

Sexual selection in the wolf spider *Hygrolycosa rubrofasciata*: female preference for drum duration and pulse rate

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The unusual form of sexual signaling, the drumming produced by the wolf spider *Hygrolycosa rubrofasciata*, allows exceptionally detailed studies of female preference patterns against signal characteristics. It is easy to manipulate the signals and to use large numbers of females in playback experiments. Males of *H. rubrofasciata* produce drums by striking their abdomen against dry leaves on the ground. Drums travel not only as substrate-borne vibrations, but also as airborne acoustic signals. Females respond sooner to drums transferred as substrate borne, but the mode of signal transfer has no effect on female preference for different types of drums. We investigated the effects of two key components of the drums, duration and pulse rate, on female choice. Previous studies have shown that the duration of the drum is both repeatable within males and variable between males. In contrast, pulse rate shows high within-male repeatability but only little variability between males. Using playbacks of manipulated drums, we found that females preferred drums of longer duration but that pulse rate had no effect on female preference. Our results suggest that drum duration may function as an indicator of male quality for choosy females. Pulse rate, on the other hand, is less likely to be an important trait in intersexual selection. Female preference for drum duration was open-ended within the natural variation of the drum durations, but it leveled off outside the normal range. Thus supernormal stimuli would not pay for males using this energetically demanding acoustic signal. *Key words*: acoustic signaling, drum duration, female choice, *Hygrolycosa rubrofasciata*, pulse rate, sexual selection, wolf spiders. [*Behav Ecol* 13:615–621 (2002)]

Acoustic signals are particularly suitable for experiments of female preference against signal properties that can be manipulated for playbacks. Female mate choice based on male acoustic signals is driven by various components or characteristics of the signals, such as calling rate, duration, intensity, dominant frequency, and song complexity (see review in Ryan and Keddy-Hector, 1992; see also Brown et al., 1996; Catchpole, 1987, 1996; Cherry, 1993; Eiríksson, 1993; Gray, 1997; Ritchie et al., 1998; Searcy and Andersson, 1986; Sullivan and Hinshaw, 1992). In invertebrates the signal components most often involved in female choice are frequency, duration, and pulse rate. Signal duration and pulse rate are important for female choice, for example, in orthopteran calls (Butlin et al., 1985; Eiríksson, 1993; Hedrick, 1986; Simmons, 1988) but also in some other insects (Jang and Greenfield, 1996), and even in spiders (Schmitt et al., 1993).

Typically, females prefer male signals of greater magnitude (e.g., longer duration, greater repetition rates and larger repertoires; Baker et al., 1986; for reviews, see Andersson, 1994; Ryan, 1988). This may be the result of females choosing signals of greater energy content, which in turn may imply that females use these signals as indicators of male quality. Indeed, there is evidence that sexual traits function as indicators of indirect genetic benefits for females in terms of good genes (e.g., Alatalo et al., 1998; Hasselquist et al., 1996; Hoikkala et al., 1998; Welch et al., 1998; for review, see Møller and Alatalo, 1999). For example, in *Drosophila montana*, females benefit

in terms of better survival of their offspring by choosing males that produce short signals with a high carrier frequency (Hoikkala et al., 1998). Females may also gain direct benefits from their preference for male sexual traits. For example, in the black horned tree cricket, *Oecanthus nigricornis*, male song correlates with body size and age, and females mating with larger males benefit directly through increased fecundity (Brown et al., 1996).

Studies of spider communication have mainly investigated the role and importance of the substrate-borne vibrations (e.g., Baurect and Barth, 1992; Rovner and Barth, 1981; Schmitt et al., 1993, 1994; Schüch and Barth, 1990). Only a few studies in spiders have even considered airborne acoustic communication (Barth, 1982; Harrison, 1969; Rovner, 1967; Stratton and Uetz, 1981; Uetz and Stratton, 1982). Furthermore, the acoustic signaling of spiders has rarely been studied from the viewpoint of indicator mechanism of sexual selection (studied by us on a single species as an exception; see Alatalo et al., 1998; Kotiaho, 2000; Kotiaho et al., 1996, 1998, 1999; Mappes et al., 1996; Rivero et al., 2000).

In the wolf spider, *Hygrolycosa rubrofasciata* (Ohlert), male sexual display consists of a series of drums produced by striking the abdomen against dry leaves on the ground. The natural habitat of the spider is open bogs and fields, and the signals are audible to humans up to a distance of 10 m. At the time of the mating season, the habitat is covered with layers of dry, deciduous leaves and dry grass. When searching for receptive females, males patrol around the habitat and stop to drum on the dry uppermost leaves on the ground (Kotiaho et al., 2000). In this complex litter habitat, drums travel as vibrations in the substrate but also as audible, airborne vibrations. Airborne and substrate-borne vibrations have basically the same structure and thus in principle convey the same information. In spiders the same sensory organs, slit sensilla, are used to detect both types of vibrations (Foelix, 1996; Hergenröder and Barth, 1983). In addition, spiders

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have sensilla (termed trichobothria) specialized in detecting air movements and low-frequency airborne vibrations (Foelix, 1996). The frequency of the drums range between 1 and 8 kHz, thus being clearly audible for the human ear (Rivero et al., 2000).

A detailed study of the characteristics of the drum of *H. rubrofasciata* males has been made (Rivero et al., 2000). This study identified two main components of the male drum, based on the within- and between-male variability: drum duration and pulse rate. Drum duration is moderately repeatable within males and considerably variable between males, while pulse rate (number of pulses divided by drum duration) is more static, having high repeatability within males but very small variation between the males (Rivero et al., 2000). In addition, drum duration is positively correlated with drumming rate (as number of drums per minute), whereas pulse rate is not (Rivero et al., 2000). Previous studies have shown that drumming rate is highly repeatable and indicates both male phenotypic (Kotiaho, 2000; Kotiaho et al., 1996; Mappes et al., 1996) and genetic quality (Alatalo et al., 1998). Furthermore, there is evidence that females prefer to mate with males of high drumming rate (Kotiaho et al., 1996; Parri et al., 1997).

In this study we first examined the unusually audible spider signal in respect to the mode of the transfer of male signals (substrate-borne versus airborne alone) and female preference. Second and most important, we examined the effect of drum duration and pulse rate on female mate choice using manipulated signals in playbacks. We expected that drum duration, as the more dynamic trait, would be more important for female preference. In particular, we examined the shape of female preference against the size of the male signal. Theoretical models have often assumed gaussian shapes for preferences against male trait (e.g., in the classic Fisherian models; Lande, 1981). However, the shapes of the preference curves have seldom been examined in any previous experiments (but see, e.g., Eiríksson, 1993, 1994; Gerhardt, 1991; Gray and Cade, 1999; Jang and Greenfield, 1996) because typically there has been only one category with increased or reduced ornaments.

METHODS

The species and the signal

The study species *Hygrolycosa rubrofasciata* is a ground-dwelling wolf spider (Lycosidae). Typical habitat of this species is open bogs and meadows where the spider occurs in patchily distributed populations. In southern Finland the mating season begins soon after snowmelt, typically toward the end of April. During this period, males move around the habitat, occasionally stopping to drum. When a male detects a female, he stops and increases his drumming rate. If the female is willing to mate with the male, she responds to the male drum by vibrating her body. This response takes place immediately after the male drum, thus making it easy to determine which male the female responded to. Before the mating the male and the female both produce a few drums while the male approaches the female ("duetting"; Kronstedt, 1996). Female response is essential for the mating to begin. Contrary to other lycosids (for review, see Forster, 1982), the vision of *H. rubrofasciata* is poor, and it is not used in mating (Parri et al., unpublished observations).

Males produce drums by striking their abdomen against dry, deciduous leaves (Kotiaho et al., 2000; Kronstedt, 1984, 1996). Males will also drum on other materials, such as paper (Kronstedt, 1984). In the laboratory, males drum on average 0.8 times/min (SD \pm 0.7, n = 423; Rivero et al., 2000). Each

drum lasts on average 1 s and consists of a series of pulses. Each pulse corresponds to a single strike of the abdomen (Figure 1). The mean pulse rate of the drum is 0.029 pulses/ms (Rivero et al., 2000). The relatively simple structure of the drum gives us an opportunity to manipulate specific characteristics of the drum and to study female preference for these characteristics in detail.

Collecting the spiders from the field

All experiments were conducted using virgin individuals of *H. rubrofasciata*. We collected spiders in late April 1995 and 1996 from two populations, Stormossa and Stenberg, in southern Finland. Spiders were placed individually into small, plastic containers (diam 3.4 cm, height 6.7 cm) with moist moss (*Sphagnum* sp.) to maintain humidity and brought into the laboratory to be weighed. Spiders were maintained in darkness at 4°–8°C to prevent them from reaching full sexual activity. Two or three days before the experiments spiders were taken to the room temperature, 20°–24°C. Spiders were fed fruit flies, *Drosophila* sp.

Mode of signal transfer

In the signal transfer experiment we tested whether the mode of male signal transfer (substrate borne versus airborne alone) affects female preference. The experiment was conducted in two setups on a 30 \times 30 cm arena, the bottom of which was covered with 2.5-cm thick foam. In the first setup (contact setup), a paper cross with four arms of equal length was placed on top of the foam. On each of the arms we marked positions for male cages at distances of 15, 10, and 5 cm from the center. On the center of the cross we marked a position for a female cage. The second setup (no-contact setup) was identical to the first one, except that the paper and the foam under the female cage were cut loose from the rest of the arena. Male and female cages were bottomless, 5.0-cm tall cylinders made out of sheets of clear acetate with a radius of 3.4 cm. In the contact setup, the intact paper cross allowed a direct substrate-borne (and airborne) contact between the female and the males, while in the no-contact setup direct substrate-borne contact did not exist. These two setups were motivated by our observations that typically in the field the leaves on which males drum are not in direct contact with the leaves on which females stand. Although there are two modes of signal transfer, airborne and substrate borne, it is still possible that females receive the signals with the help of the substrate in spite of the airborne transfer. The airborne signals may transfer into the substrate, allowing the ultimate sensory stimulus to be received as substrate borne rather than airborne. Our aim was not to study the mechanisms of receiving the airborne signals by females, but rather to determine whether the mode of signal transfer affects female preference.

Before the experiment we placed male cages at the outermost positions on each of the four arms (i.e., 15 cm away from the center). To stimulate male drumming, a female was placed into each of the male cages for 10 min and removed before the beginning of the trial. After removing the females, males were placed into the male cages. Once each of the males had started to drum, the trial was begun by placing an experimental female into the female cage at the center of the arena. We observed female behavior for 10 min. If the female did not respond during the first 10 min, male cages were carefully moved closer to the female to the distance of 10 cm. If the female did not respond during the next 10 min, we moved the males once more, to 5 cm from the female. If there was no response during the third 10 min, the trial was terminated and discarded. We avoided placing the male at the closest

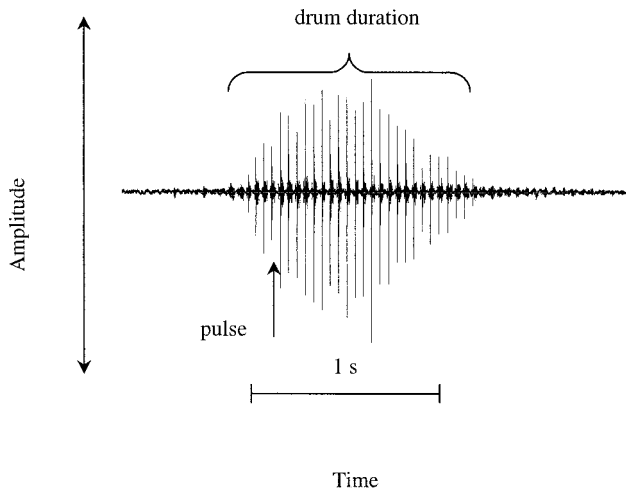


Figure 1
An oscillogram of a *H. rubrofasciata* drumming signal. Each of the pulses refers to one strike of male abdomen on the ground substrate.

distance from the start because preliminary trials had shown us that at short distances females can become overresponsive. Once a female responded, we noted the time of the response, noted to which male the female responded, and ended the trial. The duration of the trials thus varied from a few seconds to 30 min. In occasional cases where there were two males drumming so close in time to each other that it was impossible to determine whom the female responded to, the trial was discarded.

We used males and females from two populations separated by 2 km of forest. Trials were replicated 40 times with Stormossa females (20 contact and 20 no-contact setups) and 40 times with Stenberg females (20 contact and 20 no-contact setups). In each of the trials two of the males came from Stormossa and two from Stenberg. We used each male and each female only once. We compared female responsiveness between the two populations and found no difference in either time until female response (Stormossa: mean \pm SD = 5.24 \pm 7.45 min; Stenberg: 3.70 \pm 4.60 min; Mann-Whitney $Z = 0.24$, $n = 29, 27$, respectively, $p = .807$) or in the proportion of trials where the female responded (Stormossa: 29/40; Stenberg: 27/40; Yates's corrected $\chi^2 = 0.06$, $df = 1$, $n = 80$, $p = .807$). Most important, females did not discriminate between the males from the two populations (Yates's corrected $\chi^2 = 0.50$, $df = 1$, $n = 51$, $p = .478$). For this reason, all subsequent analyses were carried out with data that are pooled over the two populations.

Drum duration

For the drum duration experiment we recorded male drums using a digital recorder (Casio DA-7) attached to a Telinga microphone. For the recordings, males were placed individually in a plastic arena (diam 6.5 cm, height 4 cm) with some dry birch leaves as drumming substrate. For further details on recordings, see Rivero et al. (2000). The recordings were manipulated with sound-editing programs in a computer.

We used a total of 37 drums, each from a different male. Each drum was manipulated into four different durations by decreasing the original duration by 25% (D-25) and 50% (D-50) and by increasing the original duration by 25% (D+25) and 50% (D+50). To maintain the original structure of the drums (Figure 1), we decreased the drum duration by removing every second (D-50) or every fourth pulse (D-25),

taking care that the temporal structure of the drum (i.e., the time between successive pulses) did not change. Similarly, the duration of the drums was increased by duplicating every second (D+50) or every fourth (D+25) pulse. We used the original drum as a control for the manipulated drums. To account for the possible artifacts resulting from removing and adding pulses within the drum, the control drums were also treated by removing pulses and adding them back into their original positions. We used each original drum with its four manipulated variants to create a playback loop on the computer. Thus, each of the 37 loops consisted of 5 drums arranged in random order. The loops were replayed with a repetition rate of 4 drums/min, and each of the loops constituted one replicate.

The loops were replayed with a computer and four loudspeakers (Pioneer TS-F 1665). As a replicate we used a group of females (for groups, see below) that was divided to four loudspeakers and replayed a loop simultaneously. Females were in individual acetate cages described earlier but now with paper bottom, and thus it was possible for two observers (two loudspeakers per observer) to follow the females individually. It was possible to fit five female cages on one loudspeaker. The loops were replayed to groups of females instead of individually to increase the effectiveness of the experimental procedure; it would have been very laborious to replay a loop to each female individually. For results we calculated the proportion of responses given for each drum duration within each female group. These proportions were used in the final analysis. From previous experiments, we know that females are sensitive to the volume of the drums (Parri et al., 1997). Therefore, to elicit responses from as many females as possible and to allow females to compare between the drums, we began each playback session with a low volume. Each loop was replayed three rounds to the group of females at low volume. The volume was then increased and the loop replayed three more rounds. The volume was increased once more so that each group of the females was replayed a total of 45 drums, 15 on each of the 3 volume levels. While replaying the loops to the females we noted to which of the drums each female responded for the first time.

We used the general experimental design described above in two experiments: one with contact-only setup and the other with both contact and no-contact setup. In the contact-only setup, females were placed directly on the loudspeakers. We replayed 11 loops to a group of 16–20 females (4 or 5 females per loudspeaker) using each female only once. These females originated from the Stormossa population. The second setup, contact and no-contact setup, was conducted to determine whether the signal transfer mode (substrate and airborne versus airborne alone) affected female preference for the drum duration. We placed 26 groups of 10 females either directly on the loudspeaker (contact setup) or on a metal grid 3 cm above the loudspeaker (no-contact setup). Each female group was replayed a loop of manipulated drums once on contact and once on no-contact setup. The test was conducted in 2 successive days, and the order of contact and no-contact setups was random. These females originated from the Stenberg population. The size of female groups between the setups (16–20 and 10 females) varied because of the difference in total number of females that were available for the experiments.

We tested whether the females from the two populations differed in their preference for drum duration by comparing the proportion of females, within each replicate, that was responding to each of the drum durations. This comparison was possible to conduct in the contact setups of the above two experiments. To increase the statistical power of the tests, we pooled the proportions of females responding to decreased

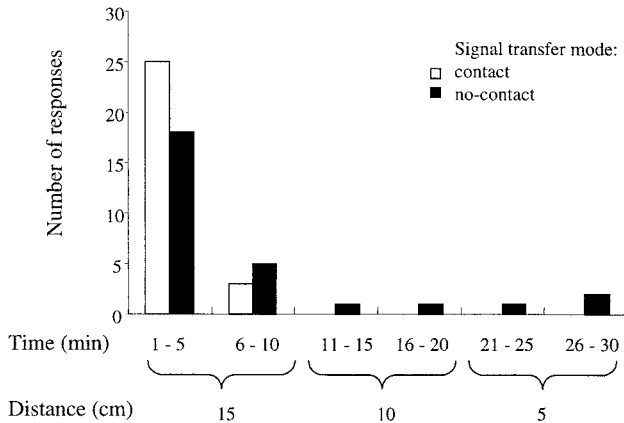


Figure 2
Number of female responses (on the y-axis) on the distance between the males and the female (on the x-axis) in the experiment on the effect of signal transfer mode. On the x-axis there are both the distance of males from the female and the corresponding time from beginning of the trial (15 cm for the first 10 min, 10 cm for 11–20 min, and 5 cm for 21–30 min). The 10-min periods within each distance are further divided into two. In the figure the lighter bars refer to the number of females responding in the contact setup, and the darker bars refer to the no-contact setup (28/39 and 28/41, respectively).

drum duration (D–25 and D–50) and to increased drum duration (D+25 and D+50). There were no differences between the two populations at any of the three drum durations (for decreased drum duration Mann-Whitney $U = 123$, for control drums $U = 109$ and for increased drum duration $U = 126$, for each comparison $n = 11, 26$, respectively; $p > .255$). Thus, for further analysis of the shape of female preference in the contact setup, we pooled the populations.

Pulse rate

We manipulated 15 drums from Stormossa males that were recorded in 1995. The mean (\pm SD) original pulse rate of these drums was 0.028 ± 0.0012 pulses/ms. The mean (\pm SD) pulse rate within the natural population in 1995 was 0.029 ± 0.0017 pulses/ms ($n = 78$) (Rivero et al., 2000). The pulse rate of the drums was either decreased or increased by 10% (P–10 and P+10, respectively) by manipulating the interpulse interval. To retain the original duration of the drums, we either added or removed individual pulses from the drums. We used the original drum as control and manipulated it as above without changing the interpulse interval. Each control drum and its two manipulated forms were used to create a playback loop. In each of the 15 loops, the order of the drums was random, and the drums were repeated at a rate of 4 drums/min. Each loop was replayed simultaneously to a group of 16–20 Stormossa females divided to four loudspeakers. Each group was used as a replicate, and each female was used only once. The playback procedure was identical to the one used in the contact setup of the drum duration experiment. We increased playback volume twice after replaying each loop five times (i.e., always after 15 drums). As in the drum duration experiment, we recorded which drum each female responded to for the first time and calculated the proportion of responses for each manipulation level within each female group. We tested the results of all experiments using nonparametric tests because the assumptions of normality of the data were not met.

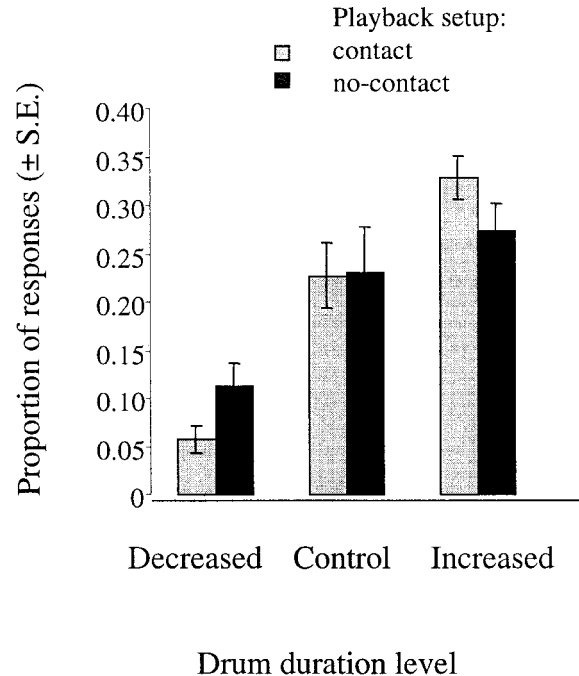


Figure 3
The proportions of female responses to the combined levels of drum duration on the contact (lighter bars) and no-contact (darker bars) playback setup. The data includes 26 groups of Stenberg females in both setups.

RESULTS

Mode of signal transfer

The proportion of the trials where the female responded to drums did not differ between the contact and no-contact setups (28/39 and 28/41, respectively; Yates's corrected $\chi^2 = 0.01$, $n = 80$, $p = .922$). However, the time until the female responded was significantly shorter in the contact than in the no-contact setup (mean \pm SD = 2.18 ± 2.13 and 6.79 ± 7.80 min, respectively; Mann-Whitney $z = 2.82$, $n = 28$ for both setups, $p = .005$). In the contact setup, all females responded to a male already from the longest distance (15 cm). In the no-contact setup, 23 females out of the 28 responded from 15 cm, while for the other females, males needed to be moved within 10 or even 5 cm from the female (Figure 2).

Drum duration

First, to test female preference for drum durations as effectively as possible, we collapsed the five levels of drum durations into three levels by pooling the female responses to the two decreased drum durations and by pooling the female responses to the two increased drum durations. This was done by using means of each combined group. The proportion of the responses given in the contact setup differed significantly between the three durations (Friedman $\chi^2 = 28.93$, $df = 2$, $n = 26$, $p < .001$, Figure 3). Females preferred the original duration over the decreased ones (Wilcoxon $z = 3.56$, $n = 26$, $p < .001$, probability level is adjusted for multiple comparisons with sequential Bonferroni correction [Rice, 1989]), and there was also a tendency for preference for increased duration over the original duration (Wilcoxon $z = 1.89$, $n = 26$, $p = .059$, probability level is adjusted for multiple comparisons with sequential Bonferroni correction). The difference between decreased and increased drum durations was significant (Wilcoxon $z = 4.34$, $n = 26$, $p < .001$, probability

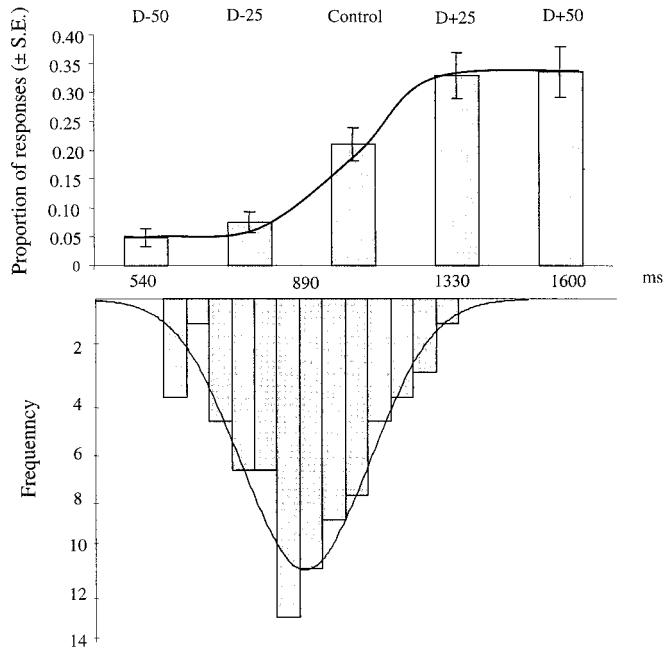


Figure 4
The proportion of female responses to the five manipulation levels of drum duration in the contact setup (upper part of the figure) and the natural range of signal duration within Stormossa population (the lower part of the figure). The control level of manipulation is positioned on the population mean. The cubic regression curve of female preference calculated from the results of the playback is drawn over the female preference bars. The playback result includes both female populations (11 groups of Stormossa and 26 groups of Stenberg females).

level is adjusted for multiple comparisons with sequential Bonferroni correction; Figure 3).

There was also a significant difference between female preference for drum durations in the no-contact setup (Friedman $\chi^2 = 7.86$, $df = 2$, $p = .020$, Figure 3). A posteriori test revealed that the proportion of responses differed significantly between decreased and increased durations (Wilcoxon $z = 2.77$, $n = 26$, $p < .018$, probability level is adjusted for multiple comparisons with sequential Bonferroni correction; Figure 3), but not between decreased and original or original and increased durations (Wilcoxon $z = 1.69$, $n = 26$, $p = .184$, and $z = 0.61$, $n = 26$, $p = .543$, respectively, probability levels are adjusted for multiple comparisons with sequential Bonferroni correction).

To test for female preference between the contact and no-contact setups, we calculated an average duration to which each of the female groups responded. This was done by assigning a value of 0.5 for each response to decreased drum duration, 1 for each response to control drum and 1.5 for each response to increased drum duration. The resulting mean durations were tested with a rank order test. There was no significant difference in female preference for drum duration between the contact and no-contact setups (Wilcoxon $z = 1.59$, $n = 26$, $p = .113$). Nevertheless, in the contact setup drums elicited female responses sooner than in the no-contact setup (mean number of drums before response \pm SD = 14.90 ± 6.10 , and 25.41 ± 6.69 , respectively; $n = 26$, Wilcoxon $z = -3.92$, $p < .001$ [as the drums were replayed in regular intervals of 15 s the number of the drums before response is equivalent to the time until response]). Thus, the mode of the signal transfer had no effect on the female pref-

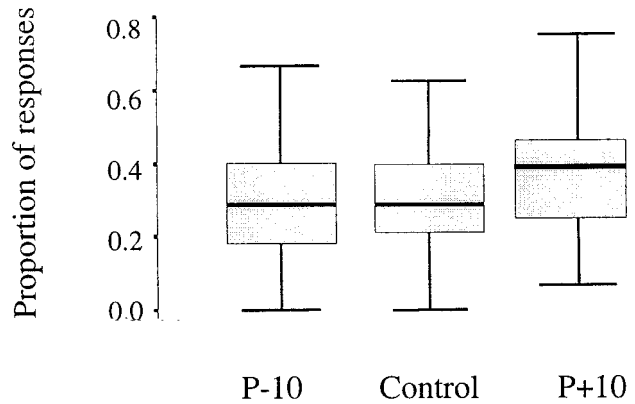


Figure 5
The proportions of female responses to the three levels of pulse rate manipulation (mean and the range). There were 15 groups of Stormossa females in the experiment.

erence for drum duration, but it affected the timing of the response.

Finally, to study the selection that female preference imposes on drum duration, we applied a curve-fitting analysis to the data from the contact setup of the drum duration experiments. The best fit to the data was given by a cubic regression ($r^2 = .29$, $F_{3,181} = 24.84$, $p < .001$; $b_1 = -3.59 \pm 1.59$, $t = -2.25$, $p < .026$; $b_2 = 4.22 \pm 1.70$, $t = 2.49$, $p < .014$; $b_3 = -1.41 \pm 0.56$, $t = -2.51$, $p < .013$). The cubic function is depicted in Figure 4 over the bars of the proportion of responses on each drum duration. Below the bars is the distribution of drum durations drawn from the field population in the same year (mean \pm SD = 981.4 ± 140.6 ms, range = $681.0\text{--}1329.7$, $n = 78$; Rivero et al., 2000). The mean duration of the drums that were used for the manipulation was 1077.5 ± 184.8 (SD) ms ($n = 37$). By comparing the female preference function to the distribution of drum durations drawn from the field population, it can be concluded that female preference is for greater than the natural mean drum duration. However, the preference is not completely open-ended, but instead the preference for even longer drums levels off after about 25% increase in drum duration.

Pulse rate

The pulse rate manipulation had no effect on female preference (Friedman $\chi^2 = 0.79$, $df = 2$, $p = .673$; Figure 5). To further compare female preference for the pulse rate as powerfully as possible, we scored every response given to the decreased pulse rate with a negative value (-1), and every response given to the increased pulse rate with a positive value (+1). Using the scores calculated for each loop separately, we calculated the mean direction for female preference within each trial. Mean directions were then compared against zero (i.e., the situation where there is no directional selection by the females). Comparison indicated that there was no directional female preference for pulse rate (mean of all the trials \pm SD = 0.034 ± 0.048 , Wilcoxon $T = 39$, $n = 14$, $p = .320$).

DISCUSSION

In the first experiment with live males, we found that signal transfer mode had an effect on female responsiveness such that females responded sooner in the contact setup than in the no-contact setup. The playback experiment on drum durations rendered the same result: females in the contact setup responded sooner than females in the no-contact setup. How-

ever, despite the delayed response in no-contact setup, the mode of signal transfer did not alter female preference for the duration of drums. In other words, when the signal is transferred only via the air, it takes longer for the female to choose between the signals, but the final preference for the signal type does not change. It is likely that the contact setups elicited faster responses from the females because the information content of the drum is more effectively transferred when in direct contact to the source of the signal. This result parallels the one found earlier with manipulations of signal volume; females respond sooner to signals replayed at higher volumes (Parri et al., 1997).

The experiment on signal duration revealed that females of *H. rubrofasciata* prefer increased drum duration over the decreased drum duration. In general, signal duration is often found to be under directional sexual selection by the females (but see also Butlin et al., 1985; Eiriksson, 1993). For example, females of the field cricket *Gryllus integer* use calling bout duration as a criterion in their mate choice, and females predominantly choose calls of greater duration (Hedrick, 1986). Another example is the lesser wax moth *Achroia grisella*, in which females choose pulse durations over the population mean (Jang and Greenfield, 1996).

Honest signaling theories of sexual selection (see, e.g., Andersson, 1994; Grafen, 1990; Johnstone, 1995) suggest that females could use the magnitude of male advertisement as an indicator of male phenotypic or genetic quality. According to this theory, females may be expected to show preference for greater magnitudes of male signals because males of poor quality cannot afford to have or maintain signals of relatively great magnitude. Such female preference may lead to an open-ended directional selection for the greater magnitude of male sexual traits.

We found that females preferred the increased drum durations, which were clearly greater than the natural population mean. In fact, female preference increased steeply with drum duration across the natural range of drum duration variation. An asymptotic level of female preference was approached after a 25% increase in drum duration. Only few natural drums reach the duration of this magnitude. Thus, it seems that females do not exhibit an open-ended preference for supernormal stimuli, but the preference levels off with the natural signals of greatest duration. Because drumming is energetically very expensive to males (Kotiaho et al., 1998), the benefits for males of using very long drums must decline steeply with drum duration.

Earlier, we found that drum duration shows high variability between males (CVs 14–30%) and high repeatability within males (0.55–0.66; Rivero et al., 2000). In addition, drum duration is correlated with another key component of the male's sexual advertisement, its drumming rate (Rivero et al., 2000). In other studies we found that females of *H. rubrofasciata* prefer high drumming rate (Kotiaho et al., 1996; Parri et al., 1997), which is an honest indicator of male phenotypic but also of heritable genetic quality (Alatalo et al., 1998; Kotiaho, 2000; Mappes et al., 1996). Thus, it is likely that females gain information about male quality via drum duration, explaining the strong directional female preference for higher drum durations.

Pulse rate manipulation did not affect female preference. In a previous study, we found that between-male variability for pulse rate was low (CV 5–7%), while within-male repeatability was relatively high (0.62–0.84; Rivero et al., 2000). Because quality indicator traits that are under directional female preference generally show both high variability within but also between males (Pomiankowski and Møller, 1995), it is plausible that pulse rate with low variability between males is not an important indicator trait. In several other studies, pulse

rate of male signals has been found to be under stabilizing rather than directional selection. For example, in a playback experiment with synthetic advertisements calls females of the natterjack toad *Bufo calamita* showed preference for the intermediate pulse rate (Arak, 1988; see also Gray and Cade, 1999).

Typically, indicator traits that honestly reflect male quality incur costs to the bearer of the trait. Several studies indicate that acoustic calls are among the most energetically demanding male sexual traits (e.g., Kotiaho, 2001; Prestwich, 1994; Vehrencamp et al., 1989). Indeed, there is some evidence that the energy requirements of signaling and male attractiveness to females might be correlated with each other: In the wax moth *Achroia grisella*, energy expenditure in signaling was highest in most attractive males (Reinhold et al., 1998). In *H. rubrofasciata*, energy consumption of drumming is, on average, 22 times higher than the energy consumption during resting (Kotiaho et al., 1998). Although the relative energy contents of drums of varying durations have not been investigated, it is likely that drums of longer duration involving a larger number of pulses are energetically more demanding to produce and thus more costly.

In conclusion, signal transfer mode had an effect on female responsiveness such that females responded sooner in the contact setup than in the no-contact setup. However, mode of signal transfer did not alter female preference for the duration of drums. Pulse rate of the drums did not affect female preference. Females did, however, show clear preference for signal duration greater than its natural mean. Because females prefer to mate with high-drumming-rate males who are in better phenotypic condition and drumming rate is correlated with signal duration, it may be that females of *H. rubrofasciata* are able to use male signal duration as an indicator of male quality. It is interesting that female preference was not entirely open ended but leveled off after signal durations above natural variation.

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