Silja Parri

Female Choice for Male Drumming Characteristics in the Wolf Spider *Hygrolycosa rubrofasciata*

Silja Parri

Female Choice for Male Drumming Characteristics in the Wolf Spider *Hygrolycosa rubrofasciata*

Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella julkisesti tarkastettavaksi yliopiston Ambiotica-rakennuksen salissa YAA303 syyskuun 18. päivänä 1999 kello 12.

Academic dissertation to be publicly discussed, by permission of the Faculty of Mathematics and Natural Sciences of the University of Jyväskylä, in the Building Ambiotica, Auditorium YAA303, on September 18, 1999 at 12 o'clock noon.

UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 1999

Female Choice for Male Drumming Characteristics in the Wolf Spider *Hygrolycosa rubrofasciata*

Female Choice for Male Drumming Characteristics in the Wolf Spider *Hygrolycosa rubrofasciata*

UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 1999

To Heikki and my parents

ABSTRACT

Female choice for male acoustic signalling and consequences of female selective mating behaviour were studied in the wolf spider *Hygrolycosa rubrofasciata*. Males of this species produce audible drumming signals that they use to attract females. These drumming sounds are audible also to human ear. When ready for mating females respond to these drummings by producing vibrations with their body. Drumming characteristics, such as drumming rate, vary between males. In this study I investigated the importance of several characteristics of the drumming signal on female choice. Females were found to prefer male signals of higher repetition rate and of greater length. Pulse rate of the signals did not affect female response behaviour. Repeatability and between male variation of the signal characteristics were used to categorise the signal traits into static and dynamic traits. Signal length was found to fulfil criteria of a trait that females could use to discriminate between males of different quality. Signal repetition rate has been found to indicate male phenotypic quality also in earlier studies. The possible consequences and benefits of female selective behaviour were studied in a selection experiment by mating females with males of either high or low drumming rate. Offspring survival and growth were compared between these two male categories. The offspring of the males with higher drumming rate were found to survive slightly better than the offspring of the lower drumming rate males. The results indicate that females of *H. rubrofasciata* might gain slight genetic, indirect benefits through their choice behaviour.

Silja Parri, University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FIN-40351 Jyväskylä, Finland

Author's address   Silja Parri
Department of Biological and Environmental Science
University of Jyväskylä
P.O. Box 35
FIN-40351 Jyväskylä, Finland

Email: pasika@cc.jyu.fi

Supervisors   Professor Rauno V. Alatalo
Department of Biological and Environmental Science
University of Jyväskylä
P.O. Box 35
FIN-40351 Jyväskylä, Finland

Docent Johanna Mappes
Department of Biological and Environmental Science
University of Jyväskylä
P.O. Box 35
FIN-40351 Jyväskylä, Finland

Reviewers   Docent Anneli Hoikkala
Department of Biology
University of Oulu
P. O. Box 333
FIN-90571 Oulu, Finland

Docent Veijo Jormalainen
Department of Biology, Section of Ecology
University of Turku
FIN-20014 Turku, Finland

Opponent   Professor Marlene Zuk
Department of Biology
University of California, Riverside
CA 92521
USA

CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications, which will be referred to in the text by their Roman numerals. I have planned, performed and am the main writer of papers I and III. I have planned and performed a significant portion of papers II, IV and V and I am the main writer of paper V.

I Parri, S., Alatalo, R.V., Kotiaho, J. & Mappes, J. 1997. Female choice for male drumming in the wolf spider *Hygrolycosa rubrofasciata*. Animal Behaviour 53: 305-312.

II Rivero, A., Alatalo, R.V., Kotiaho, J.S., Mappes, J. & Parri, S. 1999. Acoustic signalling in a wolf spider: can signal characteristics predict male quality? Manuscript (submitted).

III Parri, S., Alatalo, R.V., Kotiaho, J.S., Mappes, J. & A. Rivero 1999. Experiments on male drumming characteristics in spider *Hygrolycosa rubrofasciata*. Manuscript.

IV Alatalo, R.V., Kotiaho, J., Mappes, J. & Parri, S. 1998. Mate choice for offspring performance: major benefits or minor costs? Proc. R. Soc. B. 265: 2297-2301.

V Parri, S., Alatalo, R.V., Kotiaho, J.S. & Mappes, J. 1999. Offspring growth in a drumming wolf spider – effects of sire size and sexual attractiveness. Manuscript.

1 INTRODUCTION

1.1 Female choice and sexual selection

Sexual selection as a major type of natural selection (Arnold & Wade 1984a, b) has been one of the most extensively studied areas within the discipline of evolutionary biology (e.g. Emlen & Oring 1977, Lande 1981, Maynard Smith 1991, Andersson 1994, Andersson & Iwasa 1996). Traditionally, since Darwin (1871), sexual selection has been divided into intrasexual and intersexual selection, which refers to female choice of potential mating partners (e.g. Halliday 1983, Maynard Smith 1991). Recently, however, it has been proposed that sexual selection should be seen 'from a wider viewpoint' including also several other forms of selection (see Andersson 1994, Andersson & Iwasa 1996, Murphy 1998) and taking into consideration that all individuals might not adopt similar strategies in their mate choice (Cunningham & Birkhead 1998).

Within the last few years, both theoretical modelling and empirical testing of the theories of sexual selection have concentrated on investigating the evolution and consequences of female choice behaviour (discussed by e.g. Kirkpartick & Ryan 1991, Wiley & Poston 1996). Females are supposed to gain either direct benefits to themselves or indirect benefits, via their offspring, through their choice behaviour. In particular the indirect form of female choice has gained extensive theoretical and empirical interest, while the direct benefits have also been widely tested empirically.

1.2 Female choice for direct benefits

Direct benefits of female choice may be realised through either increased fecundity or enhanced survival. Females may be able to enhance their fecundity by choosing to mate with males that provide a higher fertilisation potential (see, for example, Brown et al. 1996, Savalli & Fox 1998). Fecundity benefits might also be gained via the nutrients that the male provides, as can be the case in katydids (Gwynne 1988) and other insects where the male provides the female with nuptial gifts (review in Thorhill & Alcock 1983). The amount of food the male provides for the female and the offspring may be correlated with the

quality of the male's territory or the quality of the nesting site (e.g. Radesäter et al. 1987, Alatalo et al. 1990). Males may also vary in the level of parental care or investment they provide for the female and the offspring, as well as in their ability to defend the brood (Norris 1990, Forsgren et al. 1996, Forsgren 1997). This 'good parent process' has been proposed to drive the evolution of male traits indicating their ability to provide parental care (Hoelzer 1989). Females might also be choosing certain types of males with the purpose of decreasing the costs of mating, such as predation or harassment during or after mating. Females of dung fly, for example, choose larger males because they are less likely to be attacked by other males during copulation (e.g. Sigurjónsdóttir & Parker 1981, see also Grafe 1997).

1.3 Female choice for indirect benefits

Most of the theoretical and also empirical testing of female mate choice has concentrated on establishing the advantages of female choice when the benefits are not obviously direct (Maynard Smith 1976, Zahavi 1977, Kirkpatrick 1982, Andersson 1986, Pomiankowski 1987, Grafen 1990a, 1990b, Iwasa et al. 1991, review in Johnstone 1995). Two main theories have been put forward to explain these cases; the Fisherian theories and the so called good genes theories (Zahavi 1977, Lande 1981, Kirkpatrick 1982, Andersson 1986, Pomiankowski 1987, Grafen 1990a, 1990b, Iwasa et al. 1991, review in Johnstone 1995). The main distinction between these two theories lies in the way they consider the female preferences to be upheld. In the Fisherian theories an important condition is that some male traits that are selected for via natural selection become encoupled with female sexual preference. Females that choose males exhibiting these traits will give birth to more successful male offspring in terms of their mating success, and the genetic preference for these male characteristics will produce a "runaway process" that would maintain both the preference and the male trait (Kirkpatrick 1982, Pomiankowski & Iwasa 1993). The good genes models, however, assume that females are, on the basis of the phenotypic expression of male secondary sexual characteristics, able to detect the genetic quality and viability of the bearer. Thus, females choosing the males of high genetic quality would gain indirect benefits in the form of increased viability of their offspring (Zahavi 1977, Andersson 1986, Pomiankowski 1987, Grafen 1990a, 1990b, Iwasa et al. 1991, review in Johnstone 1995). Fitness-related traits have, however, been thought to have a low heritability because of the strong selection acting on anything related to fitness (e.g. Falconer 1989). As a consequence, the phenomenon of female preferences for traits that do not confer any obvious benefits has been termed the "lek paradox" (Taylor & Williams 1982, Reynolds & Gross 1990, Kirkpatrick & Ryan 1991). As a resolution of the paradox it has been proposed that contrary to the expectations that directional selection for male characteristics would deplete most of the genetic variation, there would be high levels of additive genetic variation left in the traits, and indeed, due to 'modifiers' the amount of this variation may even be greater among the sexual than in the non-sexual traits (Pomiankowski & Møller 1995). The estimates of the genetic variation of sexually selected traits

based on this argument have been revised and the effect of sexual selection on fitness traits has appeared to be of a low, although significant magnitude (Møller & Alatalo 1999).

An important assumption of the good genes models is that the male phenotypic traits must be honest, in other words, producing and maintaining these traits must be costly for the males (Zahavi 1975, 1977, Grafen 1990b, b, Iwasa et al. 1991). Further, for the trait to operate as an honest handicap, these costs should be highest for the lowest quality males (Zahavi 1977, Grafen 1990a, b, Iwasa et al. 1991). This is because males that are in better phenotypic condition should be better able to bear the costs of maintaing the trait. Empirical testing of the costs of sexual traits is difficult, as reflected by the paucity of studies where such differential costs have been empirically proven (Møller 1989, Møller & deLope 1994, Mappes et al. 1996, Kotiaho 1999).

The genetic indicator mechanism has gained support in studies with several species (von Schantz et al. 1989, Reynolds & Gross 1992, Bakker 1993, Norris 1993, Møller 1994, Petrie 1994, Hasselquist et al. 1996, Sheldon et al. 1997). In the gray tree frog, for example, call length operates as an indicator of male genetic quality. The offspring of males that produce longer calls perform better at each stage of their development than the offspring of males producing shorter calls (Welch et al. 1998). There are, however, also several studies in which no evidence for the effects of male genetic quality upon offspring performance has been found (Boake 1985, Woodward 1986, Mitchell 1990, Howard et al. 1994, Semlitsch 1994).

Several characteristics of offspring performance have been used to reveal the possible indirect benefits of female mate choice. Since an individual's fitness is ultimately defined as its success to transfer its own genes to the next generation, the indirect benefits of female mate choice should be revealed as viability and reproductive success of the offspring. Viability of the offspring has been shown to be enhanced with greater levels of male sexual advertisement in peacocks *Pavo cristatus* (Petrie 1994), great tits *Parus major* (Norris 1993), fruit flies *Drosophila melanogaster* (Taylor et al. 1987) and barn swallows *Hirundo rustica* (Møller 1994). In many cases, however, offspring quality is measured using characters closely related to fitness, such as growth rate (Reynolds & Gross 1992, Welsh et al. 1998), development time (Moore 1994) and fledging condition (Sheldon et al. 1997).

Selective mating by the females is bound to entail costs (e.g. Pomiankowski 1987). Janetos (1980) suggested several different potential mate choice desicion rules varying from "random mating" to "best-of-n-males strategy". Real (1990) divided female mating costs into two basic types: direct costs and opportunity costs. Direct costs include, among others, an increased risk of predation and an increased time expenditure whilst sampling the potential mates. Opportunity costs, on the other hand, are incurred through the loss of previously encountered mates due to death, emigration or change in mating status. Females of the cockroach *Nauphoeta cinerea* and the red jungle fowl *Gallus gallus* are found to follow threshold criteria where the male trait has to exceed a certain fixed level for it to be selected (Moore & Moore 1988, Zuk et al. 1990). Study of female choice behaviour in three *Drosophila* species revealed

that females use relative criteria; female choice depends upon the variation among the available males (Hoikkala & Aspi 1993). Females of many non-lekking species are found to use sequential assessment of males (see for example Bakker & Milinski 1991) with increased costs of comparison causing decreased choosiness (see also Grafe 1997). Thus, the costs of female choice should be taken into account by any attempt to understand female preference for male characteristics.

1.4 Acoustic signals as sexual traits

Acoustic traits are among the most commonly used sexual traits (Andersson 1994). In some species, where the size of a male provides clear direct benefits to the female such as more sperm or nutrients, males have been shown to convey information about their size via acoustic signals. In the house cricket *Acheta domesticus*, for example, a male's song indicates his size, and females prefer the signals of larger males (Gray 1997, see also Simmons 1988, Brown et al. 1996). Another example of direct benefits revealed by male acoustic signalling, include cases where a male's singing rate is related to the quality of his territory (e.g. Radesäter 1987). Likewise, a male's song repertoire size correlates with male reproductive success in the great tit (McGregor et al. 1981) and in
 the sedge warbler *Acrocephalus schoenobaenus* (Buchanan & Catchpole 1997).

Several characteristics of acoustic signals make them good candidates as targets for female choice. Firstly, the traits have been shown to be repeatable within males and, also to vary between them (see for example Hoikkala & Isoherranen 1997). Indeed, repeatability and variability of the signal characteristics have been used to categorise signal components into static and dynamic (Gerhardt 1991, Castellano & Giacoma 1998). Static characteristics are highly repeatable within males with a small between male variation. These traits are often found to be used mostly for species recognition and thus to be under stabilising rather than directional selection (Gerhardt 1991, Castellano & Giacoma 1998). Dynamic characteristics, on the other hand, are also highly repeatable within males but they display a high variation between males. Thus they are the traits that are most likely to operate as indicators informing the females about the phenotypic and genetic quality of the males.

Secondly, in addition to repeatability and variability, the traits used as indicator traits in sexual selection have to be costly. Acoustic signals also fulfil this criterion. In some cases the energetic costs of producing acoustic signals are 20 times the basal metabolic energy consumption of a male (Vehrencamp et al. 1989, Wells & Taigen 1989). There is even evidence that the energetic costs of acoustic signals may vary between attractive and non-attractive males (Reinhold et al. 1998). In the spider *Hygrolycosa rubrofasciata* the energetic costs of drumming are 22 times greater than the costs of the resting metabolic level (Kotiaho et al. 1998). It has been suggested that females in general show a preference for male traits which have a greater energy content (Ryan 1988, Ryan & Keddy-Hector 1992). This could be interpreted as female choice for males that are in good condition and able to invest their energy resources into signalling. In addition to the costs of producing the sexual signals there is also solid

empirical evidence for costs to maintain the sexual signals. These costs are in general due to predation and parasitism taking advantage of the sexual signals (see Zuk & Kolluru 1998 for review).

In this thesis I investigate female mate choice in the drumming wolf spider *Hygrolycosa rubrofasciata* (Ohlert) (Lycosidae) in relation to the acoustic signalling of the males. This drumming spider is an ideal subject for the study of female preferences for different acoustic traits. The relatively simple structure of the male's signals enables the manipulation of the specific components of the signals, and thus the study of female preference. With playback experiments, using tape-recorded male signals, I studied female preference for signal length, pulse rate and the repetition rate of the signals. A detailed analysis of the signals allowed detection of correlations between these components and other male traits that have previously been found to be important for male reproductive success. The potential direct and indirect benefits of female choice behaviour were studied with a selection experiment.

2   MATERIALS AND METHODS

2.1   The study species and habitat

Hygrolycosa rubrofasciata (Ohlert) (Lycosidae) is a wolf spider which can be found in patchily located populations widely distributed over northern Europe. The species inhabits different types of habitat, both bogs and meadows. In Finland it can be found along the coastal regions as well as inland in south-eastern and northern parts of the country. The spiders used in the experiments presented in this work were collected from two site in Sipoo, Southern Finland; Stormossa (a bog habitat) and Stenberg (an abandoned field) and two sites in Sodankylä, Northern Finland; Sattanen (a bog) and Jeesiö (an abandoned field).

   H. rubrofasciata is sexually dimorphic both in terms of size and coloration. The males are somewhat smaller (mean ± SD for the southern bog population in 1995 = 16.7 ± 2.5 mg, n = 506) than the females (mean ± SD for the females of the same population in same year = 24.8 ± 4.7 mg, n = 337). Males have a dark, nearly black carapace while females are brownish and more cryptic than the males. Since *H. rubrofasciata* is a wolf spider, it lives on the ground without building any webs and it feeds on small arthropods such as springtails, mites and other spiders. The first males start drumming in the spring once the ground begins to be free from snowcover, which in Southern Finland typically happens towards the end of April and the beginning of May. The males and females, which have moulted into adulthood the previous autumn or in early spring, are ready to begin the mating season once the ambient daytime temperature has reached +10 ° C.

   The characteristic trait of the mating behaviour is the drumming display which the males produce by percussing dry deciduous leaves with their abdomen (Kronestedt 1984, 1996, own observations). These drumming signals are clearly audible to the human ear from several meters. Males drum while wandering around the habitat searching for receptive females. With mark-recapture observations we have found that the females are much more stationary than the males. When a male encounters a female it stops and drums several times. If the female is willing to copulate with the male, she responds by vibrating her body. This response is given immediately after the male drum and

it is clearly visible, although female percussions are usually not intensive enough to produce any audible sounds. The existence of such a clear response occurring shortly after the male drums allows the experimenter to determine which male or male signal the female preferred. After the female's initial response the male and the female drum several times before copulation begins ('duetting', Kronestedt 1996). Because of the size difference between the sexes males have no chance of forcing females to copulate.

In a typical year the mating season lasts for two to three weeks depending on the prevailing weather conditions, in Southern Finland males may continue drumming until early June. After the mating season the males die while at least some of the females may survive until the next season (own observation based on mark-recapture data). Mated females produce eggsacks, which they carry attached to their spinnerets (silk glands in their abdomen) until approximately mid June (in southern Finland). The newly hatched spiderlings climb onto the female's abdomen and disperse into the vegetation within a day. Juveniles mature typically after their third summer season.

2.2 Collecting the specimen

All the spiders used in the studies were collected as adults from the field immediately after the snow had melted. In order to obtain unmated females, however, care was taken to collect the females while there was still snow on the ground. Females were collected by hand while later on the greater mobility of males permitted the use of pitfall traps. After collection, the spiders were put individually into small plastic containers (film jars) with some moist moss (*Sphagnum* spp.) until they were brought to the laboratory. In the laboratory each individual was weighed (± 0.01 mg), labelled and kept in fridge temperature (+5 - 7 ° C) in order to prevent them from reaching the active sexual phase until they were used for the experiments. This is particularly important for the females, since they reach their sexual activity within a few days in room temperature. Thus by keeping the females in cool conditions until the start of the experiment we could keep them in an 'inactive' state. The male drumming rate is affected by the time of the season and, after reaching the most active phase their activity decreases towards the end of the season. Once in the laboratory the spiders were fed laboratory reared fruit flies as well as insects collected in the field.

2.3 Set-up for observing male drumming rate, tape recording the signals and playback experiments

Males of *Hygrolycosa rubrofasciata* produce drumming signals even without any females present. We determined the male drumming rate by counting the number of individual drumming signals a male produced within a given unit of time. This was done by placing the males individually on plastic arenas (sized 10 x 9 x 11 cm) with a few birch leaves as a drumming substrate. Males were kept in the containers for 1 hour before the drumming recordings began to allow them to get accustomed to the arena. Each male was then observed for

two minutes, each 2-minute observation period was repeated either five (II, IV, V) or three (II) times over two hours and the same procedure was repeated on each of two successive days. The repeatability of the drumming rates was calculated as an intra-class correlation coefficient between the successive days (see Lessels & Boag 1987). For the selection experiment (IV and V) the males were ranked according to their drumming rate with the most and least actively drumming males chosen for the subsequent matings.

The male drumming signals were tape-recorded using a Telinga microphone and a Casio DA-7 (year 1995) or a Sony TCD-D7 (year 1996) digital recorder. The recording procedure differed slightly between the years (II, III). In 1995 the males were placed in plastic cups (diameter 6.5 cm with a height of 4 cm) with a few dry birch leaves (II). In 1996 the males were placed in cylinders made of transparent sheets (height 6 cm and diameter 3 cm) which were glued onto a small piece of paper (II, III). Ten of these cylinders were arranged into a circle (diameter 35 cm) on a sheet of cardboard and the microphone was hung in the middle of the circle at a height of 35 cm from the males. In both years three separate signals were recorded from each male. The recorded drummings were then imported from the tapes into a computer and either manipulated to be used in playbacks (III) or analysed in detail to determine their different components (II).

The playback experiment upon female readiness to pay the costs of choosing between males (I) was conducted with unmanipulated signals which were replayed to the females using a tape recorder. In the signal length and pulse rate playbacks (III) drummings were manipulated using a computer program which creates a sonogram (amplitude versus time) of the signals. In signal length experiment the duration of the signals was either decreased or increased by cutting off or multiplying individual pulses within the signal. In the pulse rate experiment the inter pulse interval was either increased or decreased to produce signals which had either a higher or a lower pulse rate than the original signal. The manipulated signals as well as the original ones were used to create playback tapes, which were replayed to the females from a computer.

In all of the playback experiments the male signals were replayed to the females through loudspeakers (Pioneer TS-F 1665). In the signal length experiment (III) the female's containers were placed either right on top of the loudspeakers (contact set-up) or on a metal grid three centimetres above the loudspeakers (non-contact set-up). This was done in order to study whether female preference is dependent upon whether the signals are transmitted through the air or a substrate. In all other playback experiments (I and III) the females were right on top of the loudspeakers. Each tape or male signal was replayed to groups of 18 to 20 females, except in the playbacks studying the costs of comparison (I), in which we used groups of ten females. We observed after which of the signals each female responded for the first time, and in one of the experiments (I) how many responses each female produced in total.

The signal characteristics were analysed using a computer program (Canary 1.2, The Cornell Bioacustics Workstation) in which both an oscillogram (intensity vs time) and a spectrogram (frequency versus time) of each signal

were produced (II). The signals were analysed in two successive years, 1995 and 1996. In 1995 we analysed the signal length (mS), pulse rate (number of individual pulses/signal length), peak frequency and signal shape (as timing of the peak frequency within the signal). In addition, each signal was divided into three equal time sections and the pulse rate, average volume (dB) and peak frequency (Hz) for each section were analysed. By comparing the first and third sections we were able to determine the temporal changes within the signals. In 1996 we analysed the signal length, pulse rate and volume. In both years we estimated the between male variation of the signal characteristics, by calculating the coefficient of variation (CV) and the within male variability as repeatability (intra-class correlation coefficient, Lessels & Boag 1987).

2.4 Experiment on female signal detection and population recognition (III)

The signals that males of *H. rubrofasciata* produce travel as vibrations both in the substrate and in the air. In this experiment, we studied whether there is a difference in female response behaviour to male signals dependent upon how they receive the signals. This was studied with a signal detection experiment and also in a separate experiment upon population recognition. Female signal detection was studied on an arena, where the females received male signals either as vibrations travelling only through the air or via both the air and the substrate beneath. Females were placed in the centre of the experimental arena with or without substrate contact to four males. The distance between the males and the female was shortened from 15 to 5 centimetres until the female responded to one of the males. In each trial we had two males from both of the southern populations and a female from either of the populations.

The population recognition experiment was conducted by replaying females a tape in which male signals from two populations alternated regularly. The southern females were replayed a tape of ten signals from the both two southern populations and the northern females a tape of 20 northern signals, ten from both populations, respectively. The signals were not manipulated in any way. As in the other playback experiments, we noted the male signal after which each female responded for the first time.

2.5 Matings and rearing the offspring (IV and V)

The males with the highest and the lowest drumming rate were selected and paired with a random set of females from the same southern population as that from which the males originated (Stormossa). Each pair was placed on a plastic arena (size 10 x 9 x 11 cm) with a few dry birch leaves on the bottom as a drumming substrate for the males and a hiding place for the mating pair. We recorded the time until mating and the duration of copulation. After mating the females were placed into individual rearing containers (diameter 3.4 cm, height 6.7 cm), each of which had a cotton roll through a hole in the bottom of the container. The containers were placed onto a metal mesh tray so that it was easy to wet the cotton rolls by dipping the tray into a bucket of water. The females

were fed vestigial fruit flies and insects collected from vegetation.

After all the offspring had left the female and the eggsack, they were counted and put into two litre rearing jars. On the bottom of the jars there was some moss and a tube of water sealed with cotton to provide moisture. The offspring were fed every second day with small springtails collected from coniferous soil, and later were also fed fruit flies and field collected insects. 45 days after hatching, the offspring were removed from the jars, weighed, individually numbered and placed into individual rearing containers, similar to the ones in which the females were kept after mating. From this time onwards the offspring were fed and checked every second day and weighed every 20 days.

Body mass of the offspring of males with high and low drumming rates were compared using family means. Since male and female offspring first differed in body mass at the age of 165 days, the comparisons at 165 and 185 days of age were done separately for male and female offspring. Weights were also used to calculate the parent-offspring resemblance in body mass. All the estimates were calculated using multiple Y with one X –type regression (Sokal & Rohlf 1973) with standardised values of both parent and offspring body mass. The development time of the offspring was determined as the time from hatching until the time of moulting into adulthood.

3 RESULTS AND DISCUSSION

3.1 Male signal characteristics (II)

The detailed analysis of the signals recorded in 1995 revealed that signal length and pulse rate had high repeatabilities (0.55 and 0.84, respectively) and that signal length was also highly variable between males, while pulse rate was not (14.3 % and 5.1 %, respectively). Peak frequency and the temporal shape of the signals showed very low repeatabilities within males, whereas the temporal change in pulse rate and average volume were both significantly repeatable. The latter two traits, however, exhibited very little variation between the males. Comparisons of the signal characteristics to each other revealed only a weak association; only the pulse rate and the length of the signal tended to be negatively related. Any characteristics that exhibit a low repeatability and a low level of variation between males are not expected to play an important role in sexual selection. Thus, for the analysis of the potential relationship between the signal and male characteristics, we chose signal length and pulse rate. These characteristics were studied using a larger set of males collected from two different populations, Stormossa and Stenberg, in 1996. Standardising the recording set-up also made it possible to analyse the differences in the volume of the signals between the males. Comparisons of the signal characteristics between the successive years revealed that the signals were shorter and had a higher pulse rate in 1996 than in 1995. In both years, between male variation in pulse rate was low, while both signal length and pulse rate were highly repeatable within the males. Signal volume was positively related to signal length; longer signals were louder in both populations.

Signal characteristics can be categorised into three groups. Firstly, pulse rate and pulse rate change are static traits with a high repeatability within males but a low between male variation. Secondly, signal length is both repeatable within males and variable between males. Thirdly, signal shape, peak frequency and peak frequency change all exhibited erratic properties with a high variation between males and a low repeatability within males. In order for a trait to serve as a significant indicator trait within sexual selection and female choice it should be repeatable within males while being variable

between them (examples of such sexual traits: Alatalo et al. 1988, Pomiankowski & Møller 1995, Rowe & Houle 1996). Of all the signal characteristics that we analysed in this study only signal length seems to fulfil both of these requirements.

In particular, male drumming rate has previously been noticed to correlate with male phenotypic condition (Kotiaho et al. 1996, Mappes et al. 1996). Male body mass has in some cases also been observed to be related to the ability to bear the costs of drumming (Mappes et al. 1996). Thus to find any possible relationship between male signals and male phenotypic condition we compared signal characteristics to male drumming rate and body mass. Male body mass was correlated with signal volume in Stormossa males, but there was no such relationship within the Stenberg population. The drumming rate was related to signal length in both populations and also with volume in Stormossa males. In the preceding experiments, we have illustrated that male drumming rate is a trait directionally preferred by the selective females (Kotiaho et al. 1996, Parri et al. 1997) and an honest indicator of male phenotypic quality (Mappes et al. 1996, Kotiaho et al. 1999). Since signal length and male drumming rate are significantly correlated, it is possible that signal length also operates as an indicator of male phenotypic quality. Pulse rate, on the other hand, might operate as a characteristic related to species recognition. In several studies pulse rate has indeed been found to be under stabilising rather that directional selection (for example Schüch & Barth 1985, 1990, Ritchie et al. 1994).

3.2 Female preference for male signal characteristics (I and III)

Preferences of the females of *H. rubrofasciata* for different signal repetition rates, lengths and pulse rates were studied in two separate experiments (I and III). The results clearly show that the females responded earlier when the signals were replayed at the higher repetition rate. This result supports previous laboratory observations of male-female encounters (with three males and four females on the same arena) in which the females responded more often to males with higher drumming rates (Kotiaho et al. 1996). Also in several other studies the calling rates of males have been shown to be selected for by female choice (e.g. Sullivan 1983, Bailey et al. 1990, Sullivan & Hinshaw 1992, Jang & Greenfield 1996). Especially in anurans, the total time spent calling influences male mating success (Sullivan & Hinshaw 1992).

In our playback experiments females were found to prefer elongated signals over the shortened ones. Although the females responded earlier to the signals when they were in contact with the loudspeakers, overall, female preferences between the male signal types exhibited no clear differences between the contact and non-contact set-ups. In contrast, pulse rate manipulations did not alter female preference in any way. Signal length has, in many studies, turned out to be under directional female choice (e.g. Hedrick 1986, Sullivan & Hinshaw 1992, Jang & Greenfield 1996, but see e.g. Butlin et al. 1985). It has been proposed that directional female preference for a greater magnitude of certain characteristics of male acoustic signals would reflect a preference for greater amounts of energy invested into the signals (Ryan 1988).

This would be exhibited either as a greater energy content of individual signals or as a greater total energy invested into calling. Acoustic calls are indeed energetically very demanding to produce (e.g. Vehrencamp et al. 1989, Wells & Taigen 1989, Bailey et al. 1993, Watson & Lighton 1994). In the toad, *Bufo rangeri*, males calling at higher rates lost more weight than males with lower calling rates (Cherry 1993). Our own observations have shown that in *H. rubrofasciata* drumming is indeed very energetically demanding. The CO_2 production rate was on average 22 times higher during drumming than during rest (Kotiaho et al. 1998). We have no direct measurements of the energy requirements of different kinds of signals (see Reinhold et al. 1998) but it can be argued that longer signals should require more energy than shorter ones. When signal characteristics were compared to male drumming rate and body mass (II) it was found that signal length correlated significantly with drumming rate. Thus, the result of female preference for longer signals provides further evidence that signal length might indeed work as an indicator trait of male phenotypic condition, as does male drumming rate (Mappes et al. 1996, Kotiaho et al. 1999).

3.3 Female signal detection and population recognition (III)

In the experiment investigating the effect upon female response behaviour of the manipulation of the substrate contact between males and females, the proportion of trials in which females responded to male drumming did not differ between the contact and non-contact set-ups. The females that were in contact with the males via the substrate, however, responded earlier than those without the contact. The possibility that females may discriminate between the signals of males from two different populations was studied both within this experiment and also with a separate experiment. In both of them, there were no differences in female response behaviour between the two populations. Thus, the females do not seem to discriminate between males from different populations.

3.4 Benefits of female choice behaviour (IV and V)

For this experiment we chose males with the highest and the lowest drumming rates and mated them with a random set of females. The difference in drumming rate between these male groups corresponds to 2.8 s.d. units of ln-scaled drumming rate. Results of the experiment indicate no direct benefits from selecting actively drumming males. There were no differences between the mating characteristics of the high and low drumming rate males (time until copulation, duration of the copulation, proportion of males copulating) neither between the variables that would determine the direct female benefits (time until eggsack, eggsack carrying time or number of offspring).

Possible indirect benefits of female choice were studied by first comparing offspring body mass between the high and low drumming rate groups (V). The average body mass of the offspring did not differ between the two groups at any stage of their development. The body mass of male offspring at the age of

185 days was positively related to their initial body mass at the age of 45 days, although it was not affected by sire body mass. The body mass of female offspring at the age of 185 days, however, was unrelated to their initial body mass at the age of 45 days, but it was significantly influenced by sire body mass. The estimates of resemblance in body mass between the parents and their offspring indicate that there is a relationship between sires and the offspring at most 'stages' of their development. The estimates tended to be greater in the high drumming group but the differences were not significant. The drumming rate of sires' affected the development time of their male offspring: it took, on average, 18 days longer for male offspring of sires with a high drumming rate to reach the final moult than for offspring of sires with a low drumming rate. This result is somewhat surprising. One possible explanation could be that development time and drumming rate are in some way genetically correlated with each other. The development time of female offspring, on the other hand, was not affected by sire drumming status. There was also a difference between male and female offspring when the relationship between development time and the body mass at 145 days of age was examined. The body mass at 145 days of age represents, on average, the body mass at the final moult. Among female offspring there was a significant negative correlation between development time and body mass, but among the male offspring there was no relationship between these variables. To summarise, male and female offspring differ in their growth pattern and offspring growth is not greatly affected by sire drumming status.

Offspring survival was followed until they reached the age of 185 days, when the average family lifespans of the offspring from the different sire groups were compared (IV). There was a slight, although significant, difference in that the offspring of high drumming rate sires survived longer. By standardising both sire drumming rate and offspring survival, we were able to estimate the magnitude of the effect of sire drumming rate. This analysis revealed that the correlated response in offspring survival was 0.12 s.d. units which results in a 10.7 % increase in offspring survival for females mated with males at +1 s.d. units above the mean drumming rate compared to the survival of offspring of females mated with males of average quality.

The readiness of females to accrue costs in order to be able to compare males was investigated by presenting females with recordings of male signals at two different volumes, either simultaneously or sequentially over two successive days. Females responded sooner to the signals with a higher volume in both set-ups. The proportion of the females that chose the higher volume signal first did not differ between the simultaneous and sequential set-ups indicating that they are ready to accept the costs of waiting for another opportunity to mate. The sequential comparison set-up might indeed be quite realistic in the field where the males are actively moving and searching for females. We have estimated that in the field a female is visited, on average, by one male an hour and that during this time there will be, on average, 2.28 drumming events within a 15 cm perimeter (IV). Thus, in the field females have some opportunities to compare the males. However, in practice they are not likely to be able to 'return' to a male that they have rejected earlier. If we

assume that a female of *H. rubrofasciata* responds to the first male that drumms in the population, she would already be mating with a male that is above the average for the population. On the basis of results from Kotiaho et al. (1996) such a male would already be 0.53 s.d. units above the average drumming rate and the offspring of this female would thus gain a 5.8 % increase in survival compared to the offspring of the average male. By actively preferring males with a higher drumming rate a female would increase the benefits to some extent. The mating system of *H. rubrofasciata* represents a very good example of a system in which females, with relatively low costs of comparison, are able to increase the expected benefits of their choice. Similar systems are likely to operate in several other species, too. In other words in these systems by passively mating with any signalling or displaying male females would end up mating with a male of better than average quality.

4   CONCLUSIONS

Sexual selection has for several years been one of the most extensively studied fields in evolutionary biology (e.g. Emlen & Oring 1977, Lande 1981, Maynard Smith 1991, Andersson 1994, Andersson & Iwasa 1996). Female mate choice in particular has attracted a great deal of interest due to the strikingly diverse forms of male ornaments and displays as well as to the fact that females often discriminate between these males even when there are no obvious benefits available. In this thesis I studied female mate choice in the wolf spider *Hygrolycosa rubrofasciata.* The males' display behaviour is characterised by audible signals, which they produce by drumming dry, fallen deciduous leaves with their abdomen (Kronestedt 1984, 1996, own observation). In previous experiments it has been observed that females prefer to mate with males that drum at the highest rate (Kotiaho et al. 1996). Further, this drumming activity is a repeatable male trait which honestly indicates male phenotypic quality (Kotiaho et al. 1996, Mappes et al. 1996). In this thesis I studied, with the use of playback experiments of manipulated male signals, whether females also use specific characteristics of male drumming signals in their mate choice. By analysing the signals and their characteristics I studied whether these characteristics are related to each other or to indicator traits of male condition. Females preferred male signals replayed at a higher rate and also longer signals opposed to shorter ones. Analysis of the variability and repeatability of the signals revealed that signal length and pulse rate were highly repeatable within males, but only signal length was also variable enough between the males to qualify as an important trait in sexual selection and female choice. Signal length was also positively related to male drumming rate, a trait that indicates male phenotypic quality. Thus it could be argued that females gain information of male phenotypic quality via both male drumming rate and from the length of male signals.

An important question of this thesis was also to investigate whether females gain any benefits from their selective mate choice. The benefits, either direct or indirect, are a prerequisite for the maintenance of mate choice (see for example Majerus 1986, Kirkpatrick & Ryan 1991). The indirect benefits of female choice have in particular received wide interest since in general, the

inheritance of fitness related traits has been thought to be low (e.g. Falconer 1989). Females of *H. rubrofasciata* were not found to gain any direct benefits by mating with males exhibiting a higher drumming rate, but there was a significant, albeit slight, survival advantage for the offspring of males with higher drumming rates. By comparing the realised effects of this survival benefit to the costs that females have to face for the opportunity to choose between the males, it can be argued that with even a slight effect upon offspring survival, the females may gain significant benefits by being selective. Thus, when studying the maintenance of female mate choice for indirect benefits the costs of choice should also be taken into account. On the other hand, in the mating system of *Hygrolycosa rubrofasciata*, and probably in many other mating systems, the females can choose males of above average quality without any major costs.

26

YHTEENVETO

Koiraan kosintaäänen merkitys naaraan parinvalinnalle rummuttavalla susihämähäkillä *Hygrolycosa rubrofasciata*

Väitöskirjatyössäni tutkin naaraiden parinvalintaa sekä tästä käyttäytymisestä naaraille koituvia välittömiä ja välillisiä hyötyjä. Välittömät hyödyt vaikuttaisivat naaraan saamien jälkeläisten määrään taikka niiden kykyyn huolehtia jälkeläisistä, kun taas välilliset hyödyt parinvalinnasta tulisivat näkyviin poikasten parempana lisääntymis- taikka elinkykynä. Työssä keskityttiin koiraan tuottaman kosintaäänen ominaisuuksiin *H. rubrofasciata* hämähäkillä. Laji esiintyy Suomessa paikallisena etenkin rannikolla sekä myös sisämaassa, etenkin Itä- ja Pohjois-Suomessa. Lajin kosintamenoihin liittyy olennaisena osana rummutus, jota koiraat tuottavat rummuttamalla takaruumiillaan kuivia lehtiä tai muuta vastaavaa alustaa. Ääni on myös ihmiskorvin kuultavaa.

Aikaisemmissa kokeissa on havaittu, että koiraan rummutusaktiivisuus eli frekvenssi, jolla koiras tuottaa yksittäisiä, noin sekunnin kestäviä rummutussignaaleja, on kunkin koiraan toistettava ominaisuus ja että koiraiden elossasäilyminen korreloi positiivisesti koiraan rummutusaktiivisuuden kanssa. Naaraiden on havaittu parinvalinnassaan suosivan aktiivisimmin rummuttavia koiraita. Tavoitteena olikin ensin tutkia, olisiko koiraan rummutuksessa muita koiraan laatuun liittyviä ominaisuuksia, jotka olisivat koiraiden välillä riittävän muuntelevia, mutta yksittäisen koiraan tuottamina toistettavia toimiakseen mittarina koiraan laadusta. Tällaiset ominaisuudet voisivat toimia naaraille indikaattoreina potentiaalisten parittelukumppaneiden laadusta. Nauhoitettuja ääniä analysoimalla ja äänen sekä koiraiden eri ominaisuuksien välisiä yhteyksiä vertaamalla havaittiin, että rummutusaktiivisuuden lisäksi rummutuksen pituus voisi toimia indikaattorina koiraan laadusta mitattuna koiraan elinkykynä. Rummutuksen tiheys (yksittäisten iskujen määrä aikayksikössä) oli myös hyvin toistettava koiraan ominaisuus, mutta koiraat erosivat toisistaan tämän ominaisuuden suhteen vain vähän. Naaraiden suosivaa parinvalintaa näiden ominaisuuksien suhteen tutkittiin soittamalla naaraille manipuloituja ääniä. Kokeissa havaittiin, että naaraat valitsivat suhteellisesti useammin pidemmän kuin lyhyen äänen. Äänen tiheyden suhteen naaraat eivät osoittaneet minkäänlaista suosintaa. Yksittäisen rummutuksen pituus osoittautui rummutusaktiivisuuden lailla koiraiden välillä vaihtelevaksi ja lisäksi kullekin koiraalle tyypilliseksi ominaisuudeksi. Rummutuksen pituuden ja rummutusaktiivisuuden välillä havaittiin positiivinen yhteys, ja näin ollen voidaankin päätellä, että koiraan rummutuksen pituus voisi rummutusaktiivisuuden lisäksi toimia koiraan elinkyvyn indikaattorina. Rummutuksen tiheys puolestaan vaikuttaa ominaisuudelta, joka liittyy enemmänkin lajin tunnistukseen kuin varsinaiseen seksuaalivalintaan.

Soittokokeilla tutkittiin myös sitä, ovatko naaraat valmiita ottamaan kustannuksia mahdollisuudesta valita parittelukumppaneiden välillä, eli ovatko ne valmiita odottamaan voidakseen vertailla parittelukumppaneita keskenään. Kokeiden tulosten perusteella voidaan olettaa, että naaraat ovat

jossain määrin valmiita odottamaan tilaisuutta vertailla erilaatuisia koiraita keskenään. Tärkeänä tavoitteena oli myös tutkia, hyötyvätkö naaraat aktiivisia koiraita suosivasta parinvalinnasta. Koe tehtiin antamalla naaraiden paritella joko hyvin aktiivisten taikka vain vähän aktiivisten koiraiden kanssa ja seuraamalla sekä naaraan menestystä ja poikastuotantoa että jälkeläisten kehitysaikaa, painoa ja elossa säilymistä. Vertaamalla aktiivisten ja vähemmän aktiivisten koiraiden jälkeläistöä havaittiin, ettei koiraan laadulla ollut merkitsevää vaikutusta jälkeläisten painoon, mutta aktiivisten koiraiden koirasjälkeläiset kehittyivät hitaammin kuin vähemmän aktiivisten koiraiden. Naarasjälkeläisten kehitysaikaan koiraan laadulla ei ollut merkitystä. Kokeessa havaittiin, että rummutuksen suhteen aktiivisempien koiraiden jälkeläisillä oli jonkin verran suurempi todennäköisyys säilyä hengissä aikuisiksi kuin vähemmän aktiivisten koiraiden jälkeläisillä. *H. rubrofasciata* naaraat saavat siis jonkin verran epäsuoria hyötyjä valitessaan aktiivisimpin rummuttavia koiraita parittelukumppaneikseen. Arvioitaessa tämänkaltaisten naaraan saamien välillisten hyötyjen merkitystä naaraan suosivan parinvalinnan evoluutiolle on oleellisena osana otettava huomioon myös kustannukset, joita parinvalinnasta naaraalle aiheutuu. Koska naaraan parinvalintakustannukset vaikuttavat *H. rubrofasciata*lla suhteellisen pieniltä, saattavat verrattain pienetkin naaraan saavuttamat hyödyt jälkekäispolven elinkyvyssä olla evolutiivisesti merkittäviä. Onkin todennäköistä, että myös muissa vastaavanlaisissa pariutumisjärjestelmissä naaraat voivat parinvalinnallaan saavuttaa epäsuoria hyötyjä.

Väitöskirjatyön osatutkimusten perusteella voidaankin todeta, että *Hygrolycosa rubrofasciata* naarailla on mahdollisuus käyttää paitsi koiraan rummutusaktiivisuutta, myös rummutuksen pituutta mittana arvioidessaan koiraan sekä fenotyyppistä että geneettistä laatua. Lisäksi naaraat saavat valikoivasta parinvalinnastaan välillistä hyötyä jälkeläistensä parempana elinkykynä.

REFERENCES

Alatalo, R. V., Glynn, C. & Lundberg, A. 1990. Singing rate and female attraction in pied flycatcher: An experiment. Anim. Behav. 39: 601-603.

Alatalo, R. V., Kotiaho, J., Mappes, J. & Parri, S. 1998. Mate choice for offspring performance: major benefits or minor costs? Proc. R. Soc. Lond. B. 265: 2297-2301.

Andersson, M. 1986. Evolution of condition-dependent sex ornaments and mating preferences: Sexual selection based on viability differences. Evolution 40: 804-816.

Andersson, M. 1994. Sexual selection. 599 p., Princeton University Press, Princeton.

Andersson, M. & Iwasa, Y. 1996. Sexual selection. Trends Evol. Ecol. 11: 53-58.

Arnold, S. J. & Wade, M. J. 1984a. On the measurement of natural and sexual selection: theory. Evolution 38: 709-719.

Arnold, S. J. & Wade, M. J. 1984b. On the measurement of natural and sexual selection: applications. Evolution 38: 720-734.

Bailey, W. J., Cunningham, R. J. & Lebel, L. 1990. Song power, spectral distribution and female phonotaxis in the bushcricket Requena verticalis (Tettigoniidae: Orthoptera): Active female choice or passive attraction. Anim. Behav. 40: 33-42.

Bailey, W. J., Withers, P. C., Endersby, M. & Gaull, K. 1993. The energetic costs of calling in the bushcricket Requena verticalis (Orthoptera: Tettigoniidae: Listroscelidinae). J. exp. Biol. 178: 21-37.

Bakker, T. C. M. 1993. Positive genetic correlation between female preference and preferred male ornament in sticklebacks. Nature 363: 255-257.

Bakker, T. C. M. & Milinski, M. 1991. Sequential female choice and the previous male effect in sticklebacks. Behav. Ecol. Sociobiol. 29: 205-210.

Boake, C.R.B. 1985. Genetic consequences of mate choice: a quantitative genetic method for testing sexual selection theory. Science 227: 1061-1063.

Brown, W. D., Wideman, J. & Andrade, M. C. B. 1996. Female choice for an indicator of male size in the song of the black-horned tree cricket, Oecanthus nigricornis (Orthoptera: Gryllidae: Oecanthinae). Evolution 50: 2400-2411.

Buchanan, K. L. & Catchpole, C. K. 1997. Female choice in the sedge warbler, Arocephalus schoenobaenus: multiple cues from song and territory quality. Proc. Roy. Soc. Lond. B. 264: 521-526.

Butlin, R. K., Hewitt, G. M. & Webb, S. F. 1985. Sexual selection for intermediate optimum in Chorthippus brunneus (Orthoptera: Acrididae). Anim. Behav. 33: 1281-1292.

Castellano, S. & Giacoma, C. 1998. Stabilizing and directional female choice for male calls in the European green toad. Anim. Behav. 56: 275-287.

Cherry, M. I. 1993. Sexual selection in the raucous toad, Bufo rangeri. Anim. Behav. 45: 359-373.

Cunningham, E. J. A. & Birkhead, T. R. 1998. Sex roles and sexual selection. Anim. Behav. 56: 1311-1321.

Darwin, C. 1871. The descent of man, and selection in relation to sex. Murray, London.

Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197: 215-223.

Falconer, D. S. 1989. Introduction to quantitative genetics. 438 p., Longman, Essex, 3rd edition.

Forsgren, E. 1997. Female sand gobies prefer good fathers over dominant males. Proc. Roy. Soc. Lond. B. 264: 1283-1286.

Forsgren, E., Karlsson, A. & Kvarnemo, C. 1996. Female sand gobies gain direct benefits by choosing males with eggs in their nests. Behav. Ecol. Sociobiol. 39: 91-96.

Gerhardt, H. C. 1991 Female mate choice in treefrogs: staticand dynamic criteria. Anim. Behav. 42: 615-635

Grafe, T. U. 1997. Costs and benefits of mate choice in the lek-breeding reed frog, Hyperolius marmoratus. Anim. Behav. 53: 1103-1117.

Grafen, A. 1990a. Sexual selection unhandicapped by Fisher process. J. theor. Biol. 144: 473-516.

Grafen, A. 1990b. Biological signals as handicaps. J. theor. Biol. 144: 517-546.

Gray, D. A. 1997. Female house crickets, Acheta domesticus, prefer the chrips of large males. Anim. Behav. 54: 1553-1562.

Gwynne, D. T. 1988. Courtship feeding and the fitness of female katydids (Orthoptera: Tettigoniidae). Evolution 42: 545-555.

Halliday, T. R. 1983. The study of mate choice. In: P. Bateson (ed.), Mate choice: 3-32. Cambridge University Press, Cambridge.

Hasselquist, D., Bensch, D. & von Schantz, T. 1996. Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. Nature 381: 229-232.

Hedrick, A. V. 1986. Female preferences for male calling bout duration in a field cricket. Behav. Ecol. Sociobiol. 19: 73-77.

Hoelzer, G. A. 1989. The good parent process of sexual selection. Anim. Behav. 38: 1067-1078.

Hoikkala, A. & Aspi, J. 1993. Criteria of female mate choice in Drosophila littoralis, D. montana, and D. ezoana. Evolution 47: 768-777.

Hoikkala, A. & Isoherranen, E. 1997. Variation and repeatability of courtship song characters among wild-caught and laboratory-reared Drosophila montana and D. littoralis males (Diptera: Drosophilidae). J. Insect Behav. 10: 193-202.

Howard, R. D., Whiteman, H. H. & Schueller, T. I. 1994. Sexual selection in American toads: a test of good genes hypothesis. Evolution 48: 1286-1300.

Iwasa, Y., Pomiankowski, A. & Nee, S. 1991. The evolution of costly mate preferences II. The "handicap" principle. Evolution 45: 1431–1442.

Janetos, A. C. 1980. Strategies of female mate choice: a theoretical analysis. Behav. Ecol. Sociobiol. 7: 107-112.

Jang, Y. & Greenfield, M. D. 1996. Ultrasonic communication and sexual selection in wax moths: female choice based on energy and asynchrony of male signals. Anim. Behav. 51: 1095-1106.

Johnstone, R. A. 1995. Sexual selection, honest advertisement and the handicap

principle: reviewing the evidence. Biol. Rev. 70: 1-65.

Kirkpatrick, M. 1982. Sexual selection and the evolution of female choice. Evolution 36: 1-12.

Kirkpatrick, M. & Ryan, M. J. 1991. The evolution of mating preferences and the paradox of the lek. Nature 350: 33-38.

Kotiaho, J. S. 1999. Testing the assumptions of conditional handicap theory: costs and condition dependence of a sexually selected trait. Submitted.

Kotiaho, J., Alatalo, R. V., Mappes, J. & Parri, S. 1996. Sexual selection in a wolf spider: male drumming activity, body size, and viability. Evolution 50: 1977-1981.

Kotiaho, J. S., Alatalo, R. V., Mappes, J., Nielsen, M. G., Parri, S. & Rivero, A. 1998. Energetic costs of size and sexual signalling in a wolf spider. Proc. R. Soc. Lond. B. 265: 2203-2209.

Kotiaho, J. S., Alatalo, R. V., Mappes, J. & Parri, S. 1999. Sexual signalling and viability in a wolf spider (Hygrolycosa rubrofasciata): measurements under laboratory and field conditions. Behav. Ecol. Sociobiol. In press.

Kronestedt, T. 1984. Ljudalstring hos vargspindeln Hygrolycosa rubrofasciata. Fauna och Flora 79: 97-107.

Kronestedt, T. 1996. Vibratory communication in the wolf spider Hygrolycosa rubrofasciata (Araneae, Lycosidae). Rev. Suisse Zool. (hórs serie): 341-354.

Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. Proc. Natl. Acad. Sci. USA. 78: 3721-3725.

Majerus, M. E. N. 1986. The genetics and evolution of female choice. Trends Evol. Ecol. 1: 1-7.

Mappes, J., Alatalo, R. V., Kotiaho, J. & Parri, S. 1996. Viability costs of condition-dependent sexual male display in a drumming wolf spider. Proc. R. Soc. Lond. B. 263: 785-789.

Maynard Smith, J. 1976. Sexual selection and the handicap principle. J. theor. Biol. 57: 239-242.

Maynard Smith, J. 1991. Theories of sexual selection. Trends Evol. Ecol. 6: 146-151.

McGregor, P. K., Krebs, J. R. & Perrins, C. M. 1981. Song repertoires and lifetime reproductive success in the great tit (Parus major). Am. Nat. 118: 149-159.

Mitchell, S. L. 1990. The mating system genetically affects offspring performance in woodhouse's toad (Bufo woodhousei). Evolution 44: 502-519.

Møller, A. P. 1989. Viability costs of male tail ornaments in a swallow. Nature 339: 132-135.

Møller, A. P. 1994. Male ornament size as a reliable cue to enhanced offspring viability in the barn swallow. Proc. Natl. Acad. Sci. USA. 91: 6929-2932.

Møller, A. P. & Alatalo, R. V. 1999. Good-genes effects in sexual selection. Proc. Roy. Soc. Lond. B. 266: 85-91.

Møller, A. P. & deLope, F. 1994. Differential costs of a secondary sexual character: an experimental test of the handicap principle. Evolution 48: 1676-1683.

Moore, A. J. 1994. Genetic evidence for the "good genes" process of sexual selection. Behav. Ecol. Sociobiol. 35: 235-241.

Moore, A. J. & Moore, P. J. 1988. Female strategy during mate choice: threshold assessment. Evolution 42: 387-391.

Murphy, C. G. 1998. Interaction-independent sexual selection and the mechanisms of sexual selection. Evolution 52: 8-18.

Norris, K. 1990. Female choice and the quality of parental care in the great tit Parus major. Behav. Ecol. Sociobiol. 27: 275-281.

Norris, K. 1993. Heritable variation in a plumage indicator of viability in male great tits Parus major. Nature 362: 537-539.

Parri, S., Alatalo, R. V., Kotiaho, J. & Mappes, J. 1997. Female choice for male drumming in the wolf spider Hygrolycosa rubrofasciata. Anim. Behav. 53: 305-312.

Petrie, M. 1994. Improved growth and survival of offspring of peacocks with more elaborate trains. Nature 371: 598-599.

Pomiankowski, A. 1987. The costs of choice in sexual selection. J. theor. Biol. 128: 195-218.

Pomiankowski, A. & Iwasa, Y. 1993. Evolution of multiple sexual prefences by Fisher's runaway process of sexual selection. Proc. Roy. Soc. Lond. B. 253: 173-181.

Pomiankowski, A. & Møller, A. P. 1995. A resolution of the lek paradox. Proc. Roy. Soc. Lond. B. 260: 21-29.

Radesäter, T., Jakobsson, S., Andbjer, N., Bylin, A. & Nyström K. 1987. Song rate and pair formation in the willow warbler, Phylloscopus trochilus. Anim. Behav. 35: 1645-1651.

Real, L. 1990. Search theory and mate choice, I. Models of single-sex discrimination. Am. Nat. 136: 76-404.

Reinhold, K., Greenfield, M. D., Jang, Y. & Broce, A. 1998. Energetic costs of sexual attractiveness: ultrasonic advertisement in wax moths. Anim. Behav. 55: 905-913.

Reynolds, J. H. & Gross, M. R. 1990. Costs and benefits of female mate choice: is there a lek paradox? Am. Nat. 136: 230-243.

Reynolds, J. H. & Gross, M. R. 1992. Female mate preference enhances offspring growth and reproduction in a fish, Poecilia reticulata. Proc. Roy. Soc. Lond. B. 250: 57-62.

Ritchie, M. G., Yate, V. H. & Kyriacou, C. P. 1994. Genetic variability of the interpulse interval of courtship song among some European populations of Drosophila melanogaster. Heredity 72: 459-464.

Rowe, L. & Houle, D. 1996. The lek paradox and the capture of genetic variance by condition dependent traits. Proc. Roy. Soc. Lond. B. 263: 1415-1421.

Ryan, M. J. 1988. Energy, calling, and selection. Amer. Zool. 28: 885-898.

Ryan, M. J. & Keddy-Hector, A. 1992. Directional patterns of female mate choice and the role of sensory biases. Am. Nat. 139: S4-S35.

Savalli, U. M. & Fox, C. W. 1998. Sexual selection and fitness consequences of male body size in the seed beetle Stator limbatus. Anim. Behav. 55: 473-483.

von Schantz, T., Göransson, G., Andersson, G., Fröberg, I., Grahn, M., Helgée, A. & Wittzell, H. 1989. Female choice selects for viability-based male trait in pheasants. Nature 337: 166-169.

Schüch, W. & Barth, F. G. 1985. Temporal patterns in the vibratory courtship signals of the wandering spider Cupiennius salei Keys. Behav. Ecol. Sociobiol. 16: 263-271.

Schüch, W. & Barth, F. G. 1990. Vibratory communication in a spider: female responses to synthetic male vibrations. J. Comp. Physiol. 166: 817-826.

Semlitsch, R. D. 1994. Evolutionary consequences of non-random mating: do large males increase offspring fitness in the anuran Bufo bufo? Behav. Ecol. Sociobiol. 34: 19-24.

Sheldon, B., Merilä, J., Qvarnström, A., Gustafsson, L. & Ellegren, H. 1997. Paternal genetic contribution to offspring condition predicted by size of male secondary sexual character. Proc. Roy. Soc. Lond. B. 264: 297-302.

Sokal, R. R. & Rohlf, F. J. 1973. Introduction to biostatistics. 368 p., W. H. Freeman & Co., San Francisco.

Sigurjónsdóttir, H. & Parker G. A. 1981. Dung fly struggles: evidence for assessment strategy. Behav. Ecol. Sociobiol. 8: 219-230.

Simmons, L. W. 1988. The calling song of the field cricket, Gryllus bimaculatus (de Geer): constraints on transmission and its role in intermale competition and female choice. Anim. Behav. 36: 380-394.

Sulllivan, B. K. 1983. Sexual selection in Woodhouse's Toad (Bufo woodhousei) II. Female choice. Anim. Behav. 31: 1011-1017.

Sullivan, B. K. & Hinshaw, S. H. 1992. Female choice and selection on male calling behaviour in the grey treefrog, Hyla versicolor. Anim. Behav. 44: 733-744.

Taylor, C. E., Perada, A. D. & Ferrari, J. A. 1987. On the correlation between mating success and offspring quality in Drosophila melanogaster. Am. Nat. 129: 721-729.

Taylor, P. D. & Williams, G. C. 1982. The lek paradox is not resolved. Theor. Pop. Biol. 22: 392-409.

Thornhill, R. & Alcock, J. 1983. The evolution of insect mating systems. 547 p., Harvard University, Cambridge, Mass.

Turner, G. F. 1995. The lek paradox resolved? Trends. Evol. Ecol. 10: 473-474.

Vehrencamp, S. L., Bradbury, J. W. & Gibson, R. M. 1989. The energetic costs of display in male sage grouse. Anim. Behav. 38: 885-896.

Watson, P. J. & Lighton, J. R. B. 1994. Sexual selection and the energetics of copulatory courtship in the sierra dome spider, Linyphila litigiosa. Anim. Behav. 48: 615-626.

Wells, K. D. & Taigen, T. L. 1989. Calling energetics of a neotropical treefrog, Hyla microcephala. Behav. Ecol. Sociobiol. 25: 13-22.

Welch, A. M., Semlitsch, R. D. & Gerhardt, H. C. 1998. Call duration as an indicator of genetic quality in male gray tree frogs. Science 280: 1928-1930.

Wiley, R. H. & Poston, J. 1996. Indirect mate choice, competition for mates, and coevolution of the sexes. Evolution 50: 1371-1381.

Woodward, B. D. 1986. Paternal effects on juvenile growth in Scaphiopus multiplicatus (The new Mexico spadefoot toad). Am. Nat. 128: 58-65.

Zahavi, A. 1975. Male selection – selection for a handicap. J. theor. Biol. 53: 205–214.

Zahavi, A. 1977. The cost of honesty (further remarks on the handicap

principle). J. theor. Biol. 67: 603-605.

Zuk, M., Johnson, K., Thornhill, R. & Ligon, D. 1990. Mechanism of female choice in red jungle fowl. Evolution 44: 477-485.

Zuk, M. & Kolluru, G. R. 1998. Exploitation of sexual signals by predators and parasitoids. Quart. Rev. Biol. 73: 415-438.

Original papers

I

Female choice for male drumming in the wolf spider
Hygrolycosa rubrofasciata

by

Silja Parri, Rauno V. Alatalo, Janne Kotiaho and Johanna Mappes

II

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

by

Ana Rivero, Rauno V. Alatalo, Janne S. Kotiaho,
Johanna Mappes and Silja Parri

III

Experiments on male drumming characteristics in
spider *Hygrolycosa rubrofasciata*

by

Silja Parri, Rauno V. Alatalo, Janne S. Kotiaho,
Johanna Mappes and Ana Rivero

Manuscript, 1999

IV

Mate choice for offspring performance:
major benefits or minor costs?

by

Rauno V. Alatalo, Janne Kotiaho, Johanna Mappes and Silja Parri

V

Offspring growth in a drumming wolf spider –
effects of sire size and sexual attractiveness

by

Silja Parri, Rauno V. Alatalo, Janne S. Kotiaho and Johanna Mappes

Manuscript, 1999