

## Sexual selection in the drumming wolf spider *Hygrolycosa rubrofasciata*

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### Abstract

We have studied the significance of courtship and agonistic signalling in the wolf spider *Hygrolycosa rubrofasciata* from the viewpoint of sexual selection theory. According to the 'good genes' sexual selection theory, females base their choice of mates on traits indicating heritable viability differences and are expected to benefit through better offspring survival. During the brief mating season in early spring, males of the wolf spider *H. rubrofasciata* move around their habitat (bog, meadow or abandoned field) searching for females and drum their abdomen on dry leaves to produce short audible drummings. There are two distinct signalling types: courtship drumming in intersexual signalling and agonistic drumming in intrasexual encounters. The courtship drumming of males increases their metabolic rate and tends to increase the risk of predation. As increased courtship drumming also reduces survival, courtship drumming can be seen as an evolutionarily significant cost. However, in unmanipulated conditions there is a positive correlation between survival and courtship drumming rate. The survival cost of increased courtship drumming is condition-dependent, such that males manipulated to be in a good condition tolerate the cost of drumming better than males manipulated to be in a poor condition. The offspring of sires with high courtship drumming rate has greater viability than offspring of sires with low courtship drumming rate, and females basing their choice on male drumming benefit in terms of increased offspring viability. Therefore, male courtship drumming is a honest viability indicator for choosy females in *H. rubrofasciata*. We have also found that males with higher agonistic drumming rate have better fighting ability in male-male encounters than males with lower agonistic drumming rate, but the role of agonistic interactions in sexual selection of *H. rubrofasciata* is likely to be minor compared to that of courtship drumming. Although body mass is one of the most common sexually selected male traits among animal taxa, body mass in *H. rubrofasciata* is not correlated with male mating success or drumming rate. However, differences in body mass increase the winning probability of the larger male in agonistic male-male interactions.

**Key words:** drumming, honesty of signalling, viability, intersexual selection, intrasexual selection, wolf spider

### INTRODUCTION

Although Charles Darwin pointed out the importance of sexual selection already in 1871 in his *The Descent of Man and Selection in Relation to Sex*, it took over a century for scientists to ulti-

mately discover its power in explaining the diversity and function of secondary sexual characters. Sexual selection can be divided into two components: intra- and intersexual selection (Andersson 1994). Intrasexual selection

relates to the interactions between individuals of the same sex, and it is manifested as, for example, weapons or status signals. In intersexual selection the choosier sex, usually the female, is choosing either resources or secondary sexual traits of the opposite sex. While resource-based female choice is easy to understand due to the direct effects on female reproductive success, indirect selection affecting through offspring-performance has been debated. There are three main ideas of intersexual selection, the 'Fisherian self-reinforcing' hypothesis, the 'sensory bias' hypothesis and the 'good genes' hypothesis, that all focus on the evolution of sexual preferences for secondary sexual traits. The 'Fisherian self-reinforcing' hypothesis is based on the idea that when females prefer males with higher life-time reproductive success, their preference genes will be united in their offspring with the male's genes for higher attractiveness (Kirkpatrick 1982; Pomiankowski & Iwasa 1993). In this way both the female preference genes and the male attractiveness genes will then spread in the population. The preferred male secondary sexual traits can be neutral or even disadvantageous, the only thing that matters is that these traits must be carried by males with higher fitness. The 'sensory bias' hypothesis argues that there are pre-existing sexual preferences ('sensory bias') for certain male secondary sexual traits that females inherit from their ancestors (Ryan 1985). The preferred secondary sexual traits will spread in the population by simply utilizing this pre-existing sensory bias. According to the 'good genes' or 'handicap' hypothesis, females should prefer males displaying honest, costly secondary sexual traits that signal genes for survival (Andersson 1986, 1994; Johnstone 1995). The 'good genes' hypothesis states that as the size of a secondary sexual trait increases, male fitness increases in terms of mating success, but this is traded-off with viability which decreases as ornament size increases. Males vary in their ability to withstand the costs of secondary sexual characters so that males in poor condition have lower op-

timum level of the ornament expression than males in good condition. Thus, males in good condition have better mating success and fitness, and females mating with them will enjoy increased viability for their offspring inherited from their fathers.

The sexual signalling of the wolf spider *Hygrolycosa rubrofasciata* (Ohlert), i.e. drumming, offers a convenient way of studying both inter- and intrasexual selection. Sexual signalling rate of *H. rubrofasciata* males can be manipulated without a risk of manipulation itself having side effects. This can be accomplished by not manipulating males themselves, but manipulating only their environment; when males are placed in the vicinity of a virgin female they spontaneously increase their drumming rate. However, males of *H. rubrofasciata* produce drumming signals even without the presence of females. The signals that males of *H. rubrofasciata* produce travel as vibrations both in the substrate and in the air. Thus, it can be directly tested whether there is any difference in female response behaviour to male signals depending on how they receive the signals. Also, males of *H. rubrofasciata* produce agonistic drumming signals while encountering other males. The characteristics of tape-recorded male drumming can be manipulated to test for the importance of different components of the drum in sexual selection.

#### ECOLOGY AND LIFE-HISTORY

*Hygrolycosa rubrofasciata* is a ground-dwelling wolf spider (Lycosidae) which can be found in patchily located populations widely distributed over northern Europe. It is found along coastal regions as well as inland in south-eastern and northern parts of Finland. *H. rubrofasciata* basically inhabits two kinds of habitats: abandoned fields and other meadow habitats and half-open bogs with deciduous trees. Although there may be tens of *Hygrolycosa rubrofasciata* in a square meter of the high-density habitat, they are not readily visible, since they usually hide under leaf litter. These two habitats differ from each other in many ecological characters, e.g. in

soil moisture, pH, vegetation, soil fauna, and soil litter thickness.

#### Male drumming

In southern Finland most matings of *H. rubrofasciata* take place during sunny days immediately after the snow has melted in late April or early May. All males die during or shortly after the mating season which lasts a few weeks. During the mating season, males of *H. rubrofasciata* produce drumming signals by hitting their abdomen on dry leaves or other suitable substratum to court females (Kronestedt 1984, 1996). One drumming consists of ca. 30-40 separate pulses, lasting ca. 1 second (Rivero et al. 2000), and it is audible to the human ear up to a distance of several meters. Female spiders receive these signals both as audible airborne signals and as substrate borne vibrations. In the experiment conducted by Parri et al. (submitted) investigating the effect of the manipulation of the substrate contact between males and females on female response behavior, the proportion of trials in which females responded to male drumming did not differ between the contact and non-contact set-ups. This means that females were equally choosy for airborne signals as in situations where vibrations via the substrate were present. Thus, the acoustic component of male drumming is truly important for female choice in *H. rubrofasciata*.

Based on both mark-recapture method and direct observations in field and laboratory, Kotiaho et al. (2000) have found that males of *H. rubrofasciata* are not distributed randomly among the habitat: fewer males are found in areas that have high sedge cover and low elevation, and males spend more time on dry leaf substrate than on other substrates. Drumming rate in the field is positively correlated with dry leaf cover, and males clearly prefer dry leaves as a drumming substrate. Male drumming rate and mobility are positively correlated with temperature. Therefore, males may be sexually selected to optimize their signalling habitat by active microhabitat choice. Interest-

ingly, on forested bog habitats the availability of dry leaf litter is considerably higher than on more open meadow habitats that are dominated by grass vegetation. Male drumming is more frequent in bogs than in meadows (Vertainen et al. unpublished data). Thus, adaptive differences in male mating tactics may have evolved between these two habitat types. During the mating season, males are actively searching for receptive females, and while searching engage in agonistic encounters with other males. In these encounters males use a different type of drumming signal (Kronestedt 1984). This agonistic drumming is also audible to the human ear, but it is shorter and more intense than courtship drumming. There is no possibility for observers to confuse agonistic signal with courtship signal.

#### Life-history

Males of *H. rubrofasciata* drum while wandering around the habitat searching for receptive females. Female draglines seem to affect males, and thus chemical substances in them might be used for sexual communication. When a male encounters a female he stops and drums several times. If the female is willing to copulate with the male, she responds by vibrating her body. This response is given immediately after the male drum, and it is clearly visible like the male drumming, although female percussions are usually not sufficiently intense to produce audible sounds. The existence of such a clear response allows the experimenter to determine explicitly which male or male signal the female prefers. After an initial female response male and female, while approaching each other, drum several times before the copulation begins (the so-called duetting, Kronestedt 1996).

Mated females of *H. rubrofasciata* produce an egg sac, which they carry attached to their spinnerets (silk glands in their abdomen). After approximately three to four weeks the offspring will emerge from the egg sac. The offspring usually remain on the female's abdomen or on top of the empty egg sac for a day to chitinise their exoskeleton, after which they

disperse. The development of *H. rubrofasciata* to maturation typically lasts 2-3 years in Southern Finland depending on the prevailing environmental conditions. Male spiderlings resemble cryptic brownish female spiderlings, and only after the final moult does the typical blackish appearance of males emerge. The final moult of maturing individuals happens in autumn preceding the mating season the following spring. Each adult male cohort reproduces only during one mating season, and males die during or immediately after it. However, we have observed individually marked females surviving until the next mating season.

#### GENERAL METHODOLOGY

*Hygrolycosa rubrofasciata* can easily be collected alive by pitfall traps and by hand picking. Unmated virgin females can be collected while there is still some snow on the ground. After collection, the spiders are placed individually into small plastic containers (film jars) with some moist moss (*Sphagnum* spp.) until they are brought to the laboratory. Before experiments spiders are prevented from reaching the active sexual phase by keeping them at a cool temperature (+3-7 °C). In the laboratory *H. rubrofasciata* are fed with fruit flies (*Drosophila* spp.) and springtails.

The characteristics of male drumming can be directly manipulated to test for the importance of different components of the drum in female choice (Parri et al. 1997; Parri 1999; Rivero et al. 2000). Repeatability and variability of the acoustic signal characteristics have been used to categorize signal components into static and dynamic parts (Gerhardt 1991; Castellano & Giacoma 1998). Static characteristics are highly repeatable within individuals with a low degree of variability among them, whereas dynamic characteristics are described as being repeatable within and variable among individuals. Such studies are essential to understand the significance of signals as honest handicaps, arbitrary Fisherian traits or species recognition traits. If signal components are repeatable, highly variable among individuals,

and correlated with fitness, they may convey information about male quality. Repeatable but less variable components might serve for species recognition purposes or they might be more of the Fisherian type of traits.

#### SEXUAL SELECTION

##### Intrasexual selection

Kotiaho et al. (1997) showed that large differences in body mass and courtship drumming rate between the two rivals seem to increase independently the winning probability of the larger or more active male *H. rubrofasciata*. Kotiaho et al. (1999a) found that agonistic drumming rate indicates male fighting ability, and that relative size asymmetry and motivation to fight both contribute to fighting ability. They also found that male-male competition decreases the courtship drumming rate of subordinate males, suggesting that male-male competition limits the opportunities for female choice. While courtship and agonistic drumming rate, and body mass in particular, affect the fighting success of males, male-male interactions may, however, be of relatively minor importance in sexual selection of *H. rubrofasciata*.

##### Intersexual selection

In the wolf spider *Hygrolycosa rubrofasciata* females choose males with the highest drumming rates as mating partners (Kotiaho et al. 1996). Females disproportionately choose more males with higher drumming rate than would be expected if females exhibited passive choice, i.e. if females were randomly choosing males in direct proportion to drumming rates. The sexual signalling, i.e. drumming rate, is thus under directional female choice. Drumming rate is repeatable within males and highly variable among males (i.e. dynamic) (Kotiaho et al. 1996; Rivero et al. 2000). Female *H. rubrofasciata* also prefer higher volume of the signal and longer drumming signals of males (Rivero et al. 2000). In addition, females respond more quickly to playbacks of male signals with a higher drumming rate and volume (Parri et al.

1997). This suggests that females may use a threshold level when responding to male courtship signals, and that they are prepared to suffer costs of waiting for an opportunity to choose between different males. In addition to drumming rate, signal length is also repeatable within males and has high variability among males (Rivero et al. 2000). Likewise, signal volume exhibits moderate within-male repeatability, but in reality the differences in distance and substrate confound female perception of volume differences. Both signal length and volume are positively correlated with the rate at which males produce drumming signals. Two dynamic characteristics of the male acoustic signal, i.e. drumming rate and length, are thus most likely to operate as indicators informing the females about the quality of wolf spider males.

In contrast, pulse rate (number of pulses divided by signal length where signal length is the total duration of the signal in milliseconds), symmetry of the signal (peak time/signal length, where peak time is the section of the signal at which the maximum intensity occurs), or peak frequency (the frequency at which the highest amplitude occurs, in Hz) have not been found to be targets of female choice in *H. rubrofasciata* (Parri 1999; Rivero et al. 2000). They have low repeatability and/or small among-male variability, and are not related to any other male trait (e.g. body mass, drumming rate, or mobility). Pulse rate might operate as a static characteristic related to species recognition. In several studies on insects pulse rate has indeed turned out to be under stabilizing rather than directional selection (e.g. Ritchie et al. 1994). Indeed, many spiders use substrate-borne vibrations presumably for species recognition (e.g. Schüch & Barth 1990; Barth & Schmitt 1991). While in other animal groups the peak frequency of sexual signals may convey honest information on male size, in this spider species peak frequency is not related to male size and has low repeatability (Rivero et al. 2000).

In *H. rubrofasciata*, there is no correlation

between male drumming rate and body mass (e.g. Kotiaho et al. 1996; Mappes et al. 1996), and the body size of males does not seem to be intersexually selected (Kotiaho et al. 1996). This is surprising because body size is one of the most common sexually selected male traits among other animal taxa (Andersson 1994). In *H. rubrofasciata*, male viability is independent of body mass, even when males are stressed, large males have a small but significant survival advantage compared with smaller males (Mappes et al. 1996). There is no detectable effect of male body mass on overwinter survival (Kotiaho et al. 1999b). Interestingly, however, larger males lose proportionally more mass than smaller males. This suggests that larger males may have an additional energy expenditure because of their large body mass while overwintering, but also that large males can afford to expend more energy than smaller males.

#### Honesty of male courtship drumming

The sexual signalling of *H. rubrofasciata* is a particularly well-tested signalling system where drumming rate has really proved to be an honest viability indicator. There are three conditions that must be met before a signal can be classified as an honest signal: (I) there must be within-individual repeatability and among-individual variability in the signal, which must have an effect on mate choice; (II) there must be substantial costs of signalling in terms of increased mortality or reduced subsequent mating success; (III) there must be condition-dependence of signalling in a way that there are differential costs between individuals in different condition. Then, in a given signalling level individuals in poor condition pay higher costs than individuals in better condition.

*I. Variation and repeatability.* In *H. rubrofasciata*, there are considerable within-individual repeatability and among-male variability in drumming rate (Kotiaho et al. 1996), which have an effect on mate choice. If there was no phenotypic variability in sexual signalling, there could not be any selective pressure.

Within-individual repeatability is also important, since otherwise a signal cannot be used as a reliable source of information about male quality.

*II. Costs.* Every new signal incurs costs of production. Those costs may be physiological such as increased energy expenditure, or direct costs such as increased risk of predation. These fitness costs have rarely been found even though they play an important role for the evolution of secondary sexual traits.

*a. Physiological costs.* Drumming of *H. rubrofasciata* is energetically highly demanding to its bearer (Kotiaho et al. 1998a): During drumming, metabolic rate is 22 times higher than at rest and four times higher than when males are actively moving. Metabolic rate per unit mass is positively related to absolute body mass during sexual signalling but not during other activities. 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 (Kotiaho et al. 1998a; Kotiaho 2000).

Physiological costs are ultimately realized as an increased probability of mortality. When Mappes et al. (1996) induced a set of male *H. rubrofasciata* to increase their drumming rate by presenting females in their proximity, these males suffered higher mortality and lost significantly more weight than control males, directly verifying that drumming is costly. Within the female induced treatment group males that drummed most actively survived better than less active males.

*b. Predation costs.* In addition to physiological costs of male drumming, higher mate searching activity clearly impairs male *H. rubrofasciata* by causing a direct increase in predation risk (Kotiaho et al. 1998b). Also, there is a tendency

that more actively drumming males have higher risk of predation. Increased predation risk while drumming has led to a counter-adaptation: male drumming rate decreases drastically in the presence of a predator (Kotiaho et al. 1998b). In *H. rubrofasciata* both increased mate searching activity and drumming benefit males through sexual selection, but at the same time natural selection provokes direct balancing costs on the same traits.

*III. Condition-dependence and differential costs.* In *H. rubrofasciata*, there is a clear positive correlation between male drumming rate and survival (Kotiaho et al. 1996, 1999c; Mappes et al. 1996). When Mappes et al. (1996) manipulated the phenotypic condition of males, males in a high food level treatment maintained their drumming rate at a high level, while males with intermediate and low food levels exhibited a reduction in drumming rates. Thus, males vary in their ability to bear the costs of drumming. Kotiaho (2000) showed that when the presence of females induced males to increase their drumming rate, large males manipulated to be in good condition survived better than large males manipulated to be in poor condition, that is, there is a three-way interaction between trait expression, condition and size on survival (see also Kotiaho et al. 1996, 1999c). Therefore, survival costs of male drumming are condition-dependent, being manifested in decreased viability of males in poorer condition.

#### **Indirect genetic benefits for offspring**

In *H. rubrofasciata* females prefer males with high drumming rate. As male drumming is not known to indicate any direct benefits affecting female fecundity or survival, there may be indirect genetic benefits for offspring. Indeed, by choosing males with the highest drumming rates, females of *H. rubrofasciata* benefit through better offspring survival (Alatalo et al. 1998). The estimated correlated response in offspring viability was rather small (0.12). However, it may be sufficiently large if the costs of being choosy are small. In fact, females mate with

better-than-average males just by responding passively to a random drumming signal, since this allows more actively drumming males to be observed more frequently. The active choice by females seems to increase this benefit only slightly. In many mating systems, females obtain better-than-average males as a consequence of intense male-male competition or because of the extraordinary variance in male signalling. This may be the general solution to the lek paradox, which stems from the fact that in polygamous species females appear to copulate with a small subset of available males. Such strong directional selection is predicted to deplete additive genetic variance in the preferred male traits (Fisher 1958; Falconer 1989; Roff 1997), yet females continue to mate selectively, thus generating the lek paradox (Borgia 1979; Taylor & Williams 1982; Kirkpatrick & Ryan 1991). Most studies only report small genetic fitness benefits of female choice (review in Møller & Alatalo 1999). Our results indicate that the costs of any additional choice may be so minor that female choice for honestly signalling males may evolve even with small benefits in offspring viability.

To conclude, male drumming rate is an honest signal which indicates heritable viability for females, thus reflecting phenotypic and genetic quality of males. These results provide evidence that a good-genes process based on the costly male drumming trait, reflecting heritable viability and thus genetic benefits for offspring, is involved in the evolution of sexual selection through female choice in the wolf spider *H. rubrofasciata*.

#### FUTURE PROSPECTS

Recently, there has been much interest in estimating fluctuating asymmetry (FA) of morphological traits as a short-cut measure of overall individual quality (review in Møller & Thornhill 1998). FA deals with small differences and thus measurement error is often relatively large. However, repeated measurements and large sample sizes allow reliable estimates of fluctuating asymmetry that can be corrected for

errors. As an example, Ahtiainen et al. estimated how much fluctuating asymmetry predicts male quality in the wolf spider *H. rubrofasciata*. Pedipalps as the most repeatable of all bilateral traits in this species were measured ( $n = 804$ ) with drumming rate and mobility as fitness-related references. Our data showed a weak negative relationship between an estimate of male sexual performance and pedipalp asymmetry ( $r = -0.100$ ,  $P = 0.007$ ), which inevitably underestimates the true relationship, given the measurement error. It is possible to estimate the unbiased relationship by correcting the above correlation coefficient with effective reliability estimates of FA and sexual performance, and thus  $r$  will be  $-0.181$ . In conclusion, fluctuating asymmetry as a measure of variation in male quality at the population level is suitable only if the sample size (and/or the number of repeated measurements) is large enough to overcome the masking effect of measurement error.

Our recent interest is in the study of adaptive variation in isolated populations of *Hygrolycosa rubrofasciata* with the particular goal of conservation applications. However, this research will also have the ambition to understand evolution of adaptive variation in general. Gene flow between populations, even those located within a few hundred meters from each other, seems to be highly restricted, and we have observed adaptive genetic differences between populations on a very small geographical scale (Vertainen et al. unpublished data). We are paying particular attention to the interaction between sexual signalling and the viability of small isolated populations. These studies utilize modern quantitative genetic techniques.

#### ACKNOWLEDGEMENTS

The work was financed by the Academy of Finland.

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