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Janne Kotiaho

Sexual Selection and Costs  
of Sexual Signalling  
in a Wolf Spider



UNIVERSITY OF JYVÄSKYLÄ

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Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella  
julkisesti tarkastettavaksi yliopiston vanhassa juhlasalissa  
huhtikuun 12. päivänä 1997 kello 12.

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BIOLOGICAL RESEARCH REPORTS FROM THE UNIVERSITY OF JYVÄSKYLÄ 55

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Publishing Unit, University Library of Jyväskylä

URN:ISBN:978-951-39-8352-9

ISBN 978-951-39-8352-9 (PDF)

ISSN 0356-1062

ISBN 951-34-0961-9

ISSN 0356-1062

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Jyväskylä University Printing House,  
Jyväskylä and ER-Paino, Lievestuore 1997

*For those whom I love the most,  
Anne and my parents*

*Hello, I love you won't you tell me your name*

*— The Doors —*

## ABSTRACT

Kotiaho, Janne

Sexual selection and costs of sexual signalling in a wolf spider

Jyväskylä: University of Jyväskylä, 1997, 25 p.

(Biological Research Reports from the University of Jyväskylä, ISSN 0356-1062; 55)

ISBN 951-34-0961-9

Yhteenveto: Seksuaalivalinta ja seksuaalisen signaloinnin kustannukset  
Diss.

There are two major theories of sexual selection that both assume female choice of a costly male trait. They differ in respect to how they consider the costs of a trait; Fisherian self-reinforcing theory of sexual selection assumes no condition dependence of the costs, while viability indicator or handicap theory is based on the condition dependent costs of male trait. This thesis concentrates on sexual selection and especially on costs of male sexual signalling. As a study object I have used the wolf spider *Hygrolycosa rubrofasciata*, in which males court females with an audible drumming signal. The studies were mainly conducted in laboratory but there is also some field data presented. Females of the species actively prefer to mate with the most actively drumming males. Male drumming activity is dependent on male phenotypic condition and it is positively related to male viability. Drumming may serve as a honest indicator of viability since it provokes costs on the drumming males. More actively drumming males suffer increased mortality. This mortality may be due to energetically highly expensive drumming. There is also a possibility for direct predation costs on more actively drumming males. Especially large males suffered high energetic expenditure per mass unit. Under harsh conditions larger males seem to be better surviving suggesting that larger males may have more resources to use than smaller males. This study provides convincing empirical evidence that an viability indicator process based on costly male traits reflecting heritable viability and thus genetic benefits for offspring is involved in the evolution of sexual selection through female choice.

Key words: Conditional handicap; costs; female choice; *Hygrolycosa rubrofasciata*; indicator mechanism; predation; sexual selection; sexual signalling; viability; wolf spider.

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## LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which will be referred to in the text by the Roman numerals I - V. I have personally written papers I, III - V and performed most of the work. In paper II I have performed a significant proportion of the work.

- I Kotiaho, J., Alatalo, R. V., Mappes, J., & Parri, S. 1996. Sexual selection in a wolf spider: drumming activity, body size and viability. - *Evolution* 50: 1977-1981.
- II 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.
- III Kotiaho, J., Alatalo, R. V., Mappes, J., & Parri, S. 1997. Field and laboratory measurements of male sexual signalling and condition in a wolf spider. - Manuscript (submitted).
- IV Kotiaho, J., Alatalo, R. V., Mappes, J., Parri, S., & Rivero, A. 1997. Energetic cost of size and sexual signalling in a wolf spider. - Manuscript.
- V Kotiaho, J., Alatalo, R. V., Mappes, J., Parri, S., & Rivero, A. 1997. Male mating success and risk of predation in a wolf spider: a balance between sexual and natural selection? Manuscript (submitted).



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# 1 SEXUAL SELECTION

## 1.1 Sexual selection as a component of natural selection

Natural selection is a process that results from the heritable variation of characteristics giving rise to fitness differences between individuals. On the basis of the different nature of the fitness differences natural selection may be divided into different subsets. One division is to sexual and non-sexual selection, where non-sexual selection consists of mortality selection and differences in reproductive success beyond the sexual selection (Endler 1986). Sexual selection may be defined as fitness differences that arise from variation in traits causing differential mating success. Other aspects of reproductive success may also be included in sexual selection (Andersson 1994), but because of the difficulties in interpretations it is better to stick with the original meaning of sexual selection (Wade & Arnold 1980, Arnold 1983, Endler 1986). Therefore I will restrict the use of sexual selection to the fitness differences that arise from variation in traits affecting mating success.

Sexual selection has traditionally been divided into two major categories: competition over mates and mate choice. However, this division is not entirely clear and it has been suggested that it could be better to talk about competition over mates and competition over being chosen by a mate, in which case all of the competition would take place within one sex (e.g. Andersson & Iwasa 1996). However, since mostly the

literature still uses the division of sexual selection to competition over mates and to mate choice (see e.g. Andersson 1994), I will be using this division throughout this thesis. By definition females are the sex that produces few large and nutritious eggs and males the sex that produces outstanding numbers of small cheap sperm. Already Darwin (1871) noted that there are differences between sexes in investment to the gametes and generally the relative investment in offspring between the sexes should determine which sex is competing and which sex is choosing (Williams 1966, Trivers 1972, Andersson 1994).

In this thesis I present results of work on sexual selection in a wolf spider *Hygrolycosa rubrofasciata*. I concentrate on female choice and especially on the costs of male sexual trait. *H. rubrofasciata* is a small wolf spider (Lycosidae) occurring patchily throughout Finland in open and moist bogs and abandoned fields. Males display by drumming on dry leaves with their abdomen. Females respond to this display by shaking their body, after which the mating follows. Almost immediately after mating males engage in courtship again seeking for another female to mate with. Thus, there is no evidence for males to be investing in their offspring other than providing the sperm. Instead, females lay a clutch of eggs, which they carry with them until the spiderling hatch and disperse. Therefore, in *H. rubrofasciata* females are investing more to the offspring than males and thus one may expect females to be choosing their mating partners and males to be competing. In laboratory experiment on female choice (I), I showed how females preferentially mate with more actively drumming males. This preference is not a result of females passively responding to any signal, which would result a higher chance of response for males with higher drumming activity. Instead, females preferred males with higher drumming rate significantly more than expected from the activity differences only (I) (Fig. 1). There is also further evidence for the female choice in *H. rubrofasciata*. With a playback experiment Parri et al. (1997) demonstrated how females prefer signals occurring more frequently. Furthermore, when female movement is restricted and thus possibly female choice is slightly limited, more actively drumming males still achieved most matings (V).

## 1.2 Sexual selection with no direct benefits

There are two major theories of sexual selection that are based on female choice of a male sexual character: The Fisherian self-reinforcing theory of sexual selection and the viability indicator mechanism theory of sexual

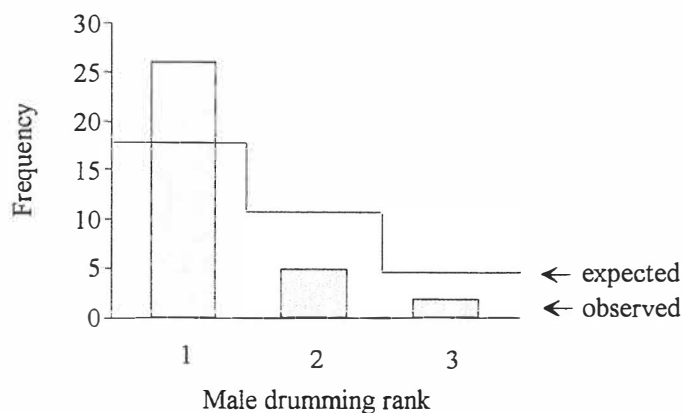


FIGURE 1 Female choice in relation to male drumming activity. In x-axis 1 represents most active males, 2 intermediately active males and 3 least active males. The expected distribution was derived from the assumption that probability of females to respond is similar after each single male drumming,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

selection. Fisherian sexual selection is based on assumptions that there is heritable variation in male trait size and that female choice is genetically coupled to male trait such that certain female genotypes will preferentially mate with certain male genotypes (Fisher 1930). When an increasing number of females prefer larger male traits there will develop an accelerating feedback for larger trait and increasing preference for the trait. This process is called runaway process. Costs of the exaggerated expression of sexual trait will finally prevent further exaggeration of the trait creating an equilibrium line between costs and benefits of the trait and thus putting the runaway process to a rest (Fisher 1930, O'Donald 1980, Lande 1981, Kirkpatrick 1982). Later modifications of the model including the cost of choice made this equilibrium to change drastically (Kirkpatrick 1982, Pomiankowski 1987a, 1988, Bulmer 1989). However, if a male trait is a target of biased mutations tending to reduce it rather than increase it then an equilibrium may be achieved and costly female choice may evolve. At equilibrium the costs of choice are balanced through females bearing more attractive male offspring (Pomiankowski 1991).

The viability indicator mechanisms theory of sexual selection is based on the assumption that a costly male trait becomes a target of female choice because it reflects a high heritable viability of the male. Zahavi (1975) was the first who really advocated the idea and named it as a handicap principle. His early handicap principle was severely criticised (e.g. Maynard Smith 1976, Davis & O'Donald 1976) because simple mathematical models suggested that it could not work. However, Zahavi (1977) disputed the criticism and proposed that if one considers not only genetic components of male condition but also male phenotypic condition

then handicaps may work. Later work has showed that handicap principle may be modelled successfully especially if condition dependence of male trait is considered (e.g. Andersson 1982, Pomiankowski 1987b, 1988, Heywood 1989, Hoelzer 1989, Grafen 1990a, b, Iwasa et al 1991). Currently accepted conditional handicap theory has two major assumptions. Firstly the trait has to be costly to produce or maintain. If there is no costs of increase in trait size the trait cannot be a honest indicator of male viability. Secondly, males in better phenotypic condition should be better able to bear the costs of increased trait size than males in poor phenotypic condition (Fig. 2).

Both of the sexual selection theories assume costs of male secondary sexual traits. These two theories differ in respect to how they consider the male ability to bear costs. In Fisherian self-reinforcing theory males are not considered to vary in their ability to bear costs and thus male condition is not considered to influence the expression of the sexual trait. Instead, the ability to bear costs differentially depending on male condition is the crux of the conditional handicap models, and male condition is assumed to be positively related to the expression of the sexual trait (Fig. 2).

In this thesis the condition dependence of male sexual signalling was studied in the laboratory by experimentally manipulating male phenotypic condition (II). Males were kept in three different food levels and their drumming activity and body mass were monitored. Males in the highest food level maintained their drumming activity while males in the lower levels decreased it. Also males body mass differed in the end of

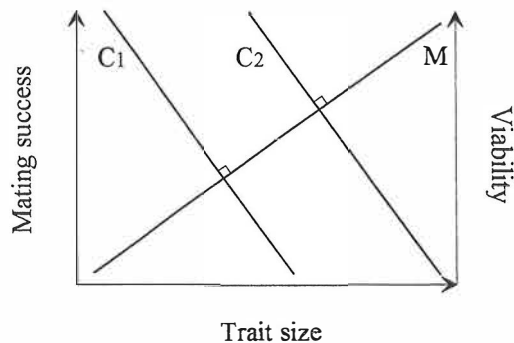


FIGURE 2 Graphical illustration of viability indicator model. Male mating success (line M) increases and male viability (lines C1 and C2) decreases with the increase of male trait size. Line C1 indicates males that are in condition 1 and C2 males that are in condition 2 (condition 2 > 1). From the graph one can see that for given size of a trait, viability of a male in better condition is higher and that the optimal trait size (intersection of lines M and C) for males in better condition is also higher.

the experiment (II). Thus it seems that male drumming activity is condition dependent. There is also a positive correlation between male drumming activity and viability in laboratory (I, II, III) as well as in the field (III). Furthermore, activity is positively correlated with another measure of male condition; males that were best able to sustain maximal physical exertion were also most active in drumming (IV). These results clearly show that in *H. rubrofasciata* male sexual trait is dependent on male phenotypic condition and that there is a positive relationship between the trait and male condition measured as viability and physical endurance. Thus, it seems that this system supports the conditional handicap theory of sexual selection fulfilling the assumption that the sexual trait is dependent on male phenotypic condition and males in good condition are better able to bear the possible costs of increased trait size. What about the costs then? The assumption in the theory is that males differ in their ability to bear costs. Therefore it is essential to demonstrate that there are costs of sexual traits.

## **2 COSTS OF SEXUAL TRAITS**

### **2.1 What are the costs of sexual traits?**

There seems to be considerable disagreement about the use of the term cost as well as the term sexual trait. In evolutionary terms, only such expression of the trait that affects negatively male fitness may be considered to be costly and only such traits that affect positively male mating success may be considered to be sexual traits. Therefore I would reserve the use of the term cost to those cases where sexual signalling ultimately leads to increased mortality or possibly to decreased fecundity, and sexual trait to those cases where male mating success is increased because of the increased expression of the trait. The increase in mating success may be due to direct female choice of the trait or it may be due to the positive effect of the trait in male-male competition resulting in increased mating success. Costs resulting from the increased sexual trait size may be divided into two broad categories: physiological costs and direct costs.

## 2.2 Physiological costs

Physiological costs such as mortality due to increased energy expenditure are often difficult to demonstrate since males are expected to optimise their level of signalling in respect to their condition in each situation. However, it is well established that sexual displays are highly energetically demanding (e.g. Halliday 1987). Increased energy expenditure of the expression of sexual trait may lead to decreased survival, but the evidence up to date is minimal relying on only one species. In the barn swallow *Hirundo rustica* experimental increase in male secondary sexual trait, the length of the outermost tail feathers, caused increased mortality (Møller 1989, Møller & deLope 1994). However, only those males that naturally, before the manipulation had shorter tails suffered increased mortality indicating that males with naturally long tails are in better condition and are able to bear the costs of increased tail length better than shorter tailed males. Prior to work presented in this thesis this was the only evidence of physiological costs causing detrimental fitness consequences. In *H. rubrofasciata* male sexual signalling activity may be manipulated without the risk of manipulation itself having any side effect. This may be accomplished by manipulating only the environment; when males are placed in the vicinity of a virgin female they spontaneously increase their drumming activity. When males induced to increase their drumming activity were compared to other males there was a significant difference in survival between the treatments. Males induced to increase their drumming activity suffered higher mortality (II) (Fig. 3). Thus, when males are induced to invest more

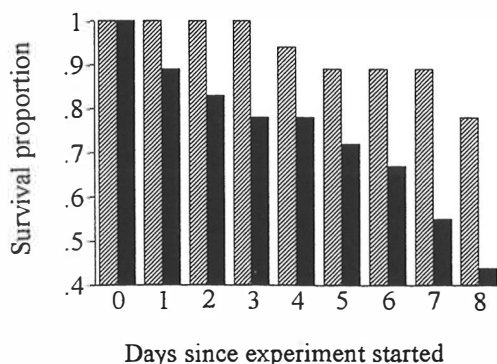


FIGURE 3 Proportions of males surviving during the experiment. Black bars represent males in high drumming rate treatment and shaded bars males in low drumming rate treatment.



to the drumming they are doing it voluntarily and presumably in relation to their phenotypic condition. This was evident since even though males with increased drumming activity suffered higher mortality, within the treatment group there was a positive correlation between drumming activity and survival (II).

With direct measurements of male metabolic rate I was able to reveal the mechanism which possibly underlies the increased mortality (IV). Male metabolic rate during sexual signalling was 22 times the basal metabolic rate. With an empirical model I showed that males that are moving around to search for females are able to drum only up to a certain number of times before reaching the maximum sustainable level of energy expenditure (Fig. 4). Interestingly the number of drums a male was able to perform was highly dependent on male body mass (IV). Thus, for larger males the maximum number of drums per minute was only 12 while for smaller males the maximum is more than three times higher. Such a differential cost of body mass on male sexual signalling should obviously have an effect on male sexual signalling activity. However, there is no correlation between male drumming activity and body mass (I, II III, IV). Furthermore, it seems that larger males may have a slight survival advantage during increased drumming activity compared to smaller males (II). Thus it seems that larger males may have proportionally more energy reserves to use than smaller males. Large size seems to benefit males also through male-male competition (Kotiaho et al. 1997a). However, even if larger males are able to repel smaller males

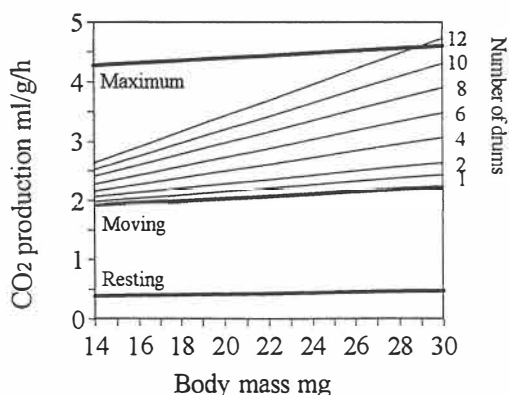


FIGURE 4 Empirical model of the increasing costs of drumming for larger males. In x-axis there is absolute body mass of the males and in the y-axis there is the CO<sub>2</sub> production per mass unit per hour. Thick lines show slopes of CO<sub>2</sub> production in relation to body mass during resting, moving and maximal exertion. Thin lines show slopes of CO<sub>2</sub> production for males that are moving and drumming 1, 2, 4...12 times. For example a 30 mg male may drum only up to 12 times before reaching the maximum sustainable level, while the corresponding number would be 39 times for 14 mg male.

in fights there seems to be no large male mating advantage (I). There is a positive correlation between male body mass and the distance moved in the field (III). Also males moving longer distances lost less mass than male moving shorter distances providing additional support for the assumption that larger males may be better able to compensate the energy requirements of different activities.

### 2.3 Direct costs

Direct costs such as predation should increase the risk of mortality in proportion to the signalling rate and basically may be independent of male condition. However, in such a case, that male condition would affect his probability to be able to escape from the predator, direct costs may be dependent on male condition and the risk would not increase directly in proportion to signalling rate. To demonstrate empirically that this is the case, one should test whether actively signalling males would be better in escaping each predation attempt. Only then one may say that male sexual signalling is condition dependent and is not increasing the risk of predation proportionally to the rate of signalling. There is plenty of suggestive data that predation may be a major cost on sexually signalling males (see e.g. Burk 1982, Andersson 1994). Majority of the data are however, observational and does not tell the magnitude of predation in field conditions. To be able to show that predation is a relevant cost one has to demonstrate firstly that predation towards signalling males occurs frequently enough to cause a threat on males and secondly that the increase in sexual signalling will lead to increase in predation risk.

I studied the possible direct costs of male sexual signalling with a predation study in the laboratory (V). As a predator I used the common lizard *Lacerta vivipara*, that is a natural predator of the species. Male sexual signalling activity decreased drastically after the lizard introduction and most males stopped their drumming altogether (V). In addition eight out of the 60 males (13.3%) were observed and taken by the lizard because of the drum. This provides evidence that predation occurs and indirect evidence that signalling may be costly for the male in terms of increased risk of predation. However, there was only a small tendency towards a negative relationship between male drumming activity and the predation order (V) giving only weak support for the assumption that more signalling males are in higher risk of being preyed. Because males reduced their drumming activity so drastically in the presence of the predator this test is not very vigorous and thus

future work will have to show if predation is provoking significant costs on signalling males.

In the same predation study (V) I studied another male trait: male mobility. In the field males are moving actively (III, Kotiaho et al. 1997b) presumably searching for females and thus fall in the risk of being noticed by lizards. In trials with three males, male mobility was a good predictor of male mating success (V). Males searching more actively thus also find more receptive females to mate with. It is not likely that male moving activity would be a target of female choice. However, since females do not move much in the field during the mating season (Kotiaho et al. 1997b), male searching activity and thus mobility could be an additional test of male quality. In any case, whether mobility is under choice or not it is obvious that since it increases male mating success there should be also counterbalancing costs on it. Male moving is energetically expensive requiring five times more energy than resting (IV). However, from the predation study it seems that the risk of predation may be more important. Males moving more were most likely to be predated (V), mobility thus imposing a significant cost on males.

### 3 CONCLUSIONS

The conditional handicap theory of sexual selection is based on the assumption that a costly male trait becomes a target of female choice because it reflects a high heritable viability of the male. In this thesis I have presented empirical evidence for the existence of the female choice on male trait that reflects male viability (I, II, III, V) and is costly to produce (II, IV, V). There is however one more crucial assumption that has not been considered in this thesis. This is the benefits that the female gets from her choice; the assumption that male trait reflects a high heritable viability. This aspect was studied with a selection experiment on male drumming activity (Alatalo et al. 1997). This experiment revealed that the offspring of more actively drumming males had a small but significant survival benefit compared to the offspring of less actively drumming males. Thus, the last assumption of conditional handicap theory of sexual selection seems to be fulfilled. I believe that the work presented in this thesis provides convincing evidence that an indicator process based on costly male traits reflecting heritable viability and thus genetic benefits for offspring is involved in the evolution of sexual selection through female choice.

## *Acknowledgements*

I am lucky in a sense that I have had two supervisors that both have helped me to see that world is not so black and white - and that I am not always right. The other one I thank for being a great opponent in verbal wars we had from sports and nationalism to sexes equality, religion and evolution. I thank her for giving me support and encouragement in my time consuming non-scientific engagements when ever I needed it even if it was in the middle of the busiest field season. The other one I thank for being such a nice chap. I thank him for being simultaneously flexible and demanding, so enthusiastic and impatient (sometimes a bit too impatient). His optimism makes the worst catastrophes look like discoveries of the century. The only thing this couple could have been giving me more is mayby opportunities for real constructive conversations. Thank you Jonna and Rauno, research presented here would not have been possible without both of your supervision. Then of course there is Silja. Probably this spider project still exists largely because of her taking care of the practical matters - sometimes she has been called "the leader" of the project. She has helped me in planning the work and in performing the work. She is the one who minds the details for me when I myself forget them. Thank you Silja. Ana Rivero I thank for all the help she provided especially with the English. She brought colour and energy to the spider group even though she never taught me to dance salsa. Thank you Ana.

I thank all my colleagues in Freda especially Pirkko Siikamäki and Matti Hovi. As my closest colleagues outside the spider project they have helped me by answering the millions of questions I have had and by giving constructive comments on my work. Pirkko and Matti thanks for bravely bearing all the disturbance. I thank Mervi and Petri Ahlroth for sharing with me the whole time we have been in the university. Jari Haimi, Matti Halonen, Taina Horne, Esa Huhta, Ari Jäntti, Esa Koskela, Jouni Laakso, Leena Lindström, Jyrki Pusenius, Tapio Mappes, Veikko Salonen, Heikki Setälä, Jukka Suhonen, Jouni Taskinen, Jussi Viitala, Hannu Ylönen I thank for being my colleague and giving support during this work (now if You were forgotten sorry and thanks). I also express my thanks to the staff of Konnevesi Research station.

I thank all my choir friends in male choir Sirkat. This brotherhood and especially friends belonging to the Male Choir Grasshoppers have helped me to forget the work on weekly basis and provided variation to the routine. Singing in this group gives me more satisfaction than you can think of. I thank also all the guys in the band that we had in Freda. This

band never really got a name but it was fun as long as it lasted. All musician's thank you.

My best friends Pekka and Anneli have provided me with a positive attitude towards life. Following them to the mountains of Lapland or to the primavel forests of eastern Finland I have been able to forget the stress of urban civilisation and feel the freedom of wild life. Thank you Pekka and Anneli, without you this thesis would not exist.

There are always the first ones and the last ones to be thanked, but I do not know which ones are more important. My mother and Father, Tuulikki and Sakari, they have always supported me in my struggle of life and career and provided resources and shelter when needed. The most important person for keeping me on the ground where people other than scientists live and preventing me from disappearing to the world of science is my dearest companion Anne. When I am lost and frustrated she shows me that there is more in the life than science. Thank you Anne, you are the one who keep me going!

## Yhteenveto

On olemassa kaksi seksuaalivalinnan teoriaa jotka pohjautuvat naaraan suorittamaan parittelukumppanin valintaan: Fisherin self-reinforcing teoria sekä elinkyvyn indikaattori-mekanismi -teoria. Molemmat teorit olettavat, että naaraat valitsevat koiraita sellaisten seksuaalisten ominaisuuksien perusteella, joiden tuottamisesta tai ylläpidosta koituu koiraalle kustannuksia. Nämä teorit eroavat kuitenkin siinä, että Fisherin self-reinforcing teoria ei oletta koiraan kunnolla olevan vaikutusta kustannusten sietokykyyn, kun taas elinkyvyn indikaattori-mekanismi -teoria puolestaan pohjautuu juuri eroon koiraiden kyvyssä sietää kustannuksia riippuen koiraan kunnosta. Tässä väitöskirjassa olen keskittynyt tutkimaan naaraan suorittamaa seksuaalista valintaa sekä erityisesti kustannuksia, joita koiraille aiheutuu seksuaalisesti valituista ominaisuuksista. Tutkimuskohteeni on juoksuhämähäkki *Hygrolycosa rubrofasciata* (Lycosidae). Tämän lajin koiraat rummuttavat kuivia lehtiä takaruumiillaan. Rummutus on selkeästi ihmisenkin kuultavissa oleva seksuaalinen signaali, ja tutkimuksessani osoitin, että sillä on tärkeä merkitys koiraan pariutumismenestykseen, koska naaraat suosivat aktiivisesti rummuttavia koiraita. Parittelussa naaras saa koiraalta vain siittiöt jälkeläistensä hedelmöittämiseen eikä mitään muita hyötyjä. Tutkimuksessa kävi ilmi, että koiraan rummutusaktiivisuus on riippuvainen koiraan kunnosta; koiraita pidettiin kolmessa ravintotasossa, ja kahdessa heikommassa ravintotasossa olevat koiraat laskivat rummutusaktiivisuuttaan. Koiraan rummutuksesta koituu koiraille myös kustannuksia. Koiraat, joita manipuloitiin rummuttamaan enemmän kuin mitä ne normaalisti rummuttaisivat, kuolivat nopeammin kuin kontrolli-koiraat osoittaen, että rummutuksesta aiheutuu koiraille kustannuksia. Vaikka koiraiden rummutuksesta aiheutuu kustannuksia, rummutus-aktiivisuuden ja koiraan elinkyvyn välillä on positiivinen riippuvuussuhde: koiraat jotka rummuttavat paljon elävät myös pidempään. Tämä korrelaatio johtuu siitä, että aktiivisesti rummuttavat koiraat ovat paremmassa kunnossa kuin vähemmän rummuttavat koiraat, ja täten sietävät paremmin rummutuksesta aiheutuvia kustannuksia. Toisinsanoen koiraat rummuttavat optimaalisella tasolla kuntoonsa nähden. Mekanismi joka aiheuttaa kuolevuuskustannuksen, näyttäisi olevan rummutuksen korkea energiankulutus; rummuttavien koiraiden energiankulutus nousi 22-kertaiseksi verrattuna perustasoon. Yksi kustannus rummutuksesta saattaisi olla myös kasvanut riski joutua saaliiksi. Koiraille, jotka rummuttivat enemmän oli taipumus joutua sisiliskon saaliiksi useammin kuin vähemmän rummuttavilla koiraille. Työssäni olen tutkinut myös koiraan koon vaikutusta seksuaalivalintaan

ja toisaalta myös luonnonvalintaan. Näyttäisi siltä, että suuresta koosta aiheutuu koiralle huomattavia energettisiä kustannuksia. Varsinkin rummutuksen aikana suurten koiraiden energiankulutus painoyksikköä kohden nousi yli kaksinkertaiseksi pienempiin koiraisiin verrattuna. Tästä huolimatta suuresta koosta näyttäisi olevan hyötyä koiraille, koska suuret koiraat, joita manipuloitiin rummuttamaan enemmän, selvisivät hengissä pidempään kuin vastaavassa tilanteessa pienemmät koiraat. Vaikuttaisi siis siltä, että suuret koiraat voivat olla paremmassa kunnossa ja siksi kestää rasitusta ja suurempaa energiankulutusta paremmin kuin pienemmät koiraat. Tässä työssäni olen testannut *H. rubrofasciata* hämähäkillä elinkyvyn indikaattori-mekanismi teorian toimivuutta ja osoittanut että teorian kaikki oletukset täyttyvät. Näinollen, elinkyvyn indikaattori-mekanismi, joka pohjautuu kustannuksia aiheuttaviin koiraan ominaisuuksiin, jotka heijastavat periytyvää hyvää elinkykyä, on osallisena naaraan valinnan kautta tapahtuvan seksuaalivalinnan evoluutiossa.



## REFERENCES

- Alatalo, R. V., Kotiaho, J., Mappes, J. & Parri, S. 1997. Lek paradox in a wolf spider - small benefits and minor costs. - Manuscript.
- Andersson, M. 1982. Sexual selection, natural selection and quality advertisement. - *Biol. J. Linn. Soc.* 17: 375-393.
- Andersson, M. 1994. *Sexual selection*. Princeton University Press, Princeton.
- Andersson, M. & Iwasa, Y. 1996. Sexual selection. - *Trends Evol. Ecol.* 11: 53-58.
- Arnold, S. J. 1983. Sexual selection: the interface of theory and empiricism. In: Bateson, P., (ed.), *Mate Choice*, 67-107. Cambridge University Press, Cambridge, UK
- Bulmer, M. G. 1989. Structural instability of models of sexual selection. - *Theor. Pop. Biol.* 35: 195-206.
- Darwin, C. 1871. *The descent of man, and selection in relation to sex*. Murray, London.
- Davis, J. W. F. & O'Donald, P. 1976. Sexual selection for a handicap: a critical analysis of Zahavi's model. - *J. theor. Biol.* 57: 345-354.
- Endler, J. A. 1986. *Natural selection in the wild*. Princeton University Press, Princeton, N.J.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Clarendon Press, Oxford.
- Grafen, A. 1990a. Sexual selection unhandicapped by the fisher process. - *J. theor. Biol.* 144: 473-516.
- Grafen, A. 1990b. Biological signals as handicaps. - *J. theor. Biol.* 144: 517-546.
- Halliday, T. R. 1987. Physiological constraints on sexual selection. In: Bradbury, J. W. & Andersson, M. B. (eds), *Sexual selection: testing the alternatives*, 247-264. Wiley, Chichester, UK
- Heywood, J. S. 1989. Sexual selection by the handicap mechanism. - *Evolution* 43: 1387-1397.
- Hoelzer, G. A. 1989. The good parent process of sexual selection. - *Anim. Behav.* 38: 1067-1078.
- Iwasa, Y., A. Pomiankowski & S. Nee 1991. The evolution of costly mate preferences. II. The handicap principle. - *Evolution* 45: 1431-1442.
- Kirkpatrick, M. 1982. Sexual selection and the evolution of female choice. - *Evolution* 36: 1-12.
- Kotiaho, J., R. V. Alatalo, J. Mappes & S. Parri 1997a. Male fighting success in relation to body size and drumming activity in the wolf spider *Hygrolycosa rubrofasciata*. - Manuscript (submitted).

- Kotiaho, J., R. V. Alatalo, J. Mappes & S. Parri 1997b. Habitat selection and sexual signalling activity in the wolf spider *Hygrolycosa rubrofasciata* (Araneae, Lycosidae). - Manuscript.
- Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. - *Proc. Natl. Acad. Sci.* 78: 3721-3725.
- Maynard Smith, J. 1976. Sexual selection and the handicap principle. - *J. theor. Biol.* 57: 239-243.
- Møller, A. P. 1989. Viability costs of male tail ornaments in a swallow. - *Nature* 339: 132-135.
- Møller, A. P. & deLope F. 1994. Differential costs of a secondary sexual character: an experimental test of the handicap principle. - *Evolution* 48: 1676-1683.
- O'Donald, P. 1980. Genetic models of sexual selection. Cambridge University Press, Cambridge, UK
- Parri, S., Alatalo, R. V., Kotiaho, J., & Mappes, J. 1997. Female preferences for male drumming in the wolf spider *Hygrolycosa rubrofasciata*. - *Anim. Behav.* (in press).
- Pomiankowski, A. 1987a. The cost of choice in sexual selection. - *J. theor. Biol.* 128: 195-218.
- Pomiankowski, A. 1987b. Sexual selection: the handicap principle does work - sometimes. - *Proc. R. Soc. Lond. B* 231: 123-145.
- Pomiankowski, A. 1988. The evolution of female mate preferences for male genetic quality. - *Oxford Surv. Evol. Biol.* 5: 136-184.
- Pomiankowski, A., Iwasa, Y., & Nee, S. 1991. The evolution of costly mate preferences: I. Fisher and biased mutation. - *Evolution* 45: 1422-1430.
- Trivers, R. L. 1972. Parental investment and sexual selection. In: Campbell, B. (ed.), *Sexual selection and the descent of man, 1871-1971*, 136-179. Heinemann, London, UK
- Wade, M. J. & Arnold S. J. 1980. The intensity of sexual selection in relation to male sexual behaviour, female choice, and sperm precedence. - *Anim. Behav.* 28: 446-461.
- Williams, G. C. 1966. *Adaptation and natural selection*. Princeton University Press, Princeton, N.J.
- Zahavi, A. 1975. Mate selection - a 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.

**ORIGINAL PAPERS**

**I**

**Sexual selection in a wolf spider: drumming activity, body size  
and viability**

By

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

Evolution 50: 1977-1981, 1996

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<https://doi.org/10.1111/j.1558-5646.1996.tb03584.x>

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**II**

**Viability costs of condition-dependent sexual male display  
in a drumming wolf spider**

By

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

Proc. R. Soc. Lond. B 263: 785-789, 1996

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**III**

**Field and laboratory measurements of male sexual signalling and  
condition in a wolf spider**

**By**

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

**Manuscript (Submitted), 1997**

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**IV**

**Energetic cost of size and sexual signalling in a wolf spider**

By

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

Manuscript, 1997

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V

**Male mating success and risk of predation in a wolf spider: a balance  
between sexual and natural selection?**

By

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

Manuscript (Submitted), 1997

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