

Female choice for male drumming in the wolf spider *Hygrolycosa rubrofasciata*

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(Received 2 January 1996; initial acceptance 7 February 1996;
final acceptance 22 April 1996; MS. number: 5121)

Abstract. Mate preferences in invertebrates have usually been studied with simultaneous choice experiments alone, which allows effective detection of any preferences but does not tell much about the strength of inter-sexual selection. Under natural conditions females frequently have to rely on sequential choice, and choosy females may incur opportunity and direct costs such as loss of time when they reject a male. Female preference in the wolf spider *Hygrolycosa rubrofasciata* for two components of male courtship signalling, rate and volume, was investigated. Both of these characteristics were tested with a sequential choice set-up and the effect of volume also with a simultaneous choice method. Females responded more quickly to male signals with a higher rate and volume. This suggests that females use a threshold level when responding to male courtship signals and that they are prepared to suffer some costs of waiting for an opportunity to choose between males.

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In his recent review [Andersson \(1994\)](#) concluded that female choice is the most commonly operating mechanism of sexual selection and that females use a variety of behavioural traits in their mate choice. Several studies have shown that male acoustic signalling, or even certain components of these signals, can be very important for female choice ([Anderson 1994](#)). Male song and singing, in parallel with exaggerated morphological traits, can be seen as ornaments, revealing the quality of the bearer. The relationship between male acoustic signalling and male mating success has been investigated quite widely, particularly among birds but also among frogs and insects (see reviews by [Searcy & Andersson 1986](#); birds: [Catchpole 1987](#); frogs: [Ryan 1991](#)). The results of these studies indicate that several components of male acoustic signalling can be selected by choosy females. Females can base their mate choice on song complexity, rate, repertoire size, volume and duration (see [Ryan & Keddy-Hector 1992](#); [Andersson 1994](#) for reviews).

Acoustic signals are also important in spiders (review in [Uetz & Stratton 1982](#)). Twenty-six families of spiders are capable of producing

sounds using different mechanisms ([Uetz & Stratton 1982](#)). In wolf spiders (Lycosidae) several species communicate by means of acoustic signals, and in many of them males have specialized organs for producing those signals ([Uetz & Stratton 1982](#)). Acoustic signals can be used for a variety of purposes, such as defence and aggression, but they also play an important role in the courtship of spiders. In some instances these acoustic signals are critical in determining whether copulation will occur ([Uetz & Stratton 1982](#)). However, although the use of acoustic signals in mating behaviour and species recognition has been described, there have not been many experimental studies on the role of male signals in sexual selection and female choice in spiders. Substrate-borne vibrations have been studied in detail in several species ([Rovner & Barth 1981](#); [Schüch & Barth 1990](#); [Barth & Schmitt 1991](#); [Schmitt et al. 1993](#); [Fernandez-Montraveta & Schmitt 1994](#); [Schmitt et al. 1994](#)). In these studies male signals have been investigated as traits of species recognition under stabilizing selection rather than as condition-dependent handicaps under directional selection (see [Kotiaho et al. 1996](#); [Mappes et al. 1996](#)).

One important element in sexual selection and female choice is the cost of choice behaviour for females, for example of actively favouring certain

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kinds of males as mates. The costs that females face can be either direct or opportunity costs (Real 1990). Direct costs include increased risk of predation, loss of time due to searching and direct aggression by other competitors. Opportunity costs include loss of a previously encountered mate because of its death, emigration or loss of mating status (Real 1990). Females can compare potential partners in two ways; simultaneously or sequentially. Simultaneous comparisons are possible when there are several potential mates present at the same time. This kind of mate comparison is possible for example in lekking species such as black grouse, *Tetrao tetrix* (Rintamäki et al. 1995) and cock-of-the-rock, *Rupicola rupicola* (Trail & Adams 1989). Sequential comparisons have been reported for example in female sticklebacks, *Gasterosteus aculeatus* (Bakker & Milinski 1991), the great reed warbler, *Acrocephalus arundinaceus* (Bensch & Hasselquist 1992) and the pied flycatcher, *Ficedula hypoleuca* (Hovi & Rätti 1994). Effects of search costs on female sampling behaviour have been investigated for example in sticklebacks where increasing costs reduce female choosiness (Milinski & Bakker 1992).

Evaluations of search and comparison costs and their significance for sexual selection in invertebrate mating systems are still rare. The experimental testing of sexual selection theories in invertebrate mating systems has traditionally been based on choice situations where females are given the opportunity for simultaneous choice between males or male signals of differing quality (see Thornhill & Alcock 1983; Bradbury 1985). However, these results might overestimate female choosiness, since the simultaneous set-up minimizes, and often even eliminates, the costs that affect female mate choice in natural mating events. These costs can be taken into account when using experimental set-ups that involve sequential choice.

In this study we investigated female preference for two characteristics of male acoustic courtship signalling, rate and volume, in a drumming wolf spider *Hygrolycosa rubrofasciata* (Ohlert 1865) (Araneae, Lycosidae). We used drumming volume to test female responsiveness in sequential versus simultaneous choice situations. Thus, our aim in this study was not to study the effect of the volume as such but rather to use it as a tool to investigate whether females are prepared to incur costs in their choice of mate. Since females of this

species respond to tape-recorded male drumming signals, we were able to carry out these experiments by playing back previously recorded male signals. We introduced the 'searching' costs for the females by presenting the different levels of male signals sequentially on successive days and thus making females wait for another opportunity to choose a male. Female preferences between sequential and simultaneous choice situations were tested using different volume levels. With these experiments it was possible to reveal the accuracy of female choice behaviour and, thus, the significance of costs to female choice.

METHODS

Study Species and Courtship Behaviour

Hygrolycosa rubrofasciata is a sexually dimorphic wolf spider. It inhabits marsh environments where the ground in spring is covered with dry leaves of willow, *Salix* spp., and birch, *Betula* spp. In southern Finland the mating season starts soon after snow melt at the end of April and lasts for approximately 1 month (personal observation). The activity of courting males peaks during the first week or so of May after which their drumming activity gradually ceases towards the end of the season. The majority of the matings are likely to take place soon after the snow melt.

The specific trait involved in courtship of this species is the drumming that males perform in order to advertise themselves to females and to other males (Kronstedt 1984; Köhler & Tembrock 1987; personal observation). The signal is produced by repeating bouts of vigorous drumming of the abdomen against the ground which is normally covered with dry deciduous leaves (Kronstedt 1984; personal observation). This percussing produces sound that is clearly audible from up to 10 m, with a peak frequency between 4 and 6.5 kHz (unpublished data). The mean duration of each drumming bout is approximately 1 s. In addition to courtship signals males produce threatening signals when they come in close contact with other males. After a female responds, males clearly change their drumming intensity. In an earlier study (Kotiaho et al. 1996) we found that females often responded to the male drumming without direct contact with the male or the leaf where the male was drumming. However, we do not exclude the possibility that substrate-borne

vibrations have some role in both inter-sexual and intra-sexual (male–male) signalling. The sound and the substrate-borne vibrations are closely related as they are produced by the same vigorous tapping on the substrate. Thus, critical features such as the inter-drum intervals, intervals between each single drum within each drumming bout, the duration of the drums and also the energy output of the signal will be reflected in the same way both in the vibrations and in the sound. Rovner (1967) has shown in *Lycosa rabida* that females respond to signals replayed by loudspeakers. In *H. rubrofasciata* females also respond to male drummings emitted by loudspeakers. When ready to copulate, females respond by shaking their body against the ground. They respond immediately after male drumming, making it easy to determine which of the males was chosen. Female response is essential for the initiation of mating; in our laboratory observations we have not observed any copulation starting without the female responding first. Copulation usually follows immediately after the female's response (personal observation). The consideration of sequential choice is realistic in this species, where males move around the habitat drumming and females are rather stationary.

Study Animals and Recording of Drumming

We collected spiders by pitfall trapping and by hand from a bog at Sipoo (60°16'N, 25°14'E), southern Finland, at the beginning of May 1994. The spiders were kept individually in containers at 6°C with moss, *Sphagnum* spp., to provide them with both moisture and food. Experiments were carried out at Konnevesi Research Station, central Finland. For individual identification both sexes were marked with a unique colour combination of small dots of paint on the carapace and abdomen. This marking method did not appear to harm the spiders.

We recorded male drumming signals during actual male–female encounters. We placed three males and four females together in an arena of 300 × 300 mm. Male drumming was recorded with a Telinga microphone and a digital recorder (Casio DA-7). From these recordings we chose one good quality (without background noise) drumming bout from 12 males to create the playbacks. All the drummings that were used in the playbacks were normal male courtship

signals with no male–male interaction or female response.

Experimental Procedure

We placed females on the top of loudspeakers (Pioneer TS-F 1665) in small plastic cups (diameter of 50 mm) with one dry birch leaf in each cup. Since we were unable to detect the physiological state of the females (whether they were ready to copulate and thus to answer the male drumming) we took several females at a time in each trial to ensure that at least some of the females would be sexually active. We carried out the sequential choice experiment using groups of 10 females in each trial; in the simultaneous choice experiment we used groups of five females. Females were allowed to habituate to the cups for 5 min before the beginning of the trials, which lasted for 90 min each. We used times from the beginning of the playback session until the first female response to compare preferences of individual females between different manipulation levels. This basic procedure was similar when testing both drumming rate and volume. In the experiment on the effect of volume we also compared the total number of female responses to different manipulation levels. All probabilities are for two-tailed significance levels.

We estimated female responsiveness by calculating the proportion of females responding out of all the females used in the experiments. In a previous choice experiment where four females and three males were free to interact with each other until one of the females responded (see Kotiaho et al. 1996 for details), 38.5% of the females responded within 60 min. In the present playback experiments, which were carried out using the same females as in the choice experiment, the overall response rate was 27% which is not different from that in the choice situation.

Drumming Rate

We investigated the effect of male drumming rate (number of separate drumming bouts per unit time) on female response rate by presenting the same drumming bout at two different rates. The high rate treatment was three drums per min and the low treatment was one drum per 3 min. These levels were selected on the basis of earlier laboratory studies in which male drumming rate was

observed in the presence of females; the mean drumming rate was 1.5 drumming bouts per min (lower quartile=0.56, upper quartile=2.46 drums per min; data used in Kotiaho et al. 1996). The rates used in this study thus fall well inside the distribution of the male's natural drumming activity. The drummings were presented to each female sequentially, in random order on successive days. We tested 80 females, 34 of which responded at least once to male drumming and were included in the analysis.

Volume Level

We investigated the effect of volume level on female responsiveness with two-level manipulations of the same drumming bout (low and high volume). Levels were chosen to be higher and lower than the mean male drumming volume (i.e. audible to humans ca 10 and 1 m away, respectively). We played back the different volumes to females with both simultaneous and sequential choice set-ups. In the former, females were able to compare the two drummings differing in volume immediately while in the latter females were forced to wait for 24 h for the other type of drumming and thus to incur clearly higher costs. We created the simultaneous choice situation by broadcasting the higher and lower volumes one after the other from the same tape alternately. In this experiment the drumming rate was three drums per min in both set-ups. We tested 75 females in the simultaneous set-up and 120 in the sequential set-up.

RESULTS

Drumming Rate

There was a clear difference in the times until first response between the experimental levels. Females responded to the higher drumming rate (three drums per min) more quickly than the lower drumming rate (one drum in 3 min; Wilcoxon $z=2.86$, $N=34$, $P<0.01$; Fig. 1). We also analysed the data using the separate groups of females that were played the same signal as independent observations for the statistical test. This analysis also gave shorter times for the higher drumming rate, although this was not quite significant (Wilcoxon $T=6$, $N=9$, $P=0.058$).

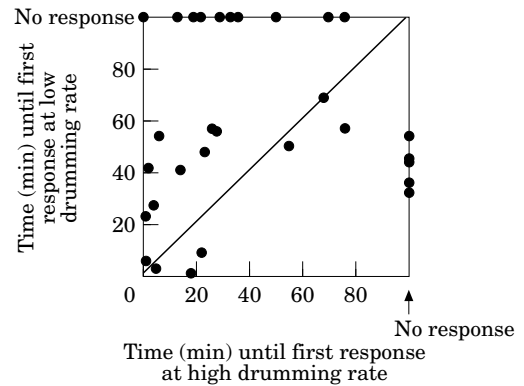


Figure 1. The time until first response of each female when the drumming was played back at a high rate (three drums per min) and at a low rate (one drum per 3 min; $N=34$). Values above the diagonal indicate that the female responded more slowly to the low than to the high drumming rate.

Volume Manipulations

Twelve females responded to the loud volume and only three of these also responded to the lower volume, in the simultaneous set-up. Females responded significantly earlier to the high volume than to the low volume (Wilcoxon $T=0$, $N=12$, $P<0.01$). These females responded in eight groups with different male playbacks. When we compared the mean times until first response for each of these groups we got the same result (Wilcoxon $T=0$, $N=8$, $P<0.01$).

Twenty-seven females responded at least once in the sequential set-up; 15 of these females responded only to loud drumming, eight to both levels and four only to the lower level. The average times until the first female response indicate that females reacted more quickly to the high than to the low volume (Wilcoxon $z=2.60$, $N=27$, $P<0.01$). Comparisons of the mean times for each female group also show that females responded more quickly to the higher volume (Wilcoxon $T=3$, $N=12$, $P<0.01$).

To find out whether there was a difference in how long it took the females to respond in the simultaneous and sequential choice situations we compared the time before first female response between these two set-ups. We did this by counting how many females chose first each of the levels and then comparing these numbers between two set-ups. There was no significant difference

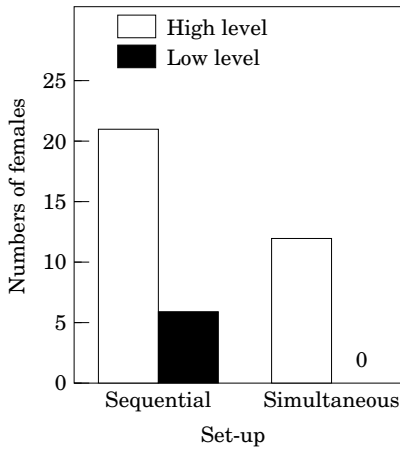


Figure 2. The first choices by each female with respect to the volume of the drumming in the set-ups with sequential ($N=27$) and simultaneous ($N=12$) presentation of the signal.

between simultaneous and sequential choice situations (Yates' corrected $\chi^2_1=1.68$, $P>0.1$; Fig. 2). Thus it seems that female *H. rubrofasciata* prefer male drumming bouts replayed at a higher volume even in a sequential setup when there are costs to waiting for another opportunity to choose a male.

We also compared the total number of female responses both within and between the simultaneous and sequential choice situations. In the simultaneous choice situation the mean number of responses (\pm SD) for the lower level was 0.75 ± 2.00 and for the higher level 8.33 ± 13.61 . Similarly, in the sequential choice situation the mean number of responses for the lower level was 3.22 ± 5.35 while for the higher level it was 11.00 ± 16.00 . The total number of responses differed statistically in both set-ups (for simultaneous choice Mann-Whitney $U=3.49$, $N_1=N_2=12$, $P<0.001$ and for the sequential situation $U=2.79$, $N_1=54$, $N_2=27$, $P<0.01$; Fig. 3). However, the proportion of females that responded more often to the higher volume compared to those that responded to the lower one did not differ significantly between simultaneous and sequential choice situations (Yates' corrected $\chi^2_1=2.84$, $P=0.092$). In other words the sequential set-up did not have any clear effect on the distribution of female response between high and low volumes, even if there was some tendency to such a difference.

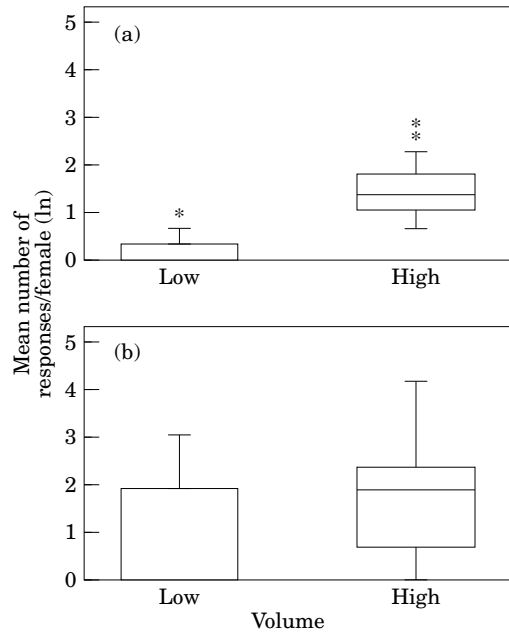


Figure 3. Female preference (median and quartiles, indicated as box and line) for each volume measured as the number of responses by each female to high and low volumes. The number of responses was ln-transformed. (a) Simultaneous choice ($N=12$); (b) sequential choice ($N=27$). Minimum and maximum values are indicated with lines and outliers with asterisks.

DISCUSSION

The playback experiments indicate that female *H. rubrofasciata* prefer to respond to male drumming signals of higher repetition rate and higher volume. These results are in accordance with a previous study in which females and males were allowed to be in contact with each other without any manipulations of male drumming signals (Kotiaho et al. 1996). In that study females preferred the males that were drumming most actively. Male drumming activity has quite a high repeatability (61.6%, Kotiaho et al. 1996), which allows for comparisons with any male secondary sexual traits that are under directional selection by the females. In addition we have shown that male drumming activity is costly, honestly revealing male phenotypic condition (Mappes et al. 1996). However, we have no similar information for the signal's volume, so in this study we used it just to compare simultaneous and sequential choice. In reality, volume is likely to depend more on the type of

substrate on each drumming occasion as well as the distance between the male and the receiver, and thus it is unlikely to be a repeatable male trait.

Both characters studied here, signalling rate and volume, are subject to female choice in several species. Male calling rate is preferred by females of several species of anuran (Whitney & Krebs 1975; Sullivan 1983; Forester & Charnowsky 1985; Schwartz 1986) and bird (Payne & Payne 1977; Collins et al. 1994). For example in Woodhouse's toad, *Bufo woodhousei*, male mating success in the field was significantly affected by its calling rate and females selected for higher calling rate in experimental observations, too (Sullivan 1983). In the grey treefrog, *Hyla versicolor*, females preferred high calling rates in laboratory conditions (Sullivan & Hinshaw 1992). Schmitt et al. (1993, 1994) have studied female response rate in two species of wandering spiders (*Cupiennius getazi* and *C. salei*) in relation to several components of the male signal. In *C. getazi* female response rates covered a larger range than the natural variation of the male signal characteristics, including amplitude range and sequence duration of the signal. In this species females did not clearly prefer male signals of greater amplitude or high repetition rate. Similarly, female response behaviour did not correlate with the attractiveness of the signal. Females responded relatively quickly after the first male signal, on average after the third. Thus, male signals in wandering spiders are used for species recognition and male competition rather than as condition-dependent ornaments in inter-sexual selection.

Female preference for calling rate, loudness or for some other characteristics of male calls can be seen as preference for more energy invested to produce sounds (Ryan 1988). Ryan (1988) proposed that males might increase the total energy input that reaches females either with increased energy content in individual calls or with an increase in the number of calls. Although it could not be stated that females select the amount of energy of the sound per se, there might be indirect selection by females for greater energy contents of male calls, as proposed also for natterjack toads, *Bufo calamita* (Arak 1988). Male calling and display behaviour are very energy demanding (Vehrencamp et al. 1989; Wells & Taigen 1989). Courtship behaviour is also very costly in *H. rubrofasciata*. Experimental manipulations of male courting activity have shown that males

stimulated to increase their drumming activity suffer higher costs (manifested as lower survival) than males drumming at a lower rate (Mappes et al. 1996). Metabolic activities and the effect of physical activities on the metabolic rates of spiders have been investigated quite widely (see Anderson 1970; Carrel 1987). However, there have not been many measurements on the effect of courtship activities on metabolic rates of spiders (but see Watson & Lighton 1994).

The sequential presentation of male drumming signals compared to simultaneous presentation did not change the female response rate significantly. Thus females can be said to be ready to pay some costs of choosing between male drumming signals of different quality. This kind of sequential comparison system might indeed be working in the field where males move actively around the habitat and court while females are rather stationary (unpublished data). It could be argued that females compare moving and courting males on the basis of their drumming performance and respond to a male that is courting at a high enough rate. Janetos (1980) proposed five decision strategies that females might be using when selecting mates. These rules include random mating, a fixed-threshold criterion, a fixed-threshold with last-chance option, an optimal one-step decision strategy and the best-of-*N*-males strategy. Our results fit best with a threshold-decision rule with practically no opportunity to return to the male encountered. There might, however, also be situations where a female could compare several males at one time and so use the pool comparison method.

Whether females of *H. rubrofasciata* are able to estimate male genetic quality on the basis of courtship characteristics has not yet been established. However, we have shown that drumming is costly to males and that they differ in their ability to bear the costs of drumming so that drumming activity could be an honest signal of male quality (Mappes et al. 1996). Furthermore we know that females prefer more actively drumming males (Kotiaho et al. 1996). Provided that male drumming characteristics have heritable components it would thus pay females to choose the more actively drumming males.

ACKNOWLEDGMENTS

We thank Konnevesi Research Station for facilities and help. In addition we thank Tanja Mattila

and Matti Halonen for their help during the experiments and Ana Rivero for checking the language. This work was financed by the Academy of Finland to R.V.A. and Wihuri Foundation to S.P.

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