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Predation risk affects courtship and attractiveness of competing threespine stickleback males

Received: 31 January 1997 / Accepted after revision: 15 April 1997

Abstract The effect of predation risk and male-male competition on male courtship behaviour and attractiveness to females was studied in the threespine stickleback (*Gasterosteus aculeatus*) by presenting dummy or live females to solitary and competing males under different predation risks. In the presence of a predator, males decreased courtship activity. Different courtship components were, however, adjusted to different extents and in opposing directions to predation risk, probably because the single components may have varied in riskiness. The presence of a competing male decreased overall courtship activity, but increased the frequency of zigzags, suggesting zigzagging to be a competitive strategy against other males. In the presence of a predator male courtship activity was not affected by a competitor. Female mate choice correlated with the males' previous frequency of zigzags towards a dummy female. However, when a live female paid attention to a male, the male decreased zigzagging and instead increased leading and fanning behaviours, probably trying to attract the female to the nest to mate. Predation risk affected the attractiveness of males as females reduced their attention to a male when he faced a predator and reduced his courtship activity. As females instead increased their attention to a competing male that had increased his courtship activity, due to decreased competition, males clearly are balancing mating opportunities against predator avoidance. When males vary in their susceptibility to predators, predation risk may thus affect mating success of competing males.

Key words Predation risk · Courtship · Female mate choice · Stickleback

Introduction

Reproducing animals have evolved various morphological and behavioural characteristics to enhance mating success. Some of these traits, like active mate searching and conspicuous displays and colours, may, however, also increase an individual's conspicuousness to predators (reviewed by Lima and Dill 1990; Magnhagen 1991). As predation would eliminate all future reproductive opportunities, animals are expected to carefully balance investment into reproduction and predator avoidance to maximize lifetime reproductive success. Traits that enhance mating success but increase predation risk should thus be reduced or modified when predation pressure is high (Lima and Dill 1990; Magnhagen 1991).

Some recent studies have examined these effects, concluding that predation risk can have profound effects on reproductive traits (reviewed by Lima and Dill 1990; Magnhagen 1991; Berglund 1993; Sih 1994). In particular, mating behaviours that increase an individual's conspicuousness to predators have been shown to be adjusted to changes in predation pressure, individuals reducing mating activity or switching to safer mating tactics when predation risk increases (e.g. Sih 1988; Sih et al. 1990; Berglund 1993; Forsgren and Magnhagen 1993; Godin 1995 and references therein; Fuller and Berglund 1996). Furthermore, mate choosiness has been found to decrease under increased predation risk, constraining the intensity of sexual selection (Forsgren 1992; Berglund 1993; Forsgren and Magnhagen 1993; Hedrick and Dill 1993; Godin and Briggs 1996), as is also predicted by models of the evolution of costly mating preferences (Hubbell and Johnson 1987; Pomiankowski 1987; Real 1990; Crowley et al. 1991; Pomiankowski et al. 1991).

How these alterations in mating behaviour affect the reproductive success of individuals is in most cases not known. If courtship behaviour plays an important part in mate attraction, changes in male courtship behaviour

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could affect the reproductive success of males. It could also decrease opportunities for careful mate choice by reducing differences between males in traits that reflect the quality of males, thus affecting female fitness due to matings with low-quality males and the relative mating success of males of different quality. Similarly, reductions in mate choosiness may affect female fitness (Real 1990; Berglund 1993; Forsgren and Magnhagen 1993; Godin and Briggs 1996) and male mating success (Hedrick and Dill 1993).

In many species males compete for females, dominant males suppressing other males. Thus the mating success of an individual depends not only on female mate choice, but also on male-male competition (discussed by Andersson 1994). As competing males may vary in their exposure to predators and therefore in their alteration of mating behaviour, predation risk could affect the relationship of dominance between males and alter their relative mating success.

Whether predation risk affects the competitive outcome of males trying to attract females by affecting male mating behaviour has, however, not been investigated. The purpose of this study is to determine whether predation risk affects courtship behaviour of solitary and competing males of the threespine stickleback (*Gasterosteus aculeatus*), and whether changes in courtship behaviour due to predation risk affect female mate choice.

Methods

Reproductive biology of the species

The threespine stickleback breeds in shallow water where males compete for territories and build and defend nests, court females under intense male-male competition, and care for the eggs (Wootton 1976). Due to conspicuous courtship displays combined with bright breeding colours the male is vulnerable to predation, although the spines and the lateral plates offer an effective defence (Hoogland et al. 1957). During courtship the male approaches the female in a series of zigzags and then attempts to lead the female to the nest to spawn by swimming directly and rapidly back to the nest. At the nest the male engages in nest activities, principally fanning behaviour. (Wootton 1976). If the female does not follow the male to the nest, the male returns to her to perform more zigzag bouts and leads.

Apparatus and procedures

Threespine sticklebacks were collected by fry traps from the littoral of the Baltic sea in southwestern Finland. They were collected in early May before they had started breeding to ensure that they had no earlier experience on breeding in this season. Sexes were held in separate brackish water holding aquaria (salinity 5.5 ppt) for 1–3 weeks on a 18:6 h light-dark cycle at 15°C. Breeding behaviour was discouraged by the lack of suitable nesting materials and the high densities of fish. Sticklebacks were fed to excess twice daily with commercial flake food supplemented with freeze-dried chironomids and wild-caught crustaceans. Several different perch (*Perca fluviatilis*), 23–25 cm long, which pose a threat to sticklebacks (Hoogland et al. 1957), were used as predators in the experiments.

Five experimental aquaria (70 × 45 × 30 cm) were divided by transparent Plexiglass partitions into four sections (Fig. 1). An

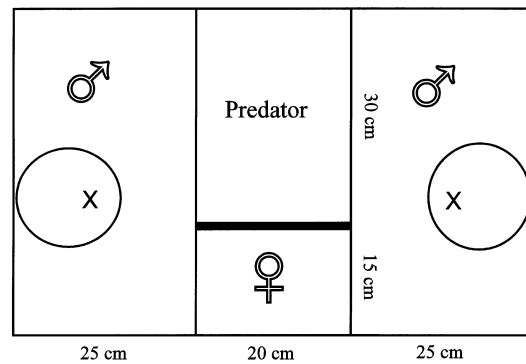


Fig. 1 The experimental aquaria. X indicates position of an artificial plant in the nesting dishes

opaque sheet prevented visual contact between the female and the predator section. The predator section was sealed, preventing olfactory contact with the other sections. White curtains with small viewing holes reduced external disturbances. A male and a plastic plant saucer (14 cm in diameter) filled with one cm of sand and an artificial plant and some *Cladophora* as nesting material were placed into each male section. The two males in each aquarium were chosen to be of the same length (± 1 mm, mean standard length = 51 mm) and outer appearance (colour and size). Only healthy males without any signs of parasite infections were chosen as parasite infections are known to affect male behaviour (see review by Milinski 1990). Two removable opaque sheets prevented males from seeing each other during nest building. If a male did not begin to build a nest within 2 days, both males were replaced by a new pair to ensure that both males were in the same breeding condition. When both males had completed a nest, i.e. they had crept through their nests (van Iersel 1953), the extent and brightness of their nuptial colouration was compared by three persons (myself and two other people). As male colour is known to affect male-male competition and female mate choice (reviewed by Rowland 1994), male pairs that were found to differ in colouration by at least one of us were replaced by a new pair.

Twenty different male pairs (40 males) were each subjected to two experiments separated by 1 day. The first experiment investigated the effect of predation risk on courtship activity of solitary males. The second experiment the effect of predation risk on courtship activity of male pairs that were competing for a female and differed in predator exposure. A realistic clay model of a gravid female was used to standardize female appearance and behaviour and to eliminate interactions between males and females which could affect the behaviour of males. Ten of the male pairs were then subjected to a third experiment, on a third day, that investigated how alterations in courtship behaviour under predation risk affect female mate choice. Live females were used in this experiment.

All experiments consisted of two treatments: control, where the predator section was empty, and a predator treatment with a predator present. Predator and control treatments were separated by 1 h and their order was reversed in half of the replicates to eliminate possible effects of treatment order. Both the predator and the female were removed between each trial to minimize any effect of habituation.

In all experiments the following male behaviours were recorded during 10 min of dummy (experiments 1 and 2) or live female (experiment 3) presentations (after 1 min of acclimation): (1) number of zigzag bouts, i.e. sequences of zigzag movements, (2) number of leads to the nest, almost invariably preceded by one or two zigzag movements that were taken as part of the leading behaviour and not included in "number of zigzag bouts", (3) number and duration (s) of fanning bouts, and (4) total time courting, i.e. time (s) spent engaged in courtship activities or within 5 cm of the partition facing the female. The experimental protocols were as follows.

Experiment 1

Effects of predation risk on courtship activity of solitary males

One of the opaque sheets was removed so that one male at a time could see into the female and the predator sections, but not into the other male's section. After 1 h a dummy was placed in the female section in a head-up posture of 45°, directed towards the male. A predator was placed in the predator section. Male courtship behaviour was recorded for 10 min.

Experiment 2

Effects of predation risk on courtship activity of competing males

To habituate males to each other the two opaque sheets had been replaced on the previous day with one small sheet placed between the predator and one of the male sections. Both males could then see each other and the dummy female, but only one of the males could see into the predator section. The experimental procedure was the same as in experiment 1, but the dummy female was directed towards the front of the aquarium. Male behaviour was recorded for both males, i.e. for all 40 males. To minimize disturbances to males only one of the males in a male pair ($n = 20$) was allowed to see the predator.

Experiment 3

Effects of altered courtship activity on female mate choice

Five live females, separated by 20 min, were presented sequentially to 10 of the competing male pairs. The experimental setup was otherwise the same as in the male competition experiment, with the same males seeing the predator. Male behaviour was recorded for both males. Female behaviour was recorded as the time spent within 5 cm of either male partition in a head-up posture facing a male. If a female did not show the head-up posture within 5 min, which indicates readiness to spawn, she was replaced by a new female. The females had all ovulated within 12 h and could neither see nor smell the predator. The same females were used in both the control and the predator treatments, except in two cases where the female had shed her eggs before the other experiment was begun.

Control experiment of treatment effects

To investigate whether repeated exposures to a dummy female and a predator affect male courtship activity, ten new pairs of competing males were exposed once a day for 3 days to a dummy female in both the presence and absence of a predator. Only one of the males could see the predator (the same one all the time). The conditions and the experimental procedures were the same as in experiment 2.

Analysis of data

Males were said to differ in activity level of a behaviour if there was at least a 10% difference in activity level between the two males in a pair. Females were considered to have a preference for one of the males when the mean time that the five females spent in contact with each male differed by at least 10%, and the majority of females (i.e. at least three) spent more time beside the preferred male. Mating preference determined by the 10% difference level has been found to correlate positively with mate choice for several fish species when actual mating is allowed (reviewed in Godin and Briggs 1996).

In the female mate choice experiment the behavioural data was averaged over the five female presentations. There was no sign of the males habituating to the female presentations as no correlation was found between the number of female presentation (1–5) and male activity level for the different behaviours (NS, Spearman rank correlation). All data sets were tested for normality. In cases where

the distribution of the data was not normal non-parametric tests were used. All probabilities are two-tailed.

Results

Male courtship activity

Dominating courtship behaviours of males in the absence of both a predator and competitor were leading and fanning the nest. The presence of a predator decreased courtship activity, with the exception of zig-zagging which increased (Fig. 2). The decrease in activity was especially marked for leads. Instead males spent more time staying still near their nests, oriented towards the predator, performing inspection behaviour every now and then (Pitcher et al. 1986).

In the presence of a competitor, males increased zigzagging, but decreased other courtship behaviours and total time courting (Fig. 2). When both a predator and a competitor was present, male courtship activity decreased, but seems to have been affected only by the predator and not by the competitor, as there was no difference in courtship activity between solitary and competing males in the presence of a predator (Fig. 2). The male who did not see the predator increased his courtship activity, with the exception of zigzagging,

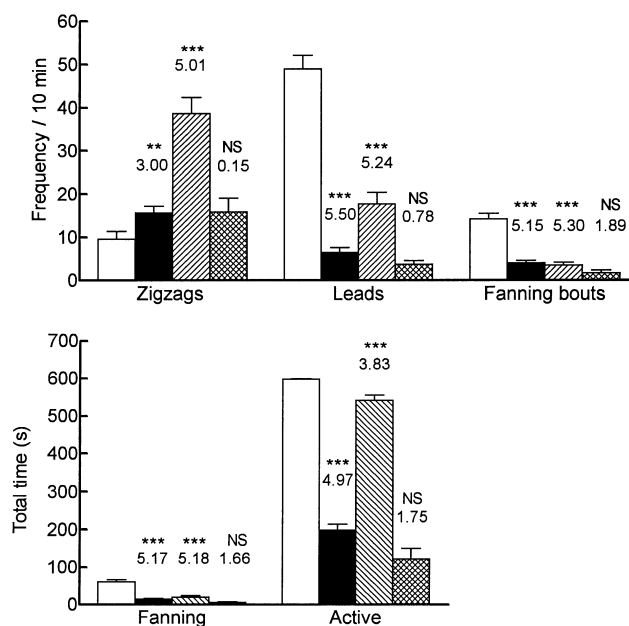


Fig. 2 Courtship behaviours (mean + SE) of males to dummy females in the absence of other fish (open bars, $n = 40$), in the presence of a predator (solid bars, $n = 40$), in the presence of a competitor (shaded bars, $n = 40$), and in the presence of both a predator and a competitor (cross-hatched bars, $n = 20$). Statistics from Wilcoxon signed rank test are given above bars. Males in the presence of a predator or a competitor are tested against males in the absence of other fish. Males in the presence of both a predator and a competitor are tested against males in the presence of a predator. ** $P < 0.01$, *** $P < 0.001$

when the competing male decreased his courtship activity (Fig. 3).

The nature of the female affected alterations in courtship activity in response to a predator, as males showed a greater decrease in leading with a dummy female than with live females (reductions of 14.25 ± 2.85 and 9.25 ± 2.68 mean \pm SE acts per 10 min respectively, $n = 10$, Wilcoxon signed rank test: $z = 2.14$, $P < 0.05$). Males also performed more leads with live females than with a dummy in the presence of a predator ($z = 2.75$, $P < 0.01$). Other courtship behaviours were not affected by the nature of the female in the presence of a predator (NS).

Female mate choice

In the absence of a predator the time that females spent close to a male correlated with the male's courtship activity, with the exception of zigzagging (Spearman rank correlation, $n = 20$, leading $r_s = 0.84$, $P < 0.001$; fanning bouts $r_s = 0.64$, $P < 0.01$; fanning time $r_s = 0.48$, $P < 0.05$; active time $r_s = 0.62$, $P < 0.01$; zigzagging $r_s = 0.13$, NS). Females preferred males that performed more leads (10/10 replicates, binomial test, $P < 0.001$) and fanning (9/10, $P < 0.05$ for both frequency and duration), whereas total time active (8/10, NS) and the frequency of zigzags (7/10, NS) seemed to have less effect on female mate choice.

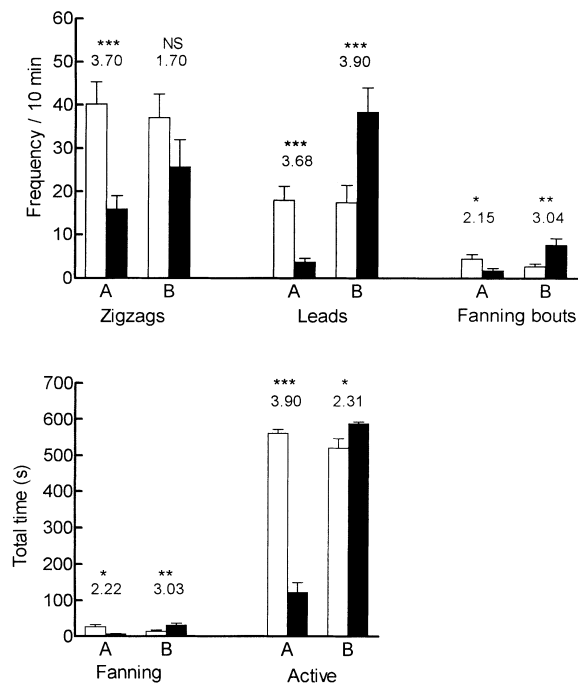


Fig. 3 Courtship behaviours (mean + SE) of competing males to a dummy female in the absence (*open bars*) and presence (*solid bars*) of a predator. (*A* male who could see the predator when it was present, *B* male who could not see the predator). Statistics from Wilcoxon signed rank test are given *above bars* ($n = 20$). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

As high courtship activity of a male preferred by females may be due to males increasing courtship activity when females pay attention to them, the time that females spent in contact with a male was compared with the male's activity with a dummy female that shows no male preference. A positive correlation was then found with the frequency of zigzags ($n = 20$, $r_s = 0.59$, $P < 0.01$). No correlations were found with other courtship behaviours ($-0.25 < r_s < 0.20$, NS). Similarly females preferred males that had performed more zigzags with a dummy (9/10, binomial test, $P < 0.05$), whereas other behaviours could not be shown to be associated with female mate choice ($< 7/10$, NS).

Female behaviour obviously affected male behaviour as males performed more leading (Wilcoxon signed rank test, $n = 20$, $z = 2.33$, $P < 0.05$) and fanning (frequency: $z = 3.15$, $P < 0.01$, duration: $z = 2.53$, $P < 0.05$) and tended to perform less zigzagging ($z = 1.71$, $P < 0.10$) with live females than with a dummy. Time active did not differ between dummy and live female presentations ($z = 0.52$, NS).

Females decreased their attention to the male that saw the predator and had decreased his courtship activity, and increased their attention to the male that did not see the predator and had increased his courtship activity (Fig. 4). In the presence of a predator females always preferred the male that did not see the predator (10/10, binomial test, $P < 0.001$). This male also had

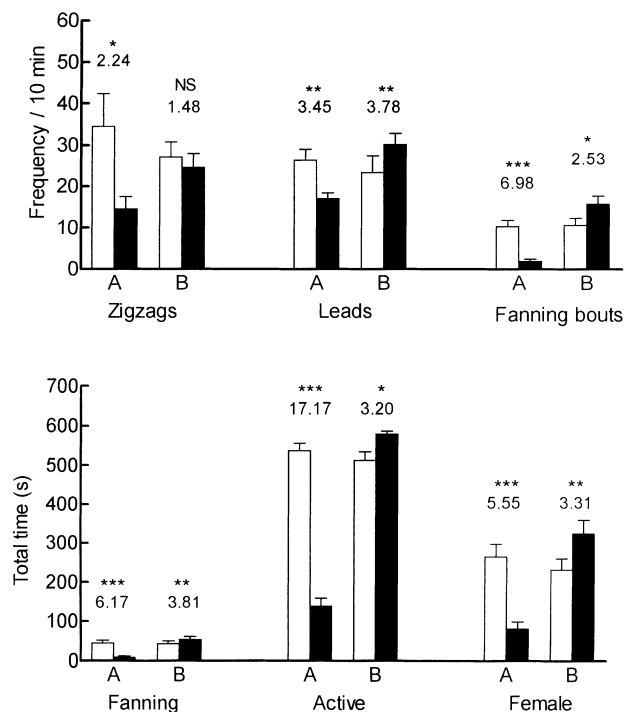


Fig. 4 Courtship behaviours (mean + SE) of competing males to live females, and the time that females spent close to respective male, in the absence (*open bars*) and presence (*solid bars*) of a predator (*A* male who could see the predator when it was present, *B* male who could not see the predator). Statistics from paired *t*-test are given *above bars* ($n = 10$). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

higher activity levels than the other male for all investigated behaviours. In all 6 replicates where females in the absence of a predator had preferred the male who could see into the predator section, the females changed their mate choice towards the other male when the predator was added and the preferred male decreased his courtship activity.

Control experiment of treatment effects

Courtship activity of the ten control male pairs did not vary over the 3 days of observation. The response to the dummy female was unchanged between days, both in the absence and presence of a predator, for both males that could see, and males that could not see the predator (NS, repeated measures ANOVA on all of the investigated behaviours). This is in accordance with other studies that have found no effect of repeated dummy female presentations on male total courtship activity (Bakker and Rowland 1995).

Discussion

Alterations in courtship behaviour

Predation risk altered courtship behaviour of both solitary and competing males. The decrease in total courtship activity in the presence of a predator is in accordance with studies in other species with conspicuous courtship displays (Endler 1987; Magurran and Seghers 1990; Magurran and Nowak 1991; Berglund 1993; Forsgren and Magnhagen 1993; Godin 1995; Fuller and Berglund 1996). However, this study also showed that males can adjust different components of courtship to different extents, and in different directions in response to predation risk. The reason for the decrease in leading and the increase in zigzagging of solitary males in response to increased predation risk could be due to males seeing more of the predator when they swim to the nest than when they stay near the female. In addition leads could be more risky than zigzagging as they may show the predator the way to the nest, which may be fatal if the predator is also a predator on eggs. Males thus seem to be able to adjust the behaviours to the risk that they incur.

The greater predator induced reduction in leads with a dummy female than with live females suggests that males adjust their alterations in courtship behaviour and risk-taking to their mating probability. As the purpose of leading is to attract females to the nest to mate, males may show a greater reduction in leading with a dummy than with live females as they get no response from a dummy and most likely perceive their probability of succeeding in leading the female to the nest as low. These results should however be interpreted with caution as the encounter with an unresponsive dummy female is an

unnatural situation and could affect the male's later response to live females. Further studies are required to determine the effects of expected mating success on responses to predation risk.

The presence of a competitor reduces total time spent courting and all courtship activities except zigzagging. This suggests that males subdue each others courtship activity and that zigzagging, in addition to being directed to a female, is a competitive strategy against other males. During zigzagging a male exposes his entire colour signal (McLennan and McPhail 1990), and as nuptial colour has been shown to be an important determinant of dominance between males (Bakker and Sevenster 1983), males may try to subdue competing males by promoting their signal display by increased zigzagging.

An increase in aggressive behaviour, due to the presence of a competitor, could have contributed to the decrease in total courtship activity, as aggressive and sexual behaviours have been found to be mutually inhibitory (Sevenster 1961; Wilz 1972). During the experiments aggressive interactions between males were, however, not discerned, probably because the males could not freely interact and had time to habituate to each other (Rowland 1988). However, the result that a male increases his courtship activity when a competing male decreases his courtship, due to the presence of a predator, shows that males are affected by the courtship activity of competing males. When a male reduces his courtship activity, he also decreases his intimidating effect on other males, perhaps because the exposure of his colour signal is decreased.

Interestingly a competitor had no effect on males courtship activity when a predator was present. Predation risk thus overrides any effects of competition on courtship behaviour. This is explained by the different effects that predators and competitors have on a male's lifetime reproductive success. Predators may end an individual's life and eliminate all future reproductive opportunities whereas a competitor usually affects only current mating opportunity.

Female mate choice

The time that a female spends in contact with a male correlates with the male's courtship activity, with the exception of zigzagging. This could, however, be due to a male increasing his courtship activity when a female pays attention to him due to other components of his behaviour or to colouration. The association between a male's frequency of zigzags with a dummy and the time that females spend close to him however suggests that females do discriminate between males on the basis of courtship activity. A high frequency of zigzags may attract females to a male, but when females pay attention to the male, he reduces zigzagging and instead increases leading and fanning behaviours, thereby trying to entice females to the nest.

The importance of courtship activity in female mate choice has been debated. Most studies have found no relationship between male courtship intensity and female mate choice (e.g. Ward and FitzGerald 1987; Milinski and Bakker 1990), with one exception (Rowland 1995). This may be due to most studies using live males and females and therefore being unable to separate between cause and effects of high male courtship activity and female mate choice. In addition the frequency of zigzags, which usually has been related to female mate choice, do not necessarily reflect female mate choice when the female is paying attention to the male, as found in this study.

High rates of zigzags have, however, been proposed to expose a male's entire colour signal to a female (McLennan and McPhail 1990). As the intensity of male colouration has been shown to affect female mate choice (reviewed by Rowland 1994) and reflect male condition (Milinski and Bakker 1990), high rates of zigzagging should be expected to enhance the potential for female mate choice based on the quality of a male. In this study the males were chosen to be as equal as possible when it comes to outer appearance. It is however possible that also small differences in colour between males were emphasized during zigzagging and affected female mate choice, especially as the white background should have increased the contrast to the red nuptial colouration. However, as nuptial colouration does not immediately decrease under the threat of predation risk (personal observation), which courtship behaviour does, the significant decrease in the females' attention to a male when he reduces his courtship activity shows that courtship activity plays an important part in mate attraction.

The importance of zigzagging in attracting females may also explain the increase in zigzagging when a competitor is present. In addition to try to subdue each other by increased zigzagging, males may try to entice females toward themselves, away from an other male.

As females decrease their attention to a predator exposed male that reduces his courtship activity and instead increase their attention to a male that increases his courtship activity, due to decreased competition, predation risk may affect the reproductive success of males. Males thus appear to be balancing reproductive success against predator avoidance.

Both male-male competition and predation risk thus affect courtship activity and attractiveness of males. When predation risk is low male courtship activity and attractiveness to females are affected by competitors. Males are subduing each others courtship activity and probably adjusting their courtship activity and colour signal to the quality of competing males. This gives females better opportunities to evaluate males and choose the best one. Under increased predation risk courtship activity and attractiveness to females is affected by the males' susceptibility to predators and their alteration of courtship activity. This could decrease or increase sexual selection, depending on whether male susceptibility to predators is random or not.

Acknowledgements I thank Kai Lindström, Veijo Jormalainen and two anonymous referees for valuable comments on earlier versions of the paper. My research was supported by Ella and Georg Ehrnrooth Foundation, Waldemar von Frenckell Foundation and the Swedish Cultural Foundation in Finland.

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Communicated by N. Metcalfe