODS

(a) *Metabolic rate measurements*

We collected individuals for this study before the mating season in May 1996 from a bog at Sattanen, Northern Finland (67°30′ N, 26°40′ E). All spiders were collected within 48 h just after the snow had melted. We housed spiders individually in small plastic jars filled with soft cellulose paper. Jars were moistened regularly and food (*D. melanogaster* fruit flies) was available continuously. Spiders were maintained for six weeks at 4 °C, after which they were transported to Denmark for measurements of metabolic rate.

Before measuring metabolic rates, we measured the drumming rate and the body mass of males. To measure drumming rate, we placed each male in a small plastic arena (10 cm × 15 cm) with some dry birch leaves. The number of drums was counted three times for 2 min and the procedure was repeated on three consecutive days. Body mass was measured to the nearest 0.1 mg. Body mass was measured only once, because earlier we found (Kotiaho *et al*. 1996; Kotiaho 1998) that male body mass is highly repeatable (0.82–0.99%). No significant relationship was found between male drumming rate and body mass (Spearman's $r = 0.17$, $n = 30$, $p > 0.3$). This result is consistent with our earlier results from field and laboratory, that there is no correlation between these two traits (Spearman's $r = 0.08$–0.31, $p > 0.1$ for all; Kotiaho *et al*. 1996, 1998*b*).

We used the CO_2 production (ml CO_2 h^{-1}) as a measure of the metabolic rate. CO_2 production was measured with a CO_2 analyser model LI-6251, which used flow-through CO_2 respirometry, connected to Sable Systems data acquisition and analysis software Datacan V (Sable Systems, Salt Lake City, UT). Males were inserted into a cylinder-shaped test chamber (length 50 mm, diameter 13 mm) that was plugged from both ends with a rubber plug. CO_2 and moisture were removed from the incoming air by filtering the air through soda lime and silica gel before it passed into the test chamber. From the test chamber the air with CO_2 produced by the spider was led through another moisture-absorbing silica gel filter to the CO_2 analyser. The air flow was 150 ml min^{-1} and all measurements were made at 25 °C. Before starting each measurement session, males were allowed an acclimation period of 5 min. Between the measurements the test chamber was washed with water and dried with soft cellulose paper.

Spiders used in the measurements were not in postabsorptive state, instead food was made unavailable only 1 h before the measurements. This method was used because lack of food significantly reduces male drumming rate (Mappes *et al*. 1996). In fact, the postabsorptive state is not likely to be a natural state for animals in the wild. Therefore, when measuring energetic costs of behaviour, the natural state of the individuals should be preferred over the postabsorptive state. Furthermore, the absorptive state of individuals may not affect the relative magnitude of the results because all spiders were kept and measured in similar conditions.

The CO_2 production of resting males was measured several times during different days. We included in our analyses only those measurements that were taken after the male had been motionless for at least 5 min. Each measure was a mean CO_2 production over a period of 2–5 min. For the 30 males measured, the number of measurements per male ranged from 1–9 and the total time that measurements lasted for ranged from 2–44 min. In the analysis we used a mean value from all of the measurements.
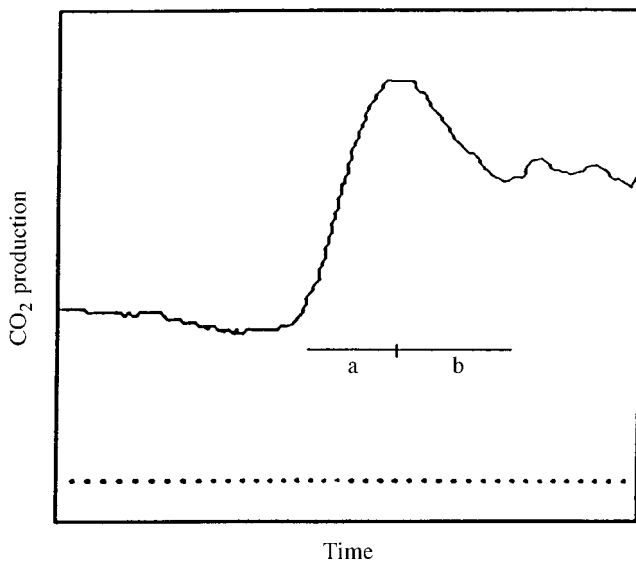
Figure 1. Slope of CO_2 production during male drumming. The slope is a real example of one single drumming followed by moving. The graph is an output produced by Sable Systems DATACAN V software. The estimate of the area under the decreasing phase of the slope (b) is 1.4 times larger than the area of increasing part (a). Thus the whole area under the curve is 2.4a.

Measuring the CO_2 production of moving males was more difficult because males tend not to move continuously but stop for short periods of time. To qualify as a reliable measurement, however, males were required to move continuously and therefore, the number of measurements per male is smaller (between one and six) and the total number of individuals with reliable measurements was 19. Each measure was a mean CO_2 production over a period of 1–5 min and the total time that measurements lasted for ranged from 1–32 min.

To measure metabolic rate during drumming, males were not allowed to move before measurement. If the male was moving the measurement had to be discarded as we could not tell apart the source of CO_2. One drumming bout lasts *ca.* 1 s and often males start moving soon after the drumming. For this reason we could not calculate directly the whole area under the CO_2 production curve (figure 1). Thus, we calculated the area under the increasing phase of the curve and summed this with an estimate of the decreasing phase of the curve. We calculated the difference between the increasing and the decreasing phase of the curve by letting a small amount of CO_2 into the empty measurement chamber and calculating the area under the increasing phase and the area under the decreasing phase separately. The shape of the curve was not symmetrical and the area of decreasing phase was 1.4 times larger than the area of increasing phase. Thus, by calculating the CO_2 production under the increasing phase of the curve and multiplying this by 2.4, we get the CO_2 production during a single drumming bout (figure 1). Because a single male drumming lasts *ca.* 1 s, this corresponds to the male energy consumption during 1 s. Thus, the measure of the drumming CO_2 production is different from all other measurements in that absolute CO_2 production is measured during 1 s, whereas all other measures of CO_2 production are averages over a longer time interval. This difference results from the different nature of the activities; males pursue all of the other activities more-or-less continuously, whereas they have been observed to drum at most nine times per min.

Table 1. *Mean, s.e.m., minimum and maximum of CO_2 production* $(\mathrm{ml\,CO_2\,g^{-1}\,h^{-1}})$ *during resting, moving, maximal exertion and drumming*

	n	mean	s.e.m.	min–max
resting	30	0.22	0.007	0.17–0.33
moving	19	1.02	0.048	0.77–1.40
maximal	28	2.21	0.086	1.33–2.86
drumming	22	4.80	0.493	1.32–8.78

The value of CO_2 production during drumming used in the analysis was a mean value from between one and six measures, and we obtained measures from 22 males.

Spiders, like many other animals, do not in any circumstances voluntarily lie on their back. If they are forced into that position they immediately try to turn back on their feet. We exploited this behaviour to measure the maximal sustainable metabolic rate of the males. We repeatedly turned males on their back by rapidly turning the test chamber and continued to do so until the male was unable to correct its position. We calculated the maximal sustainable metabolic rate as the mean CO_2 production per second during 30 s; 15 s in each direction from the maximum peak of the CO_2 production curve. We also measured the time males were able to sustain this maximal exertion.

(b) *Morphological measurements*

The hypothesis we wanted to test with morphological measurements was whether differences in male morphology could explain the observed size-dependent CO_2 production during drumming. The spider body is composed of the cephalothorax (prosoma), to which the legs are attached, and the abdomen (opisthosoma), which is attached to the cephalothorax with a very narrow pedicel (waist). Because *H. rubrofasciata* males drum by hitting their abdomen against dry leaves, the relative mass of the male abdomen may be of some importance; if masses of cephalothorax and abdomen are not isometrically related this might explain the positively size-dependent energy expenditure during drumming.

Males ($n=93$) were collected during the spring of 1997 from the same population in northern Finland as males for the metabolic rate measurements. Spiders were housed as described earlier at $4\,°C$ until they were measured.

Drumming rate and mobility of the males was measured before the morphological measurements. Each male was placed in a small plastic arena ($10\,\mathrm{cm} \times 15\,\mathrm{cm}$) with some dry birch leaves. The arena was divided into four equal parts and the mobility was measured as the number of times the male crossed a line between the parts. Drumming rate and mobility were measured five times for $2\,\mathrm{min\,d^{-1}}$ and the procedure was repeated three times.

For morphological measurements, males were killed by placing them individually in a jar containing chloroform gas. Each male was kept in the jar for a few minutes before being measured. Males were weighed to the nearest 0.1 mg and subsequently placed under a binocular microscope where their abdomens were separated from the cephalothorax by cutting the pedicel from the joint between cephalothorax and the pedicel with a scalpel. There was no detectable loss of haemolymph due to cutting the pedicel. Cephalothorax and abdomen were then weighed separately to the nearest 0.1 mg.
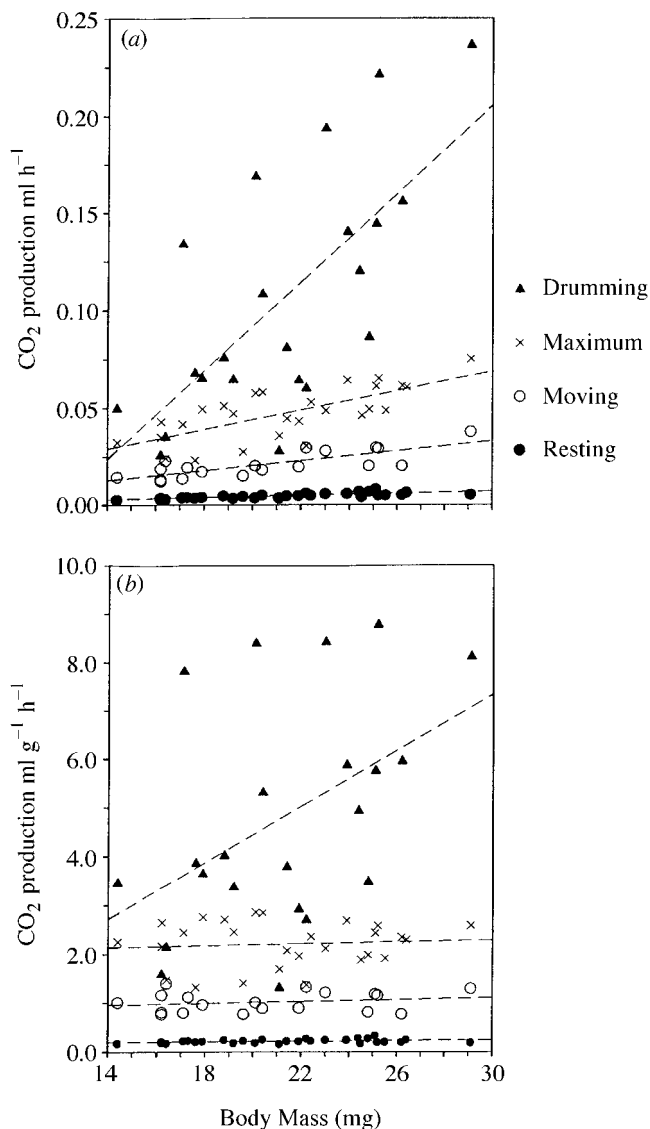
Figure 3. Empirical model of the increasing costs of drumming for larger males. Male CO_2 production per unit mass per hour is plotted on the y axis, absolute body mass is on the x axis. Thick lines represent the CO_2 production during resting, moving and during maximal exertion. Thin lines represent the CO_2 production of a moving male that is drumming 2, 4, 6, ..., 12 times per minute. For example, a 30-mg male that is moving may drum only up to 12 times before reaching the maximum sustainable level. For a 14-mg male the same number would be 39 times. Calculations are based on data presented in figure 2.

Figure 2. (*a*) Linear regression between male body mass and CO_2 production (ml CO_2 h^{-1}) during resting ($y = -0.01 \times 10^{-3} + 2.76 \times 10^{-3}x$; $r^2 = 0.61$, $F_{1,28} = 43.20$, $p \ll 0.001$); during moving ($y = -4.81 \times 10^{-3} + 1.27 \times 10^{-3}x$; $r^2 = 0.60$, $F_{1,17} = 25.85$, $p \ll 0.001$); during maximal exertion ($y = -5.59 \times 10^{-3} + 2.48 \times 10^{-3}x$; $r^2 = 0.52$, $F_{1,26} = 28.29$, $p \ll 0.001$); and during drumming ($y = -134.82 \times 10^{-3} + 11.34 \times 10^{-3}x$; $r^2 = 0.49$, $F_{1,20} = 18.98$, $p \ll 0.001$). (*b*) Linear regression between male body mass and CO_2 production per unit mass (ml CO_2 g^{-1} h^{-1}) during resting ($y = 0.15 + 0.003x$; $r^2 = 0.10$, $F_{1,28} = 2.99$, $p = 0.095$); during moving ($y = 0.83 + 0.010x$; $r^2 = 0.04$, $F_{1,17} = 0.65$, $p = 0.430$); during maximal exertion ($y = 2.00 + 0.010x$; $r^2 = 0.01$, $F_{1,26} = 0.18$, $p = 0.673$); and during drumming ($y = -1.31 + 0.288x$; $r^2 = 0.22$, $F_{1,20} = 5.69$, $p = 0.027$).

3. RESULTS

(a) *Metabolic rate measurements*

Male CO_2 production per unit mass was significantly different between each of the activities (Friedman ANOVA, $\chi^2 = 43.88$, d.f. $= 3$, $p \ll 0.001$; Wilcoxon signed-rank test between each of the activities, for all $T \leqslant 1$, $n = 15$, $p \ll 0.001$). Male CO_2 production during drumming was 22 times higher than during resting and more than twice as high as during maximal exertion (table 1).
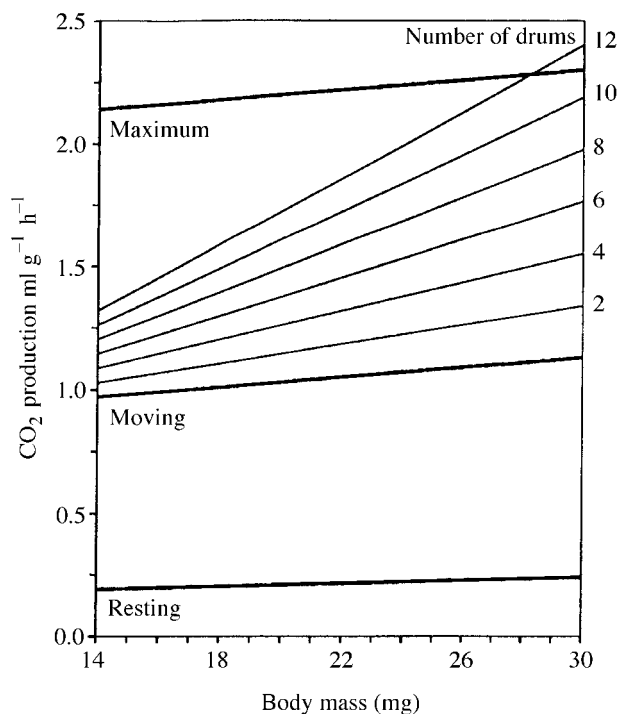
CO_2 production during all of the activities was positively dependent on body mass (figure 2a). However, when CO_2 production was calculated per unit mass, resting, moving and maximal exertion were independent of absolute body mass (figure 2b). The drumming CO_2 production was still dependent on male body mass (figure 2b). The slope of drumming CO_2 production per unit mass was also significantly different from the slopes of other activities (resting, $t = 2.36$, d.f. $= 48$, $p = 0.022$; moving, $t = 2.30$, d.f. $= 37$, $p = 0.027$; maximal exertion, $t = 2.27$, d.f. $= 46$, $p = 0.028$). Slopes between resting, moving and maximal exertion did not differ (for all, $t < 0.6$, d.f. $= 42$–54, $p > 0.5$).

The time for which males were able to sustain the maximal exertion (mean 225 s, range 124–396 s) was positively correlated with drumming rate (Spearman's $r = 0.41$, $n = 28$, $p = 0.030$). The time was also positively correlated with the CO_2 production during maximal exertion (Spearman's $r = 0.49$, $n = 28$, $p = 0.008$), but not with CO_2 production during other activities (for all, Spearman's $r < 0.22$, $n = 18$–28, $p > 0.3$). Body mass of the males did not seem to have any influence on the time for which males were able to sustain the maximal exertion (Spearman's $r = 0.05$, $n = 28$, $p > 0.6$). There was no relationship between male drumming rate and CO_2 production during maximal exertion (Spearman's $r = 0.22$, $n = 28$, $p = 0.267$), or between drumming rate and CO_2
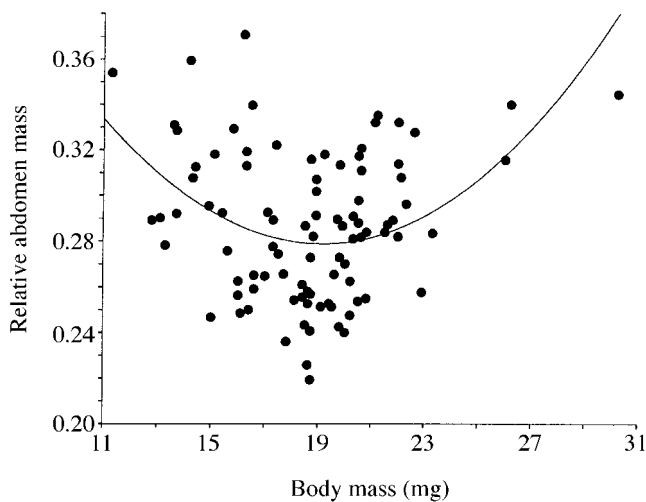
Figure 4. Quadratic relationship between relative abdomen mass and absolute body mass of the males.

production during the other activities (for all, Spearman's $r < 0.05$, $n = 19–30$, $p > 0.7$).

If we consider our measure of the maximum metabolic rate as an upper limit the male is able to perform, it seems that larger males are not able to drum as much as smaller males before reaching this limit (figure 3). If we assume that a male is moving all the time during one minute and stopping only for drumming, which is supported by observations in nature, then a male with a body mass of 30 mg would be able to drum only 12 times per minute before reaching the upper sustainable metabolic rate, whereas a male of 14 mg may drum up to 39 times per minute (figure 3). This empirical model clearly demonstrates the differential costs of body mass for males during sexual signalling.

(b) *Morphology measurements*

Male body mass averaged 18.59 mg and 28.7% of this was attributable to the abdomen. There was a quadratic relationship between the relative abdomen mass and overall body mass of males ($r^2 = 0.19$, $F_{2,90} = 10.45$, $p \ll 0.001$; $b_1 = -0.032 \pm 0.007$, $t = -4.49$, $p \ll 0.001$; $b_2 = 8.26 \times 10^{-4} \pm 1.81 \times 10^{-4}$, $t = 4.57$, $p \ll 0.001$) (figure 4). The positive b_2 slope indicates that the relative abdomen mass was higher for heavier males. If males are divided to five equal categories according to their overall body mass (< 15 mg, $15–17$ mg, $17–19$ mg, $19–21$ mg, and > 21 mg), the relative proportion of abdomen mass for these categories was 31.2%, 29.0%, 27.0%, 27.8% and 30.8%, respectively. This indicates that relative abdomen mass is larger for largest males but also for the smallest males.

There was no relationship between body mass and drumming rate (Spearman's $r = 0.128$, $n = 93$, $p = 0.218$), or body mass and mobility (Spearman's $r = 0.187$, $n = 93$, $p = 0.072$). However, when we compared drumming rate and mobility to the residuals from the quadratic regression between relative abdomen mass and body mass, there were negative relationships: both drumming rate and mobility were negatively related to the residuals (Spearman's $r = -0.215$, $n = 93$, $p = 0.039$ and $r = -0.271$, $n = 93$, $p = 0.009$, respectively). These negative relationships indicate that males with relatively smaller abdomens

are drumming and moving more than males with relatively larger abdomens.

4. DISCUSSION

There is evidence from a variety of species that sexual displays are energetically demanding (e.g. MacNally & Young 1981; Prestwich & Walker 1981; Taigen & Wells 1985; Ryan 1988; Vehrencamp *et al.* 1989; see also Andersson 1994). However, to demonstrate that increased energy consumption has fitness costs, one has to show a negative relationship between energy consumption and survival or some other viability measure. This is not a simple task for empirical research as animals generally signal at an optimal level in relation to their phenotypic condition, so that any possible costs may be hidden under the positive correlation between the expression of the sexual trait and viability.

In this study, we discovered that drumming of *H. rubrofasciata* males is energetically 22 times more demanding than resting. Drumming was also 4.5 times more demanding than moving, and in most cases the metabolic rate during drumming seemed to be even higher than the maximal sustainable metabolic rate. However, males do not drum continuously, which may allow them to achieve bursts of high metabolic activity exceeding the maximum sustainable level (see figure 3).

Male drumming rate was positively correlated with the direct measure of male physical condition, namely the time the male was able to sustain the maximal exertion. Therefore, it seems that males that drum more are in better condition and thus also better able to bear the possible costs of increased energy expenditure. In a previous experiment on *H. rubrofasciata*, it was apparent that despite the existing positive correlation between male drumming rate and viability (Kotiaho *et al.* 1996, 1998b), the males' capability to sustain experimentally increased drumming rate was reduced (Mappes *et al.* 1996). Recalling that drumming increased the energy expenditure 22-fold compared with resting, and that males induced to drum more suffered higher mortality, it seems that increased mortality of actively signalling males is due to high energetic costs of drumming.

Body mass had a major impact on the energy expenditure of the males. Larger males suffered increased energy expenditure during any activity and particularly so during sexual signalling. Interestingly, CO_2 production per unit mass during drumming was positively dependent on absolute body mass, which indicates that larger males paid over twice the energy costs per unit mass as smaller males. This result is somewhat counterintuitive, however, as normally the relative metabolic rate is expected to decrease with body size (e.g. Hemmingsen 1960; Kleiber 1965; Reiss 1989). In figure 3 we show that larger males are capable of drumming only up to 12 times per minute before they reach the maximal sustainable level. For smaller males the corresponding number is more than three times higher; they may drum up to 39 times before reaching the maximal level. These aspects provide strong evidence that larger males suffer increased energy expenditure, and consequently costs, because of their size.

To explore the mechanism underlying the higher energy need of larger males during drumming, we examined the morphology of differently sized males. These measurements revealed a quadratic relationship between the relative mass of the abdomen and the overall body mass. This relationship indicates that larger males have relatively higher abdomen mass. This could partly explain the increased energy requirement of larger males during drumming: drumming with a relatively larger abdomen requires larger amounts of energy relative to drumming with relatively smaller abdomen. The probable effect of the relative abdomen size is supported by the fact that males with relatively heavy abdomen were less mobile and less active in drumming. However, also some other factors needs to be to incorporated, as the smallest males also had relatively heavy abdomens.

In spite of the increased cost of drumming in the largest males, the relationship between drumming rate and body mass is flat (Kotiaho *et al.* 1996, 1998*b*; Mappes *et al.* 1996). Thus, it seems that larger males are able to compensate for the increased energy expenditure of drumming. This compensation could be accomplished through increased food consumption. Although this has not been investigated specifically, Kotiaho (1998) conducted an experiment where males were kept on different food regimes. He found that at the beginning of the experiment the correlation between body mass and drumming activity was flat as expected, but after 20 days on food regimes there was a significant negative correlation in males that were kept on a low food regime. The correlation was still flat on a high food regime, supporting the idea that larger males need more energy than smaller males to maintain similar drumming activity. However, from the current results it seems possible that the absolute body mass may generally be irrelevant for the male drumming activity and the important determinant is the relative size of male abdomen.

In conclusion, it seems that the evolution of honest, condition-dependent sexual signalling in *H. rubrofasciata* wolf spiders may be attributable partly to the general morphology of spider males. Drumming by moving the whole abdomen is highly costly in its energy demand and consequently drumming without energy consumption is not possible and cheating is not an option. In fact, extensive energy expenditure during vigorous drumming incurs costs that have detrimental fitness effects; males induced to drum more suffer increased mortality (Mappes *et al.* 1996; Kotiaho 1998). Furthermore, because highly actively drumming males sire offspring that have higher survival than offspring of poorly drumming males (Alatalo *et al.* 1998), it seems that male drumming activity is indeed a reliable indicator of male heritable viability and thus allows female preference for actively drumming males to evolve.

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