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

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Summary

1. Traits that benefit males through sexual selection are simultaneously expected to impair males by provoking costs through natural selection. If we consider the two male fitness components, mating success and viability, then we may expect that the increase in male mating success resulting from a larger trait size will be counter-balanced by an increase in viability costs.

2. We studied the benefits and costs of male mate searching and sexual signalling activity in the wolf spider *Hygrolycosa rubrofasciata*. In the field, males search females actively and court them by drumming dry leaves with their abdomen. Females have been shown to prefer males with high drumming rate. Male moving and especially drumming is energetically highly demanding and drumming results in significant mortality costs.

3. Our objective in this study was to determine whether male mate-searching activity or drumming activity affect male mating success and the risk of males being predated.

4. It was evident that both higher mate-searching activity and higher drumming activity benefited males by increasing their mating success. Higher mate-searching activity clearly impaired males by causing direct increase in predation risk. There was also a slight tendency that more actively drumming males had higher risk of predation and from all of the predated males 13.3% were caught directly after they had drummed. Furthermore, male drumming activity decreased drastically in the presence of the predator.

5. We conclude that in *H. rubrofasciata* both increased mate-searching activity and drumming activity benefit males through sexual selection, but at the same time natural selection provokes direct balancing costs on the same traits.

Key-words: cost, *Hygrolycosa rubrofasciata*, mating success, predation risk, sexual signalling.

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Introduction

The expression of a sexual trait is expected to reflect a balance between natural and sexual selection (e.g. Endler 1982; Andersson 1994). In other words, the costs of producing a larger trait is likely to increase in parallel to the benefits gained through the increased size of the trait. Since fitness of a male may be ex-

pressed as viability times mating success, a trait may be expected to have a beneficial effect through sexual selection by increasing mating success, and an impairing effect by decreasing viability through natural selection. It is well documented that increased size of a sexual trait benefits the male through sexual selection by increasing his mating success (see, e.g. Andersson 1994, pp. 132–142; Johnstone 1995; Pomiankowski & Møller 1995). However, the evidence for natural selection balancing these benefits by provoking significant viability costs on the males bearing the increased size of the trait is not equally strong. The costs resulting from the increased size of a sexual trait

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may be direct (e.g. predation) or physiological (e.g. increased energy consumption). Physiological costs are difficult to demonstrate since animals normally display at an optimal level in respect to their condition, and thus it is likely that one cannot detect immediate increase in mortality. However, to qualify as a real cost causing detrimental fitness consequences, physiological costs have to ultimately increase the risk of mortality. Evidence for such physiological costs is limited to a few experimental studies (Møller 1989; Møller & de Lope 1994; Mappes *et al.* 1996).

Direct costs causing immediate mortality or reduced mating success are easier to determine than physiological costs. However, to show that direct costs have a balancing role, it is not enough just to observe that predation or parasitism occurs. Instead, it is necessary to show that predation or parasitism occurs frequently enough to be a significant threat for males and that there is a significant positive relationship between the expression of the sexually selected trait and the risk of predation or parasitism. There is some evidence that the need of the sexually signalling male to make himself conspicuous to females simultaneously increases the risk of being detected by predators or parasites (reviewed by Burk 1982; Thornhill & Alcock 1983; Sakaluk 1990; Magnhagen 1991; see also Andersson 1994). In particular, acoustic sexual signalling has been shown to be exploited by predators and parasites (e.g. Walker 1964; Cade 1975; Soper *et al.* 1976; Mangold 1978; Bell 1979; Doolan & Mac Nally 1981; Tuttle & Ryan 1981; Sakaluk & Bellwood 1984; Ryan 1985) but evidence for correlation between signalling activity and predation risk is nonexistent.

Hygrolycosa rubrofasciata (Ohlert) is a ground-dwelling wolf spider (Lycosidae) in which males move around the habitat actively and court females by drumming dry leaves with their abdomen. One drumming consists of ≈ 30–40 separate pulses and lasts ≈ 1 second (Kronestedt 1996). The sound produced is clearly audible and it has been demonstrated to be a target of female choice (Kotiaho *et al.* 1996; Parri *et al.* 1997). There is a positive correlation between male drumming activity and survival (Kotiaho *et al.* 1996), but experimental increase of male drumming activity causes also increased mortality (Mappes *et al.* 1996). Male drumming activity is energetically highly demanding (Kotiaho, unpublished data), and the increased mortality of actively drumming males is likely to be the result of increased energetic expenditure during the sexual signalling.

In this paper we report the results of two studies on the wolf spider *Hygrolycosa rubrofasciata*. Our objective comprises two components: the benefits and the costs of male mate searching and drumming activity. First, we focused on the possible benefits by determining whether male mate-searching activity or sexual signalling activity affect male mating success. Secondly, we focused on the possible direct costs by determining whether mate-searching activity or sexual signalling activity affect the risk of predation.

Methods

Spiders and predators (common lizard *Lacerta vivipara*) for the study were collected during April and early May 1996 in Southern Finland (60°16′N and 25°14′E). Lizards were collected from three populations separated by 500–1000 m and spiders from one of the populations. Lizards are natural predators of the spiders and both species occur sympatrically in all three sites. Spiders were housed individually in small plastic jars and food (*D. melanogaster*) and moisture were provided *ad libitum*. Lizards were housed outdoors individually in glass terrariums (20 × 25 cm) and food (other spider species and mealworms) and water were available continuously. One day before using the lizards in the test, food was removed from the terrarium to ascertain that lizards were motivated to hunt. After the tests lizards were released to nature.

MOBILITY, SEXUAL SIGNALLING AND MATING SUCCESS

We studied male mating success in relation to mobility and drumming activity in a plastic arena (450 × 450 mm), the bottom of which was covered with paper and dry birch leaves. We divided the arena into four equal rectangles and placed one unmated female in the centre of one of the rectangles in a small cotton net cage (diameter 30 mm). A circle (diameter 140 mm) around the female cage was cut loose from the paper covering the rest of the arena. We did this to prevent the vibrations resulting from male drumming and female responses to reach the opposite sex from a longer distance than from which they normally respond. Prior to the study we tested females with playbacks of male drumming to ensure they were all responsive and thus virgin and willing to mate. It is easy to determine unequivocally when and with which male a female is willing to mate because a receptive female responds immediately after the chosen male drumming bout by shaking her body vigorously.

In each trial ($n = 32$) we released three individually marked males into the centre of the rectangle opposite to the rectangle containing the female cage. Male mobility (i.e. how many times a male crossed the line separating the rectangles) and drumming activity were counted during the test until one of the males succeeded in mating with the female. We did not let the pair copulate, but we considered the male to have succeeded in mating when he had located the female, was drumming within 30 mm of the centre of the female cage, and the female responded to the male drumming. We had 15 receptive females and each of them was used in up to three trials. Each of the 96 males was used only once.

MOBILITY, SEXUAL SIGNALLING AND PREDATION

We studied the risk of predation in relation to male mobility and drumming activity in a similar plastic arena (450×450 mm), the bottom of which was covered with sand and dry birch leaves. We divided the arena into nine equal-sized squares and released three individually marked males to the arena. First, we observed the males for 10 min counting their mobility (number of line crossings) and drumming activity. Before the lizard was introduced into the arena, males were directed to one of the corners of the arena. The lizard was then released in the opposite corner. We observed male mobility and drumming activity until the lizard had eaten two of the spiders. Thus, we obtained the rank in which the males would have been predated. Each of the 10 lizards were used in three trials and all of the 90 males were used only once. Altogether we had 30 trials.

STATISTICAL TESTS

The design of the study generates non-independent observations when we analyse the effects of the lizard on the males (predation order vs. mobility and drumming activity). Thus, while the number of males was 90, the number of independent observations was only 30 (the number of the trials). To overcome the statistical problems we calculated a Pearson correlation coefficient between predation order and drumming activity and mobility for each of the 30 trials separately and tested whether the average of these coefficients is different from zero. All the probabilities are for two-tailed tests.

Results

MOBILITY, SEXUAL SIGNALLING AND MATING SUCCESS

Males that were most actively moving had higher mating success than less actively moving males (Fig. 1a).

Moving activity of the successful male was significantly higher than the mean of the two unsuccessful males (Wilcoxon paired rank test $z = 3.85$, $n = 31$, $P \ll 0.001$). Also, male drumming activity had a positive effect on male mating success (Fig. 1b). The drumming activity of the successful male was significantly higher than the mean of the two unsuccessful males (Wilcoxon paired rank test $z = 3.34$, $n = 32$, $P < 0.001$). There was no significant relationship between male mobility and drumming activity (Spearman's $r = 0.16$, $n = 96$, $P = 0.126$), and therefore, it seems that both male mobility and drumming activity increased male mating success independently.

MOBILITY, SEXUAL SIGNALLING AND PREDATION

Male moving activity had a strong negative effect on the predation order of the males (Paired t-test $t = 5.47$, d.f. $= 29$, $P \ll 0.001$) (Fig. 2a). Lizard introduction did not seem to affect average male mobility (Wilcoxon signed rank test $z = 0.50$, $n = 90$, $P > 0.6$). Drumming activity of the males decreased drastically after the lizard introduction and many males stopped drumming altogether (mean drumming activity per minute before and after the lizard introduction was 1.60 and 0.43, respectively, Wilcoxon $z = 7.61$, $n = 90$, $P \ll 0.001$) (Fig. 3). Among all the predated males, 13.3% (8/60) were captured during, or immediately after, the drumming bout, while the expectation based on mean drumming activity would have been only 1.2% (0.7/60) males. There was also a non-significant tendency of more actively drumming males to be predated more rapidly (Paired t-test, $t = 1.71$, d.f. $= 19$, $P = 0.104$) (Fig. 2b).

Discussion

In this study male mate-searching activity increased male mating success. In the field, males are much more mobile than females and may move more than 30 m per day (Kotiaho, unpublished data). Male mobility
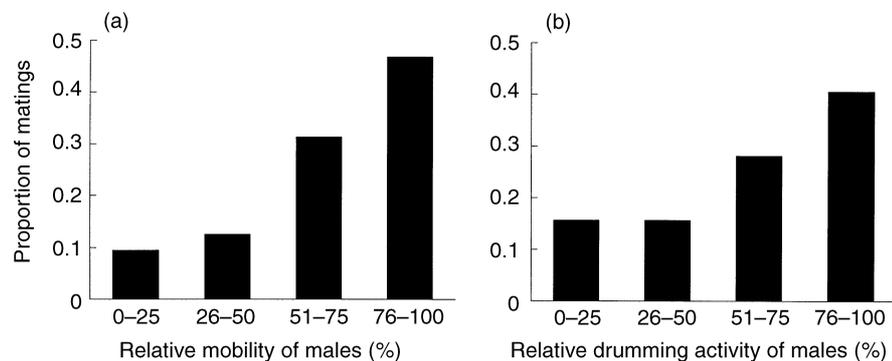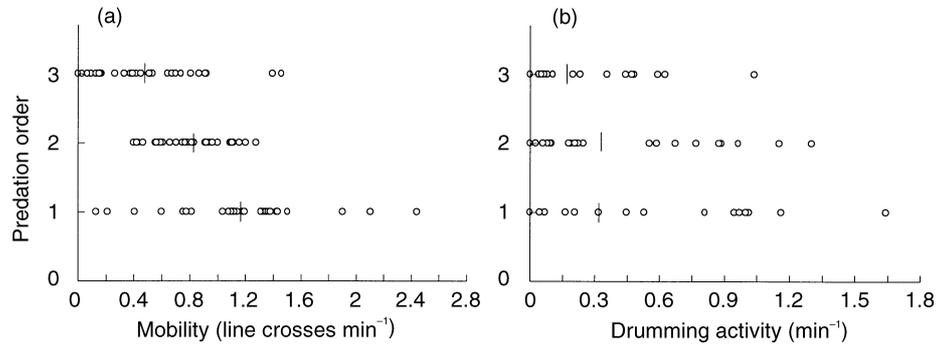

Fig. 1. (a) Proportion of matings falling into each quartile of male relative mobility. (b) Proportion of matings falling in each quartile of male relative drumming activity.

Fig. 2 (a) Scatter plot between predation order and male mobility per minute. Line indicates the mean. Mobility is ln-transformed. (b) Scatter plot between predation order and male drumming activity per minute. Line indicates the mean. Drumming activity is ln-transformed.
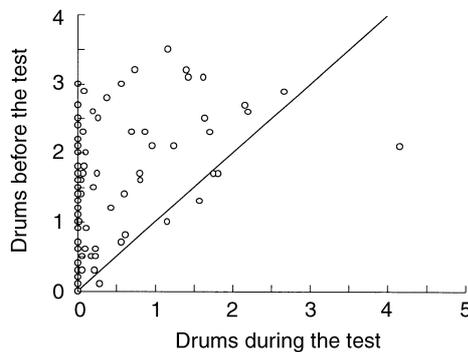
Fig. 3 Scatter plot between male drumming activity before and during the test. Solid line represents the one to one line.

is probably not directly a target of female choice but it greatly affects male mating success. Because females do not move much, male ability to move could be an additional test of male condition. There is evidence that males that are moving more lose less mass, indicating that they may indeed be in better condition (Kotiaho, unpublished data). From our results it is evident that males that are moving more have higher mating success and thus higher mobility seems to be favoured through sexual selection. Also, male drumming activity increased male mating success. Previously we have found, with two different studies, that females preferentially choose males that are most actively drumming (Kotiaho *et al.* 1996; Parri *et al.* 1997). Thus, there is a good reason to believe that male drumming activity is indeed increasing male fitness through increased mating success.

Because male mobility and drumming activity both seem to affect male fitness positively, it is evident that some costs will appear to hinder the mobility or drumming activity. Costs other than direct ones may be difficult to detect because animals are normally behaving optimally in respect to their condition. This is evident in *H. rubrofasciata* where male drumming activity and male viability are positively correlated (Kotiaho *et al.* 1996), but with experimental increase

of drumming activity significant mortality costs emerge (Mappes *et al.* 1996). This mortality may be explained by the extremely high energetic requirement of male drumming (Kotiaho, unpublished data). Also, male mobility increases male energy consumption significantly compared to resting metabolic rate (Kotiaho, unpublished data). However, there is no evidence that moving would cause serious physiological costs on males. In this study we found evidence that male mobility affected and drumming activity tended to affect the risk of predation. There was a highly significant negative relationship between the predation order and the moving activity of the males. Thus, males that were most actively moving had significantly higher risk of being predated than males moving less actively. There was also a negative but not quite significant relationship between predation order and male drumming activity. Thus, it seems that more actively drumming males may also be under higher risk of predation. This is supported by the observation that eight males were taken immediately during or after their drumming while the expectation according to mean drumming activity was only 0.7 males. Male drumming activity was also significantly lower in the presence of the predator than before it, indicating that when males observe the presence of the predator they decrease their drumming activity.

The reason why male drumming activity did not have very clear effect on predation order may be due to males decreasing their drumming activity so drastically; many males stopped their drumming altogether. When the difference between male drumming activity is small then random effects may affect male predation order more than differences in drumming activity, and the power of the test becomes small. Therefore, the importance of predation as a significant balancing factor on drumming activity remains to be tested in future work. However, predation does occur and it has potential to be a significant threat for males.

In conclusion, male mobility and male drumming activity benefit males by increasing their mating success, but also impair males by provoking predation

costs. Thus, in *H. rubrofasciata* for a given trait size there may be a balance between the benefits obtained trough sexual selection and costs incurred by natural selection.

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