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## SEXUAL SELECTION IN A WOLF SPIDER: MALE DRUMMING ACTIVITY, BODY SIZE, AND VIABILITY

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**Abstract.**—Females are often believed to actively choose highly ornamented males (males with extravagant morphological signals or intense sexual display), and ornaments should be honest signals of male viability. However, this belief is relying only on some pieces of empirical evidence from birds. Our study reports active female choice on sexual display that indicates male viability in spiders. We established trials in which we studied female choice in relation to male courtship drumming activity and body size. Females chose the most actively drumming males as mating partners, but the body size of the males did not seem to be selected. Male drumming activity turned out to be a good predictor of male viability, whereas male viability was independent of male body mass. Our results suggest that by actively choosing mates according to male drumming performance, but independently of male body mass, females are preferring viable males as mates. Because *Hygrolycosa rubrofasciata* males do not provide obvious direct benefits to their offspring, females may gain some indirect benefits; offspring may have higher chance of survival, or the offspring may inherit the attractiveness of their father.

**Key words.**—Female choice, good genes, *Hygrolycosa rubrofasciata*, male viability, sexual selection, wolf spider.

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In mating systems in which males do not provide any short-term benefits for females, females are supposed to base their choice on some indicator of male genetic quality. By choosing males according to this quality indicator, females are expected to gain long-term benefits through increased offspring fitness. Traits that are correlated with male viability may serve as an index of male quality. Females are commonly believed to mate with the most viable males, and this prediction is supported by some recent evidence. Alatalo et al. (1991) studied female choice on males in black grouse. They found that females preferred to mate with the most dominant males and that the preferred males were most viable.

Møller (1988, 1991) showed with barn swallows that females prefer males with larger ornaments and that the degree of ornamentation is positively related to male viability. Moreover, Göransson et al. (1990), Hill (1991), Kempnaers et al. (1992), and Petrie (1992) showed with birds that male mating success is positively related to male viability. Thus, there are only few studies examining the relationship between male viability and male character chosen by females; and to our knowledge, there is no direct evidence from invertebrates that females would be preferring viable males as mates (but see Wilcockson et al. 1995).

There is, however, evidence of female preference for other male traits in invertebrates. Simmons (1986, 1987) found that female field crickets prefer to mate with large-bodied males. In field crickets, body size is heritable and thus can serve as an index of male quality. In spiders, there is plenty of data showing that body size is important in intrasexual competition (e.g., Riechert 1978; Christenson and Goist 1979; Suter and Keiley 1984; Wells 1988; Watson 1990; Faber and Baylis 1993), but female preferences have not been studied (but see Elgar and Nash 1988).

Acoustic communication and characteristics of song have often been studied in sexual selection, and they have been shown to influence mate choice in several animal groups, especially in insects, birds, and frogs (see Searcy and An-

dersson 1986 and Andersson 1994 for a review). In spiders, acoustic communication is not common and has been described only for some species (e.g., Rovner 1967, 1975, 1980; Harrison 1969; Rovner and Barth 1981; Stratton and Uetz 1981; Kronstedt 1984). In most cases, the function of acoustic communication in spiders seems to be the stimulation of females, but direct experiments are missing.

Although the function of female preference for body size and different song characteristics is well documented with variety of taxa, strong evidence for the adaptive significance of these preferences is still largely missing. In our study, the objective was to explore whether females actively choose particular males and if so, how do females benefit by choosing these males. This was studied by observing the female choice on male drumming activity and body mass, and examining how well these characters predict the male viability.

### MATERIALS AND METHODS

#### *Study Organism and Site*

*Hygrolycosa rubrofasciata* (Ohlert 1865) is a ground-dwelling wolf spider (Lycosidae) inhabiting marsh habitats with moss (*Sphagnum* spp.) and birch (*Betula pendula*) or willow (*Salix* spp.). Males court females by percussing dry leaves with their abdomen that is thickened and covered with specialized hairs (Kronstedt 1984; Köhler and Tembrock 1987). Rovner (1967) showed that lycosid spiders are able to detect airborne sounds, and drumming of *H. rubrofasciata* is also audible by the human ear up to a few meters. In Finland, the development of *H. rubrofasciata* takes 3 yr. It overwinters the first and second time in subadult stage and the third time in adult stage. The mating season begins immediately after snow melt in April, and males will court until the first half of June, even if most of the matings are likely to take place in a rather short period in May. Males are not found later in the season, and presumably they die after the mating season. Males do not provide parental care, nuptial

gifts, or any other obvious direct benefits other than sperm for females. Males are not cannibalized before, during, or after copulation.

Spiders were collected using pitfall traps and by hand-picking from a marsh in Sipoo, southern Finland (60°16'N and 25°14'E) between April 22 and May 10, 1994. Spiders were housed individually in plastic containers at 6°C in darkness. The bottom of each container was covered with moss (*Sphagnum* spp.) to provide humidity and a microhabitat similar to the natural environment of spiders. The moss was changed frequently enough to provide sufficient food (other arthropods) for spiders. Spiders were marked individually by placing a small dot of paint on the dorsal surface of the carapace, abdomen, or both. No adverse effects of this treatment were evident.

#### Measurement of Female Choice

Female choice was observed during the last week of May and the first 2 wk of June in plastic arenas (300 × 300 × 150 mm), the bottoms of which were covered with dry birch leaves. Three males and four females were placed randomly in each cage for 60 min. In nature, we have observed up to six males displaying in areas of similar size. Females are difficult to detect during the mating season because of the relatively low mobility compared with males. However, before and after the mating season we can find several females in such a small areas. Four females were used to ensure that there were at least one receptive female in each trial. A verbal description of male courting activity (frequency of drumming bouts) and female responses were taperecorded and later transcribed. Males were allowed to habituate for 10 min in the arena before the females were introduced, but males started their normal drumming behavior immediately allowing us to estimate drumming activity also before females were present.

When females are willing to mate they respond immediately after a male courtship drumming by shaking their body vigorously. Thus, it is easy to see which male is chosen. Observation was terminated after the first female responded, because from other studies (unpubl. data) we know that females as a rule mate with that firstly chosen male. The same females could be tested up to three times, but after the female responded for the first time it was not used anymore. If a female did not respond during the third trial, it was considered as unreceptive and was not included in the analysis. Each male was used only once.

#### Male Drumming Activity, Body Size, and Viability

Drumming activity of 18 males was measured in five different days during the laboratory period in 1993. Using this data, we tested the repeatability of the male drumming performance. Males were drumming on average ( $\pm$  SD)  $1.12 \pm 0.68$  times per minute. Variance of drumming activity was greater between the individuals than variation within the individuals (ANOVA,  $F_{16,51} = 3.51$ ,  $P < 0.001$ ), and the repeatability of drumming activity was 61.6% (Sokal and Rohlf 1969).

Male and female body masses were measured with a Sauter AR 1014 analytical balance to the nearest 0.1 mg. Body masses were taken only once; according to our observations in

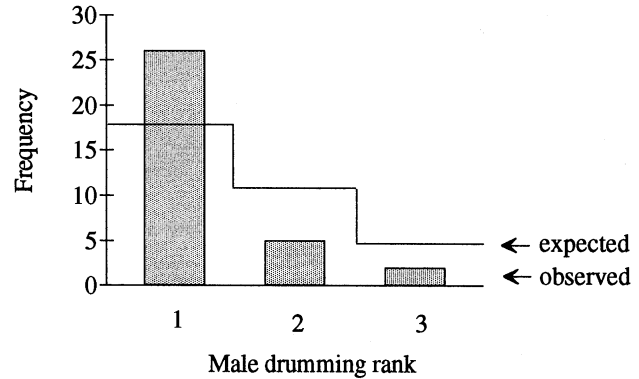


FIG. 1. Female choice in relation to male courting activity. 1, most active males; 2, intermediately active males; and 3, least active males. The expected distribution was derived from the assumption that probability of females to respond is similar after each single male drumming bout being directly proportional to male drumming rates (=passive choice).

1993 individual body masses do not significantly change during the laboratory period under similar conditions. Indeed, the repeatability of the size was extremely high (99.4%) (ANOVA,  $F_{17,72} = 153.51$ ,  $P \ll 0.001$ ) (Sokal and Rohlf 1969).

Survival was measured over a 1-mo period from mid-May to mid-June 1994. We recorded the survived males in the end of the 1-mo period. Males were housed in similar manner as described earlier. Even though absolute survival pattern in the laboratory is likely to be different from the natural conditions, we expect that males in good condition would survive longest in both situations. Most males used in the female choice trials were the same males used in the viability measurements. However, we included in our tests only those trials in which one of the females responded to a male and thus, there was not enough statistical power to test directly female choice on male viability.

#### RESULTS

In 33 cases, females responded to male courtship drumming. The three males in each trial were drumming in different activity level, and in 26 cases out of the 33, females selected the most actively drumming male (Fig. 1). To determine whether this was a result of passive attraction or active preference, we tested female choice against the different drumming activity of males. As a null hypothesis (i.e., passive attraction), we assumed that females are equally likely to respond after each single drumming bout of any male. Thus, the likelihoods of choosing any of the three males should directly be reflected in the proportions of drumming bouts performed by these males. This was tested with a simulation that considers the different rate of drumming for each male separately for every trial. We let the simulation run 10,000 times to get the estimate of the probabilities for observed or more discrete distribution of female choice. The simulation was repeated 25 times to get the 95% confidence intervals for the estimate. The probability of 26 or more of the most active males to become selected by chance alone was 1.01% (0.97, 1.04). Probability for five or fewer of the

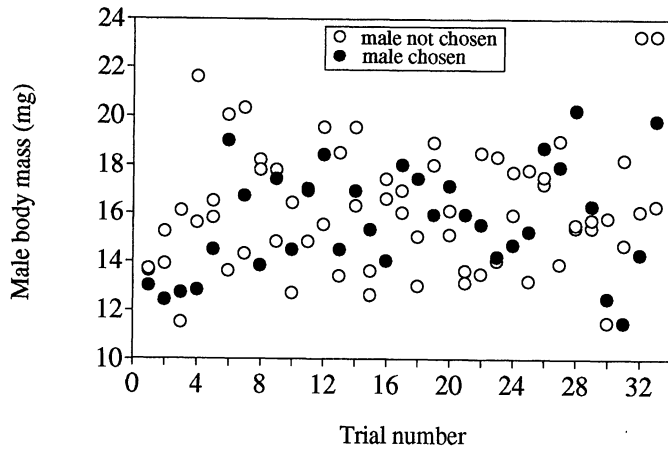


FIG. 2. Female choice in relation to male body mass in each three-male trial.

secondly active males to become selected by chance was 3.42% (3.34, 3.50) and for two or fewer for the least active males 27.34% (27.18, 27.50) (Fig. 1). Thus, females seem to actively choose the most actively drumming males.

Although the presence of females increased male drumming activity, there was a positive correlation between male drumming activity before and after female introduction ( $r_s = 0.658$ ,  $n = 99$ ,  $P < 0.001$ ). Thus, we can exclude the possibility that the high drumming activity of the successful male could be a consequence rather than a cause of female choice.

We were also interested whether body mass of males influence the female choice. We compared the body masses of males that became selected by females to those males that were unsuccessful. We found no indications that females would choose males according to their body mass (two-sample  $t$ -test,  $t = 0.30$ ,  $df = 30.4$ ,  $P > 0.7$ ) (Fig. 2). We also compared male body mass and drumming activity to determine the possible covariance between these traits, but there seemed to be no relationship at all (Fig. 3).

Among 103 males 23 did not survive through the 1-mo

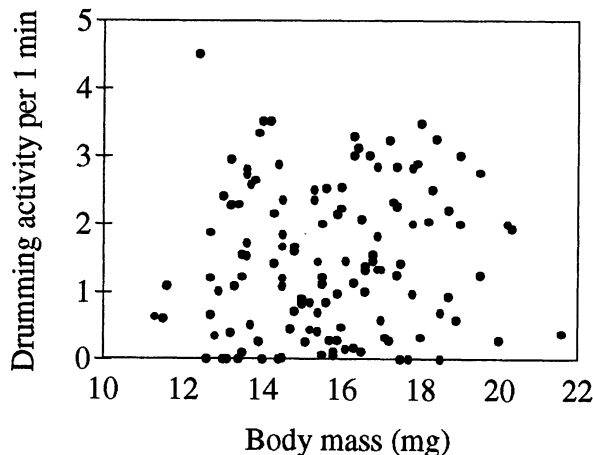
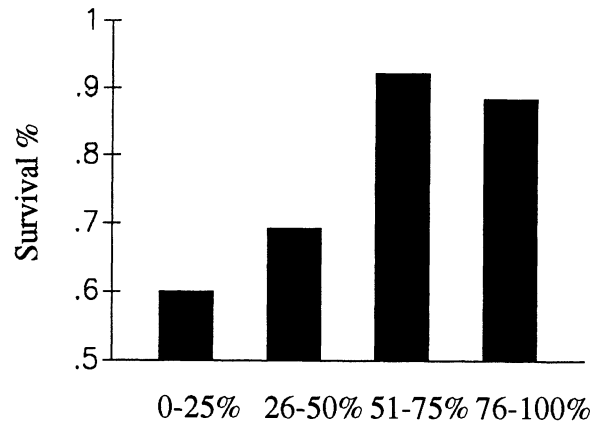


FIG. 3. Relationship between male body mass and drumming activity. Pearson's  $r = 0.078$ ,  $n = 126$ ,  $P > 0.35$ .



Relative drumming activity of males

FIG. 4. Unweighted logistic regression for survival and drumming activity. Coefficient for drumming activity is 0.569,  $df = 101$ ,  $P = 0.021$ .

observation period. Survivors had been more actively drumming than males that died (Fig. 4). Body mass tended to be a bit larger in males that survived (Table 1) but the tendency was far from significant (two-sample  $t$ -test  $t = 1.21$ ,  $df = 38.8$ ,  $P > 0.2$ ). Furthermore, when logistic regression was applied to test whether body mass and/or drumming activity was a good predictor of male survival, body size was found to be unimportant (Table 2A). The analysis of deviance revealed that only the drumming activity significantly improved the model, whereas body size had no significant effect (Table 2B). Therefore, drumming activity alone seems to be the predictor of male survival.

#### DISCUSSION

There is some empirical evidence from lekking (e.g., Alatalo et al. 1991; Petrie 1992) and nonlekking birds (e.g., Göransson et al. 1990; Hill 1991; Møller 1991; Kempenaers et al. 1992) that male viability is positively correlated with secondary sexual traits preferred by females. There is also scarce evidence from mammals (Byers et al. 1994) that females choose more vigorous males. However, there is no such evidence from other taxonomic groups. Here we demonstrated that *H. rubrofasciata* wolf spider females prefer males that are most actively drumming and that male drumming activity and survival are positively correlated. Somewhat surprisingly in contrast to many insect studies (e.g., Wilcockson 1995; Pomiankowski and Møller 1995) females did not seem to

TABLE 1. Body mass and activity differences between males that survived through the observation period and males that died. ( $N$ , number of males; +, survived; -, died; mass, mg; activity, drumming bouts per minute).

	Alive	$N$	Mean	(SD)
Mass	+	80	15.6	(2.1)
	-	23	15.0	(2.3)
Activity	+	80	1.7	(1.2)
	-	23	1.1	(1.0)

TABLE 2. A. Unweighted logistic regression of survival. B. Analysis of deviance. First row tests whether M and A improves the intercept-only model, second row whether A improves the model when I and M are already in the model, and the third row whether M improves the model when I and A are already in the model. Degrees of freedom is the difference in the number of the independent variables in the two models. *P* is computed from the  $\chi^2$  of the difference. (I, intercept; A, activity; M, mass).

A.					
Predictor variables	Coefficient	Std. error	Coeff./SE	<i>P</i>	
Constant	-1.3164	1.7973	-0.73	0.464	
Activity	0.5429	0.2474	2.19	0.028	
Mass	0.1189	0.1177	1.01	0.313	
Deviance	102.22				
<i>P</i> -value	0.420				
Degrees of freedom	100				
B.					
Model	Deviance	Difference	df	Tested for	<i>P</i>
I	126.41 <sub>(dI)</sub>	24.19 <sub>(dI-dIMA)</sub>	2	M+A	0.000
I+M	124.67 <sub>(dIM)</sub>	22.45 <sub>(dIM-dIMA)</sub>	1	A	0.000
I+A	103.27 <sub>(dIA)</sub>	1.01 <sub>(dIA-dIMA)</sub>	1	M	0.315
I+M+A	102.22 <sub>(dIMA)</sub>				

choose males according to male body mass. Furthermore, male body mass was not associated with survival or drumming activity. Thus, it seems that male body mass is unimportant or has only minor importance for female choice of *H. rubrofasciata*. This may allow the high variation observed in male body masses (range 10.6–21.6 mg, CV = 14.02, see also Fig. 3). However, there is evidence that larger body mass benefits males in intrasexual encounters (Kotiaho et al. unpubl. data). There were occasional interactions between males also during our choice experiments, but this did not lead to reduced drumming in smaller males and, thus, there were no observable effect on female choice.

Spiders are poikilothermic, and their normal resting metabolic rates are about half of those measured for other poikilothermic animals of equal mass (Anderson 1970). Furthermore, Miyashita (1969) and Anderson and Prestwich (1982) showed that for several species of spiders the regressions between resting metabolic rate and body size have virtually zero slopes. This may explain why body size was not associated with male survival; metabolic rate and thus energy expenditure of males is independent of body size. However, during activity heart rate of spiders may increase rapidly (e.g., Carrel 1987). Courtship drumming of *H. rubrofasciata* males is likely to be energetically demanding. Thus, males that are drumming actively may be in better condition and more vigorous than males that are not courting or are courting at low drumming rate. Even though it seems that male body size is not important for female choice, there is a possibility that variation in body size may affect differently the energy expenditure during high drumming activity. Thus, it may be that during the similar activity levels, larger males suffer increased energy expenditure compared to smaller males.

In nature, *H. rubrofasciata* males are very mobile, whereas females are quite sedentary during the mating period (Kotiaho et al. unpubl. data). This indicates that females may be minimizing the risk of predation and the amount of energy

used for mate selection. Therefore, males have to face any increased risk of predation (see Vollrath and Parker 1992) and spend more energy for moving and finding receptive females. Thus, staying sedentary during mating season may be an additional mechanism for females to test male condition, because moving increases rapidly the energy expenditure of spiders (Carrel 1987), and males of *H. rubrofasciata* actively search females in addition to display courtship drumming.

Females are often demonstrated to prefer some signals or components of courtship (for a review see Andersson 1994, pp. 132–142), but there is frequently a controversy about what females may gain from choosing these particular mates. Females are expected to choose attractive males to get more attractive offspring and thus benefiting through increased offspring mating success or to get offspring that have higher chances of surviving because they have inherited the good genes. Recently, evidence supporting these expectations have started to accumulate (e.g., Watt et al. 1986; Norris 1990, 1993; Gilburn et al. 1992, 1993; Pomiankowski and Møller 1995; Wilcockson et al. 1995). Our study indicates that *H. rubrofasciata* females are actively choosing the most actively drumming males as their mates. We were able to show that these actively drumming males are also more viable than other males. Thus, providing that *H. rubrofasciata* females do not get any immediate benefits that we were not able to measure, for example, disease-free copulation or good quality sperm, this mating system may also be supporting the good gene models. However, to determine whether the choice of *H. rubrofasciata* females has adaptive value, heritability of the selected trait needs to be estimated.

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