Acoustic signalling in a wolf spider: can signal characteristics predict male quality?

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While there has been considerable interest in female choice for male sexual signals, there have been few studies of the underlying information that different aspects of the signal calls convey. Such studies, however, are essential to understand the significance of signals as honest handicaps, arbitrary Fisherian traits and/or in species recognition. We studied the somewhat exceptional system of audible drumming in the wolf spider, *Hygrolycosa rubrofasciata*. We estimated the repeatabilities of signal components, the levels of between-male variance, the symmetry of the signal, the correlations between different aspects of drumming and their correlations with body weight. While in other taxa the frequency of audible signals may convey honest information of male size, in this species signal frequency was not related to male size and had a low repeatability. The pulse rate within each drum was highly repeatable but had a relatively small between-male coefficient of variation. In previous studies on this species, these traits were not important for male mating success. Among the traits directionally preferred by females, signal volume had considerable repeatability. Signal length was repeatable with high variability between males. In one population, signal length and volume were positively correlated with the rate at which males produced the drumming signals, a trait essential for male mating success. Thus, while signal length may reliably indicate male quality, other signal characteristics such as peak frequency and symmetry were not repeatable or were static and not related to any other male traits.

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Sexual selection has produced highly variable types of signals for mate attraction (Andersson 1994). Two rival hypotheses are currently emphasized as an explanation of female choice for male sexual signals. They may represent arbitrary aesthetic traits as initially envisioned by Fisher (1930; see also Kirkpatrick 1982; Pomiankowski et al. 1991) or they may be indicators of male condition (Zahavi 1975; Grafen 1990; Iwasa et al. 1991). There is, however, an alternative possibility: that the signals are under stabilizing selection and act merely as traits for species recognition (Ryan & Rand 1993). The latter hypothesis has influenced many of the earlier studies in sexual selection and is partly linked with the Fisherian hypothesis (see Lande 1981; Iwasa & Pomiankowski 1995).

Female choice has been studied across many taxa and acoustic signals are among the most commonly studied

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sexual traits (see e.g. Andersson 1994). However, further information about signal components, their repeatabilities, variabilities and correlates is needed to understand the roles of the signals involved in sexual communication. If male signals act as viability indicators, we would expect them to be both positively correlated with other fitness-related traits and highly variable in the level of expression between males (Alatalo et al. 1988; Pomiankowski & Møller 1995; Rowe & Houle 1996). In contrast, Fisherian traits are not expected to be variable and, owing to their arbitrary nature, correlations with other traits are unlikely. Gerhardt (1991) used a similar framework in his division of call characteristics of frogs into static (highly stereotyped within and between males) and dynamic (highly variable) properties. He suggested, with evidence from treefrogs, that static properties are under stabilizing or weakly directional female preferences, while dynamic properties are strongly directionally preferred by females (see also Castellano & Ciacoma 1998).

Sounds are commonly used in sexual signalling across many animal taxa. In many anurans, calls are under female choice and the dominant frequency often reveals male size (see Andersson 1994 for a review). Nevertheless,

research on frogs and toads has focused on the role of call properties in species recognition (Gerhardt 1988, 1991; Ryan & Rand 1993). In birds the focus has been on song repertoire, the size of which may indicate male condition (e.g. Lampe & Espmark 1994) and to some degree even heritable viability (Hasselquist et al. 1996). Among insects the main emphases have been in identifying species recognition and signal variability between species (e.g. Butlin et al. 1985; Eiríksson 1993; Charalambous et al. 1994; Ritchie et al. 1994) and the directional female preferences for signal properties (Hedrick 1986; Simmons 1988; Bailey et al. 1990; Tuckerman et al. 1993; Aspi & Hoikkala 1995; Jang & Greenfield 1996). In *Drosophila montana* and *D. littoralis,* for example, the signal components targeted by females are highly repeatable and vary considerably between males (Hoikkala & Isoherranen 1997). In many orthopterans call properties (frequency, intensity and phrase number) are related to male size (Bailey 1985; Simmons 1988; Tuckerman et al. 1993; Brown et al. 1996) but not in all species (for reviews, see Andersson 1994; Zuk & Simmons 1997).

Many spiders use substrate-borne vibrations, presumably for species recognition (Rovner & Barth 1981; Schüch & Barth 1990; Barth & Schmitt 1991; Schmitt et al. 1993, 1994; Fernandez-Montraveta & Schmitt 1994). In the wolf spider *Hygrolycosa rubrofasciata* (Lycosidae (Ohlert)), the drumming signal is transmitted through both the substrate and the air (S. Parri, R. V. Alatalo, J. S. Kotiaho, J. Mappes & A. Rivero, unpublished data), being loud enough to be clearly audible to the human ear (Kronestedt 1984, 1996). Drumming rate (drumming signals per unit time) is highly repeatable within each male and also variable between males. It is significantly dependent on male condition (Mappes et al. 1996) and females appear to prefer males with the highest drumming rate (Kotiaho et al. 1996; Parri et al. 1997). The drumming rate might thus act as a handicap, particularly as the signals are costly to produce (Mappes et al. 1996; Kotiaho et al. 1998a). Playback experiments have confirmed that females prefer actively drumming males (Kotiaho et al. 1996; Parri et al. 1997), pulses of high volume (Parri et al. 1997) and relatively long signals, while pulse rate is not important in female choice (S. Parri, R. V. Alatalo, J. S. Kotiaho, J. Mappes & A. Rivero, unpublished data).

We studied the drums of *H. rubrofasciata* males, analysing the repeatabilities, between-male variabilities and correlations between the different components of the signal. In addition, we searched for associations between these components and male size and drumming rate. Any aspects of the drum that are not repeatable within the male are unlikely to be important in sexual selection. If signal components are repeatable, highly variable between males and correlated with the drumming rate they may convey information about male condition. Repeatable but less variable components might serve for species recognition purposes and/or be a Fisherian type of trait. Our previous experiments allowed us to predict that signal length and volume would be of the former type, and pulse rate of the latter (Parri et al. 1997; S. Parri, R. V. Alatalo, J. S. Kotiaho, J. Mappes & A. Rivero, unpublished data). We also analysed the asymmetry of the pulse characteristics over the signal to see whether the males differ in how they maintain the signal characteristics within each signal.

METHODS

Study Species

Hygrolycosa rubrofasciata inhabits open bogs and meadows. The sexual display of males consists of a series of drums produced by hitting the abdomen against the substrate. In the field these sounds are produced against dry deciduous leaves. During the mating season, which in southern Finland begins after snowmelt in late April, males move around the habitat searching for receptive females, which are more stationary than the males. When a male discovers a female, he stops nearby and increases his drumming rate. If the female is sexually receptive, she responds to the male by producing similar but less intense vibrations with her body. Before copulation, male and female exchange a few further drums ('duetting', see Kronestedt 1996). Females choose the most actively drumming males as mates and drumming rate reflects male viability (Kotiaho et al. 1996; Mappes et al. 1996). Male size, on the other hand, does not influence female preferences in this species, although there is evidence that it confers advantages in male–male competition (Kotiaho et al. 1996, 1997) and a survival benefit at times of stress (Mappes et al. 1996).

Male Collection and Recordings

Spiders were collected after snowmelt in 1995 and 1996 from two sites in Sipoo, southern Finland, located 2 km from each other but differing in the type of habitat: Stormossa (a bog) and Stenberg (a meadow). Males were immediately transported to the laboratory where they were weighed to the nearest 0.1 mg and placed individually in plastic film containers, the bottom of which had been covered with moss (*Sphagnum* sp.) to ensure constant humidity. As male weight is highly repeatable in this species (Kotiaho et al. 1996), we used it as a measure of male size. All males were kept individually in a refrigerator at 5–6°C and fed fruit flies until drumming rate measurements and drum recordings were made.

In 1995 we obtained drumming rates by placing the males individually in plastic boxes (8 × 10 × 11 cm), each containing three or four dry birch leaves. Males were kept at room temperature (ca. 22 ± 2°C) for 1 h before the data were collected. We counted the number of drums produced by each male for five 2-min periods over 2 h, on 2 consecutive days. From these observations we calculated the mean drumming rate (drums/min) for each male. To calculate the repeatability of drumming rate (intraclass correlation coefficient, Lessells & Boag 1987) on consecutive days, we used the male drumming rate estimates for each day. In 1996 we used a similar method to measure male drumming rate but we counted the signals for three 2-min periods on 2 consecutive days. There is thus a
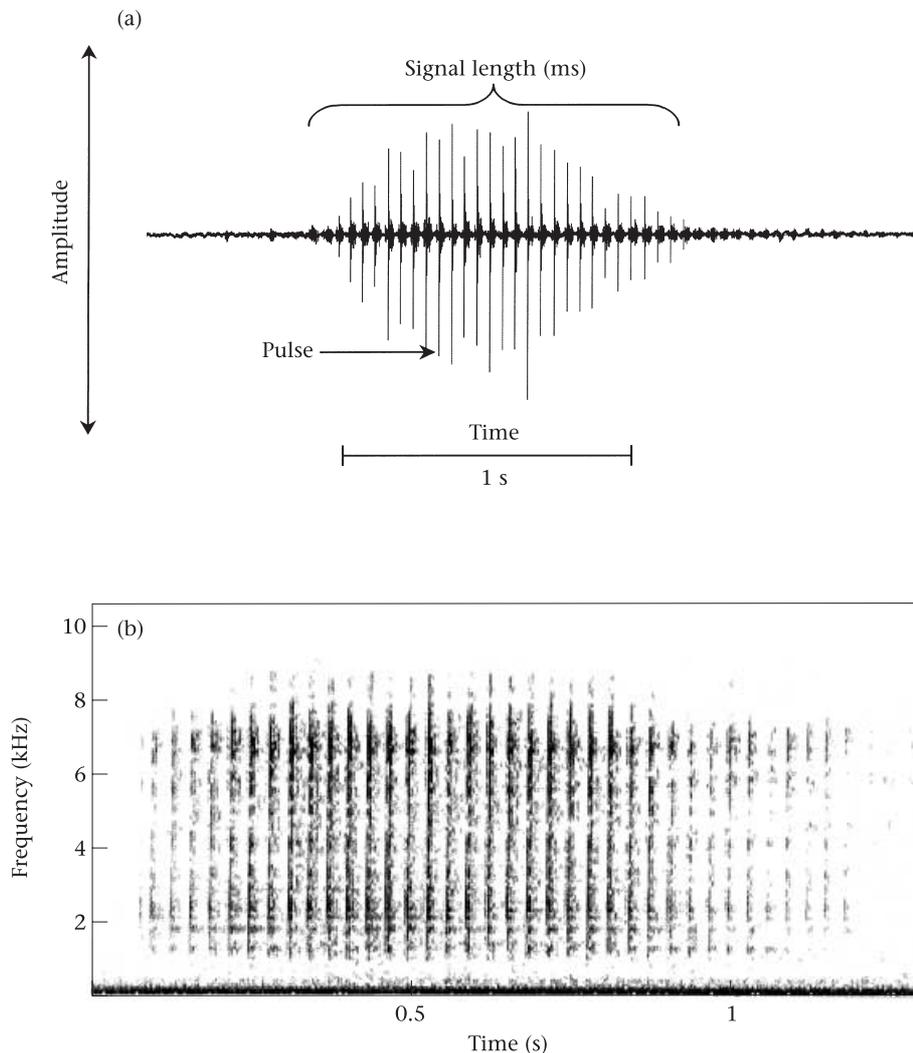
(a)

(b)

Figure 1. (a) An oscillogram and (b) a spectrogram of a typical drumming signal of *Hygrolycosa rubrofasciata*. In (a) each vertical line corresponds to one pulse, which is produced by a single hit of the male's abdomen against the substrate.

difference in the time each male was observed each day (10 min in 1995 and 6 min in 1996) which may affect the accuracy of the repeatability estimates.

For the signal recordings in 1995, Stormossa males (*N*=78) were placed individually in plastic containers (4 cm high, 8 cm in diameter) with two or three dry birch leaves. For recordings we used a digital recorder (Casio DA-7) attached to a Telinga microphone. Males were kept in the recording containers until they had produced a minimum of three drums against the dry leaves. In 1996 the drumming substrate was standardized to reduce variation in the drums from the uneven leaf substrate. We used new containers that consisted of a cylinder of plastic acetate (6 cm high, 3 cm in diameter) to the bottom of which a small square of paper (3.5 × 3.5 cm) was glued. In each recording session 10 cylinders, each containing a male, were arranged around a circle (inner diameter 35 cm). The microphone was hung in the middle of the circle, 35 cm above the males. Males were kept in the cylinders until they had produced three drums, at which point they were replaced by a new male. We used a Sony

TCD-D7 recorder attached to a Telinga microphone and recorded 207 males from Stormossa and 104 males from Stenberg.

Signal Analysis

For signal analysis, we used a sound-analysing computer program (Canary 1.2, Cornell Bioacoustics Workstation, Ithaca, New York, U.S.A.). The drums of *H. rubrofasciata* consist of a series of equally spaced pulses increasing in amplitude towards the middle and decreasing again towards the end (Fig. 1a), with a frequency band that varies broadly between 1 and 8 kHz (Fig. 1b). For each signal, an oscillogram (amplitude versus time) and a spectrogram (frequency versus time) were created. Several components of the 1995 males' signals were thus analysed in detail: signal length (total duration (ms) of the signal), pulse rate (number of pulses divided by signal length); and peak frequency (the frequency (Hz) at which the highest amplitude occurred). The latter has also been

Table 1. Analysis of drums from recordings of Stormossa males in 1995

	$\bar{X}\pm SD$	CV (%)	Repeatability$\pm$SE
Traits			
Drumming rate (drums/min)	0.79±0.65	82.4	0.48±0.05**
Length (ms)	981.40±140.63	14.3	0.55±0.06**
Pulse rate (pulses/ms)	0.029±0.002	5.1	0.84±0.03**
Peak frequency (kHz)	5.29±0.91	17.2	0.15±0.07*
Signal shape (relative peak time)	0.38±0.08	19.9	0.09±0.07
Trait variation (sections III–I)			
Pulse rate (pulses/ms)	−0.001±0.009**	3.1	0.63±0.07**
I section	0.029		
II section	0.029		
III section	0.029		
Average volume (dB)	−3.4±1.37**	7.1	0.32±0.07**
I section	−34.2		
II section	−33.1		
III section	−37.6		
Peak frequency (kHz)	−0.30±0.94**	17.7	0.09±0.07
I section	5.51		
II section	5.18		
III section	4.85		

Means±SD, coefficients of variation, CV (Sokal & Rohlf 1981), and repeatabilities (Lessells & Boag 1987) for each of the signal components (traits) and for the change in signal components between the first and last segments of the signal (trait variation). N=78 except for drumming rate for which N=423 males. Asterisks symbolize significant values in the one-way ANOVAS used to calculate the repeatabilities (df=77, 233, except for drumming rate where df=1, 422). The significance of trait variation was tested with a repeated measures ANOVA. SE of repeatabilities was calculated after Becker (1984).
*P<0.05; **P<0.001.

referred to as fundamental frequency (e.g. Simmons 1988).

To analyse the shape of the signals and the temporal change within them, we divided each drum into three equal-time segments. For each segment we calculated pulse rate (from five randomly chosen successive pulses), peak frequency and volume (the average intensity of the segment in dB, standard reference pressure level of air taken as 20 µPa). For each of these signal characteristics, we calculated the temporal change in the signal by subtracting the values for the third and first segments of the drum. Calculation of the peak time, that is, the section of the signal at which the maximum intensity occurs, allowed us to estimate the shape of the drum ((peak time/signal length) × 100), that is whether the signal was skewed to the right (<50%), symmetrical ($\simeq$50%) or skewed to the left (>50%).

From the detailed analysis of the signal carried out in 1995 we could identify potentially important signal components for mate choice on the basis of the between- and within-male variability. We reanalysed these components, signal length and pulse rate, in 1996 with a larger number of males. In addition, standardizing the drumming substrate by replacing the leaves by a sheet of paper allowed us to compare signal volumes between males.

In both years, we calculated (1) the repeatability (Lessells & Boag 1987) of each of the signal components as a measure of within-male variability and (2) the coefficient of variation (CV=(SD/mean) × 100) as an index of between-male variability.

RESULTS

Signal Description

A typical drumming bout lasted ca. 1 s with an average of 29 separate pulses. Signal length and pulse rate were highly repeatable within males (Table 1). The highest within-male repeatability, for pulse rate, was accompanied by the lowest between-male variability. Peak frequency, on the other hand, showed low repeatability and a relatively high coefficient of variation (Table 1). This is expected when, as in this case, the frequency of a signal depends on the nature of the substratum against which the drums are produced. Furthermore, peak frequency was independent of male size (Spearman correlation: r_S= 0.048, N=78, NS). All three of the signal components decreased significantly towards the end of the signal (repeated measures ANOVA: pulse rate: $F_{2,154}$=40.94, P<0.001; signal volume: $F_{2,154}$=611.45, P<0.001; peak frequency: $F_{2,154}$=17.1, P<0.001). The maximum volume intensity appeared between the first and second thirds of the signal, which was therefore right skewed, although the repeatability of signal shape was very low (Table 1).

All the correlations between the signal components in 1995 were close to zero (Table 2). There was a weak relationship between signal shape and the temporal change in signal volume, which is by definition expected. There was also a slight, negative correlation between length and pulse rate; longer signals were less 'dense'. However, the power of the tests is low because of the multiple comparisons.

Table 2. Spearman coefficients of correlation for the signal components and the temporal changes in the signal, in 1995

	PR	PKF	Shape	PR	PKF	Volume
				Temporal changes in signal		
Length	−0.33*	+0.14	−0.17	−0.14	+0.14	−0.21
Pulse rate (PR)	—	−0.02	−0.05	+0.17	−0.12	+0.06
Peak frequency (PKF)	—	—	+0.12	+0.07	−0.18	+0.10
Signal shape	—	—	—	+0.04	+0.07	+0.26*
PR change	—	—	—	—	+0.04	+0.06
PKF change	—	—	—	—	—	+0.13

Sequential tablewise Bonferroni correction (Rice 1989) at 0.05 significance level applied to the coefficients. Stormossa population: $N=78$.
*$P<0.05$.

Table 3. Analysis of drums from recordings of Stormossa and Stenberg males in 1996

	Stormossa			Stenberg		
	$\bar{X}\pm$SD	CV (%)	Repeatabilities±SE	$\bar{X}\pm$SD	CV (%)	Repeatabilities±SE
Drumming rate (drums/min)	0.43±0.44	97.0	0.45±0.05*	0.44±0.39	90.0	0.21±0.05*
Length (ms)	773.03±230.04	29.8	0.62±0.03*	789.52±238.62	30.2	0.66±0.05*
Pulse rate (pulses/ms)	0.030±0.002	7.7	0.75±0.03*	0.030±0.002	6.5	0.68±0.04*
Volume (dB)	−24.02±3.81		0.49±0.04*	−24.15±3.73		0.55±0.05*

Means±SD, coefficients of variation, CV, and repeatabilities for each of the signal components. The relative nature of decibels did not allow the calculation of CVs for volume. Asterisks symbolize significant values in one-way ANOVAS used to calculate the repeatabilities (Stormossa: $df=206, 616, N=207$; Stenberg: $df=103, 304, N=104$ except for drumming rate, where $df=410$ for Stormossa and 320 for Stenberg). SE of repeatabilities was calculated after Becker (1984).
*$P<0.001$.

Signal Characteristics and Male Quality

From the 1995 analysis we identified three signal components with high repeatabilities that may be indicative of male condition: signal length, pulse rate and volume (although the latter could not be standardized in 1995). Pulse rate and pulse rate change, in contrast, were less variable than volume or signal length (Table 1). To examine these traits further, we compared male size and drumming rate with several signal characteristics. For this, purpose we used the larger data set from 1996.

The characteristics of the signal differed between the two data sets recorded with slightly different set-ups (see Methods). In 1996 signals were shorter with a higher pulse rate than in 1995 (Tables 1, 3; Mann-Whitney test: signal length: $Z=7.19, N_1=78, N_2=207, P<0.001$; pulse rate: $Z=4.05, N_1=78, N_2=207, P=0.001$). In both years, however, high repeatabilities for pulse rate were associated with the lowest coefficients of variation (Tables 1, 3). Repeatability of signal length was also high in 1996, although its coefficient of variation was considerably higher than in 1995. As mentioned above, in 1996, the standardization of the recording conditions permitted a comparison of overall signal volume across the males. In both populations, the average signal volume was highly repeatable (Table 3). Drumming rate was also repeatable within males although there was a difference between populations (Table 3).

In 1996, the relationship between signal length and pulse rate was nonsignificant, and the correlation coefficients were considerably smaller than in 1995, despite the larger sample size (Table 4). A comparison of overall signal volume across the males revealed a significant positive correlation between signal length and volume: in both populations longer signals were louder. In Stormossa males, there was a nonsignificant positive relationship between pulse rate and signal volume, suggesting that louder signals had a higher pulse rate, but in Stenberg this correlation was negative.

Stormossa males were significantly larger than Stenberg males (Stormossa: $\bar{X}\pm$SD$=17.66\pm0.55$ mg, $N=207$; Stenberg: 15.29 ± 2.28 mg, $N=104$; Mann-Whitney test: $Z=6.98, P<0.001$). The average drumming rates of the

Table 4. Spearman's coefficients of correlation for the different components of the male's signal for both populations in 1996

	Pulse rate		Volume	
	Stormossa	Stenberg	Stormossa	Stenberg
Length	−0.11	−0.08	0.44**	0.32*
Pulse rate	—	—	0.17	−0.10

Sequential tablewise Bonferroni correction at 0.05 significance level applied to the coefficients. Stormossa: $N=207$; Stenberg: $N=104$.
*$P<0.05$; **$P<0.001$.

Table 5. Spearman coefficients of correlation between male characteristics and signal components in 1996

	Length		Pulse rate		Volume	
	Stormossa	Stenberg	Stormossa	Stenberg	Stormossa	Stenberg
Drumming rate	0.33**	0.35**	−0.11	−0.11	0.22*	−0.04
Weight	0.06	0.01	0.08	0.13	0.26*	0.10

Sequential tablewise Bonferroni correction at 0.05 significance level applied to the coefficients. Stormossa: $N=207$; Stenberg: $N=104$.
*$P<0.01$; **$P<0.001$.

males from the two populations, however, did not differ from each other (Table 3; Mann-Whitney test: $Z=1.45$, $P=0.146$). There was a significant positive correlation between male drumming rate and signal length for both populations (Table 5). In Stormossa males, higher drumming rates were also positively correlated with louder signals. Weight, on the other hand, did not correlate with signal length but was positively correlated with signal volume in Stormossa males.

DISCUSSION

The properties of the drumming signal in *H. rubrofasciata* fall into three categories. First, pulse rate and pulse rate change were static (CV 3–8%), and were highly repeatable within males (0.63–0.84). Thus, individual males differed consistently from each other, but the relative differences between males were small. Second, signal length was both highly variable between males (CV 14–30%) and repeatable for individuals (0.55–0.66). Average volume was equally repeatable (0.49, 0.55), but the relative index in decibels did not allow calculation of CVs. Average volume change within the signals was an intermediate trait, with some repeatability (0.32). Third, there were properties of the signal, such as peak frequency, signal shape and peak frequency change that were dynamic with high CVs (17–20%), and with little or no repeatability (0.09–0.15).

Traits that are not repeatable within individuals are unlikely to be important in sexual selection, since the inconsistent signal would not allow any sexual selection to take place. Compared with the sound-signalling systems of many other animal groups, the acoustic signals of *H. rubrofasciata* are relatively simple in structure. Furthermore, the signal requires the external substrate of dry leaves, which may explain the great variability in peak frequency with highly variable peaks over the range 1–8 kHz. In wandering spiders, however, fundamental frequency is important, since females respond to their species-typical frequencies in a stabilizing manner (Schüch & Barth 1985, 1990).

The pulse rate within drums was highly repeatable, even though differences between males were small. In a playback experiment we found that females do not discriminate between signals based on pulse rate within the range of its natural variation (S. Parri, R. V. Alatalo, J. S. Kotiaho, J. Mappes & A. Rivero, unpublished data). It may be that pulse rate serves some function in species recog-

nition, but the female preferences are not very specific, allowing the differences between males to be highly repeatable without any major evolutionary consequences. Pulse rate might be expected to be sensitive to male condition, since one would expect denser pulses to be energetically more demanding. However, directional preferences for denser pulses have not been reported, while stabilizing selection has frequently been implied in spiders (Schüch & Barth 1985, 1990), insects (Ritchie et al. 1994) and amphibians (Klump & Gerhardt 1987; Sullivan & Leek 1987; Gerhardt 1991). Thus, pulse rate might serve a general function in species recognition, suggesting that other traits such as signalling rate may provide more honest signals of male condition (see Mappes et al. 1996). In *H. rubrofasciata*, pulse rate was not related to male mass or drumming rate, even though there was a tendency for a negative correlation between pulse rate and signal length, suggesting a possible trade-off against a trait that is under directional female preference. Pulse rate change was highly repeatable, but again it was not correlated either with male drumming rate (Spearman correlation: $r_S=-0.12$, $N=71$, NS) or male body mass ($r_S=0.11$, $N=78$, NS).

Playback experiments have confirmed that, even though drumming rate itself is probably an important determinant of male mating success (Parri et al. 1997), females are more likely to respond to loud and long signals (Parri et al. 1997; S. Parri, R. V. Alatalo, J. S. Kotiaho, J. Mappes & A. Rivero, unpublished data). Signal length was positively related to male drumming rate. It was also highly repeatable, and varied between males, as is the case for many male ornaments (see Alatalo et al. 1988; Pomiankowski & Møller 1995; Rowe & Houle 1996). This suggests that it may provide consistent information about male quality. Volume also has some features consistent with a handicap, but its association with drumming rate is weak and its repeatability is low. Loudness of the signal is confounded by proximity of the male and substrate type thus making it unlikely to carry reliable information about male quality.

In some taxa, such as frogs (see Andersson 1994) and some orthopterans (Bailey 1985; Simmons 1988; Tuckerman et al. 1993; Brown et al. 1996), signal properties have been associated with body size. In one of the two populations we studied, volume was weakly correlated with male size, with larger males having louder signals. Overall, however, the signal was not particularly informative of male size and there is no strong

association between male size and drumming rate itself (Kotiaho et al. 1996, 1999a). Body mass of mature males is highly repeatable during the mating season (0.99, Kotiaho et al. 1996, 1999a) and highly variable (CV 14.9–17.6% in the three samples used here), but we have no evidence that larger males have higher mating success (Kotiaho et al. 1996), even if very large males have a good chance of winning male–male combats (Kotiaho et al. 1997, 1999b). It seems that in the mating system of *H. rubrofasciata*, where males move around signalling for any responsive females, male size does not increase the chances of obtaining matings.

In conclusion, the analysis of signal properties and their correlations reveal clear differences with some traits being highly variable and erratic, while others are highly repeatable with low variation between males. The latter traits, which include pulse rate and pulse rate change, may be suitable for species discrimination to avoid inter-specific hybridization. Other traits are highly variable but with some repeatability, such as signal length, which may provide honest indicators of male quality. Females indeed prefer longer signals (S. Parri, R. V. Alatalo, J. S. Kotiaho, J. Mappes & A. Rivero, unpublished data). The result fits well with the idea that directional female preferences should be directed to energetically demanding aspects of the call (see Klump & Gerhardt 1987; Gerhardt 1991; Bailey et al. 1990; Jang & Greenfield 1996). Indeed, the drumming rate itself, which is correlated with signal length, seems to provide an even better indicator of male quality in this species. Females prefer males with the highest drumming rate (Kotiaho et al. 1996; Parri et al. 1997) and drumming rate incurs significant survival (Mappes et al. 1996; Kotiaho et al. 1998b) and energetic costs (Kotiaho et al. 1998a). In addition there is a slight survival advantage for the offspring of males with higher drumming rates (Alatalo et al. 1998). Drumming rate is highly variable between males, but is still a consistent character of individual males.

Acknowledgments

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