

SHORT COMMUNICATION

Negatively condition dependent predation cost of a positively condition dependent sexual signalling

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Abstract

Predation is considered as an important factor constraining the expression of sexual signals. Nevertheless, direct quantitative evidence for predation provoking significant viability costs on individuals signalling at high rates is scarce. Moreover, it is unclear whether high rate signallers are able to balance presumably increased predation costs. We examined whether a condition dependent audible sexual signal, drumming, makes *Hygrolycosa rubrofasciata* male spiders more prone to predation by pied flycatchers (*Ficedula hypoleuca*), and whether sexual signalling rate is related to escaping ability once attacked. When birds were given a choice between two spider males manipulated to drum either one or three bouts per minute using playbacks, naïve birds attacked the males randomly regardless of the drumming rate. However, experienced birds chose significantly more often the males with high signalling rate. When spiders were allowed to escape, males with high sexual signalling rate tended to be better at escaping attacks than males with low sexual signalling rate. This study provides evidence that high signalling rate increases the risk of predation, but simultaneously males with high mobility, which correlates positively with signalling rate seemed to be better at compensating this cost.

Introduction

Sexual selection has favoured extravagant ornaments in many species, and natural selection has in turn constrained the extravagance (Darwin, 1871; Andersson, 1994). In other words, females prefer males with a strong sexual signal, but at the same time viability costs through physiological mechanisms (Vehrencamp *et al.*, 1989; Kotiaho *et al.*, 1998a; Kotiaho, 2001; Ahtiainen *et al.*, 2005) or predation (see review by Zuk & Kolluru, 1998; Rosenthal *et al.*, 2001) are likely to increase. Predation costs typically originate from either exploitation of the conspicuous sexual signal by predators or the sexual signals may handicap the signalling individuals and

therefore make them an easier target for their predators (Andersson, 1994). For instance, acoustic sexual signals frequently seem to be exploited by predators (Walker, 1964; Bell, 1979; Burk, 1982; Sakaluk & Bellwood, 1984; Sakaluk, 1990; Magnhagen, 1991; Kotiaho *et al.*, 1998b) and negative selection by predation or parasitism is suggested, in general, to increase with the enhancement of the sexual signalling (e.g. Endler, 1982; Andersson, 1994; Zuk & Kolluru, 1998; Stuart-Fox *et al.*, 2003). Despite the obvious potential for predation to impose significant fitness costs on sexual signalling, the direct empirical evidence for quantitative costs is surprisingly scarce (cf. Kotiaho, 2001; but see Zuk & Kolluru, 1998; Zuk *et al.*, 1998; Godin & McDonough, 2003).

Concurrently the favoured theory of sexual selection assumes that because sexual signals are costly to produce they are expected to evolve condition dependent expression, leading to the probability that they may function as honest indicators of heritable quality of males

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for the choosy females (Andersson, 1994; review in Møller & Alatalo, 1999; David *et al.*, 2000; Tomkins *et al.*, 2004). Thus, it is evident that costs of signalling play a considerable role in good genes sexual selection: First, sexual signalling must be costly in terms of reducing the fitness of the signaller, and these costs should increase in parallel with the increasing investment in signalling (e.g. Grafen, 1990; Johnstone & Grafen, 1992). Second, the marginal costs of signalling must be less for males in good condition than for males in poor condition (Grafen, 1990; Rowe & Houle, 1996; Tomkins *et al.*, 2004). In other words, individuals in better condition should have a lower cost/benefit ratio for a given rate of signalling.

Since the empirical evidence for direct fitness costs created by predators on sexual signals is scarce (cf. Kotiaho, 2001; but see Zuk & Kolluru, 1998) it is not well understood whether predation costs increase in proportion to the expression of the signal or whether they are related to the condition of the males. For instance, empirical evidence indicates that males with high signalling rates may alter their behaviour when predators or parasitoids are present (see Candolin, 1997, 1998; Kotiaho *et al.*, 1998b; Hedrick, 2000; Lewkiewicz & Zuk, 2004). Such plastic responses to the presence of a predator may compensate for the predation costs of increased sexual signalling. If individuals in better condition are better at escaping predation, and if signalling rate is positively dependent on condition, then the condition dependent escape rate would reduce the cost of signalling in males that are signalling the most, thus fulfilling the assumptions of good genes sexual selection theory (cf. Kotiaho, 2001).

In the mating season male wolf spiders *Hygrolycosa rubrofasciata* (Ohlert, 1865) (Araneae: Lycosidae) produce acoustic sexual signals by drumming their abdomens against dry leaves (Kronstedt, 1996). One drumming consists of approximately 30–40 separate pulses, lasting approximately 1 s (Rivero *et al.*, 2000), and drumming is audible to the human ear up to several meters. Drumming imposes physiological costs by increasing male metabolic rate 22-fold compared to the metabolic rate at rest (Kotiaho *et al.*, 1998b). Manipulation of the food levels of the males has an effect on their signalling rates (Mappes *et al.*, 1996; Kotiaho, 2000) indicating that signalling rates are condition dependent. Furthermore, males manipulated to signal at a higher rate suffer increased mortality although in unmanipulated conditions males with higher signalling rate have better survival (Mappes *et al.*, 1996; Kotiaho *et al.*, 1996, 1999; Kotiaho, 2000). In other words, drumming is a condition dependent signal, being manifested as decreased viability of highly signalling males in poorer condition (Mappes *et al.*, 1996; Kotiaho, 2000). Furthermore, there is also a tendency that predation may impose a survival cost on male signalling (Kotiaho *et al.*, 1998b). *Hygrolycosa rubrofasciata* females use male drumming to choose their mate, and prefer males with the highest drumming rates

(Kotiaho *et al.*, 1996; Parri *et al.*, 1997). Also, male mobility is positively associated with male mating success (Kotiaho *et al.*, 1998b). By choosing males with high drumming rate, females derive indirect benefits as the offspring of males with high-drumming rates have better survival than the offspring of males with low-drumming rates (Alatalo *et al.*, 1998). Therefore in *H. rubrofasciata*, male courtship drumming seems to be an honest indicator of male genetic quality (review in Ahtiainen *et al.*, 2001).

The aim of this study was to investigate whether predation can act as a viability cost promoting honest expression of the sexual signals as expected by the theoretical work. To test this hypothesis we first determined whether the drumming is costly in terms of increased predation risk (see also Kotiaho *et al.*, 1998b). Second, and more important, we tested whether males' condition, estimated through sexual signalling rate (see Mappes *et al.*, 1996; Kotiaho, 2000), affects the male's ability to escape from predation. In the first experiment we examined whether high sexual signalling rate makes *H. rubrofasciata* males more prone to predation by pied flycatchers (*Ficedula hypoleuca*), a species that can act as a natural predator of these spiders. In the second experiment, we tested in a multiple choice arena whether males with high sexual signalling rate are more likely to escape from predation than males with low sexual signalling rate.

Materials and methods

Experiments were carried out at Konnevesi Research Station (Central Finland). We ran two separate experiments: the cost experiment that we will describe first was run in 2001 and the escape ability experiment that we describe was run in 1999.

Predator

We captured migratory pied flycatchers (*F. hypoleuca*) from the forests around Konnevesi Research Station at the time they arrived in Finland before the nesting period (cost experiment: $n = 30$; escape ability experiment: $n = 12$). Pied flycatchers are nearly exclusively insectivorous, capturing prey in flight and from the ground. On average 10% of the prey items given to nestling includes Arachnida (Lundberg & Alatalo, 1992). The Central Finland Regional Environment Centre gave us a permission to capture and keep the birds in captivity (cost experiment: N:o LS-18, Dn:o 0901L0218/254; escape ability experiment: N:o LS-17/99, Dn:o 0999L0253/254). The Ethical Committee of University of Jyväskylä gave permission to conduct the experiments (cost experiment: 7/27.2.2001; escape ability experiment: 7/26.4.1999). Birds were housed individually in illuminated cages ($65 \times 80 \times 65 \text{ cm}^3$ high) and provided with mealworms (*Tenebrio molitor*) and water *ad libitum*. After the

experiment, all birds were released at the sites where they were originally captured.

Spiders

We collected *H. rubrofasciata* males using pitfall traps from a bog in Sipoo, Southern Finland (60°16'N and 25°14'E) at the beginning of the mating season (cost experiment (2001): $n = 380$; escape ability experiment (1999): $n = 159$). In the field we placed each spider in a small plastic film jar with some moss (*Sphagnum* spp.) for transport and storage. We kept spiders at a low temperature (ca. +10 °C) to suppress their activity. Individuals of this species die after the mating season, and by keeping the activity levels low we could keep them in better condition for a longer time. In the laboratory, we weighed spiders to the nearest 0.1 mg with an analytical balance (AND HA-202M). After body mass measurements, spiders were kept at +5 ± 2 °C in darkness. Spiders were provided food (*Drosophila melanogaster*) and water *ad libitum*.

Measurements of spiders' sexual signalling rate

For sexual signalling rate and mobility measurements, we took each male randomly from the sample of all specimens, and placed them individually in plastic arenas (125 × 88 × 110 mm³ high). We covered the bottom of the arenas with a white copy paper (8 × 4 cm²). To enable mobility measurements, we divided each arena with a line into two equal rectangles. In each arena, we placed two dry birch leaves as drumming substrates. We illuminated the laboratory with fluorescent tubes and with 40 W bulbs placed 30 cm above the floors of the arenas to increase the light intensity and temperature, which have positive effects on spider activity (Kotiaho *et al.*, 2000).

We measured signalling rate as the number of drumming bouts, and mobility as the number of times the male crossed a line between the two rectangles. Measurements were repeated five times for 2-minute periods for each spider during each trial day. To improve measurement accuracy we repeated the measurements on consecutive days (cost experiment on 3 days; escape ability experiment on 2 days). For comparison the signalling rate and mobility measures were adjusted to time because the observation times between the experiments differed (cost experiment 30 min, escape ability experiment 20 min). Between the trial days, males were fed fruit flies (*D. melanogaster*), and kept in cool temperature (+5 ± 2 °C) in darkness. On the day prior to signalling rate measurements, we kept males in the laboratory in an ambient temperature of +31 ± 1 °C for 2 h to trigger their sexual behaviour. Repeatabilities for signalling rate and mobility across trial days were significant but moderate at best (cost experiment: signalling rate $R = 0.35$ [Confidence intervals (CI): 0.28–

0.41], $F_{379,760} = 2.64$, $P < 0.001$; mobility $R = 0.30$ (CI: 0.23–0.36), $F_{379,760} = 2.30$, $P < 0.001$; escape ability experiment: signalling rate $R = 0.49$ (CI: 0.32–0.57); $F_{158,159} = 2.96$, $P < 0.001$, mobility $R = 0.46$ (CI: 0.37–0.60); $F_{158,159} = 2.69$, $P < 0.001$) (for methods see Lessells & Boag, 1987; Krebs, 1989). Signalling rate and mobility were positively correlated in both experiments (cost experiment: $r_s = 0.624$, $n = 380$, $P < 0.001$; escape ability experiment: $r_s = 0.733$, $n = 159$, $P < 0.001$ see Fig. 1).

Cost experiment

We used a playback experiment to test the predation pressure birds create on males manipulated to signal at two different rates (high vs. low rate). To measure the predation cost of the drumming rate, we placed a spider in each of two containers ($\varnothing = 25$ cm) both containing a

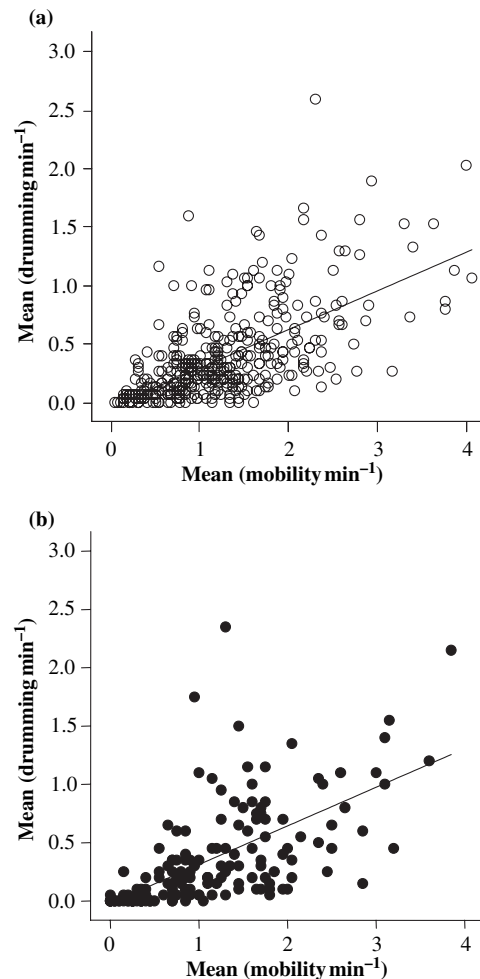


Fig. 1 The correlation between the mobility and drumming rate of the spiders in the (a) cost experiment and (b) escape ability experiment.

loudspeaker in the aviary ($3.4 \times 3.9 \times 2.5 \text{ m}^3$ high) (see Fig. 2). We placed a piece of styrofoam on top of the loudspeakers to silence the spiders' own drumming. Instead we broadcasted previously recorded (digital recorder Sony TCD-D7, see details in Rivero *et al.*, 2000) playback drumming of the *H. rubrofasciata* males. Each drumming sound was used only once. Drumming sounds were similar with respect to pulse rate, signal length, signal volume, peak frequency and symmetry (see also Rivero *et al.*, 2000). We chose drumming rates, which corresponds to the high and low signalling rates in nature (Alatalo *et al.*, 1998). One loudspeaker was drumming three times per minute (high rate) and the other was drumming one time per minute (low rate).

Before the birds were tested they were habituated to feeding from the container placed in the middle of the aviary. During customization, we released a bird in the aviary that had only one perch inside. After the bird had landed on the perch, we switched off the lights and placed a mealworm in the container. We used switching off the lights as the conditioning stimulus for food. The birds could not see what was in the containers from their perch (see Fig. 2), and therefore in the actual experiment with spiders we could test, which of the containers (drumming either one or three times per minute) drew the attention of the birds. Birds had been conditioned to feeding from the containers without the sound.

We tested simultaneously whether the males' ability to escape predation was related to their own signalling rate (high sexual signalling rate vs. low sexual signalling rate). To test this, the spiders used in the cost experiment were males, which were first divided into two groups according to their own signalling rate, either 'high sexual signalling rate' or 'low sexual signalling rate'. For both groups we allocated 80 males (from 380

males for which the sexual signalling rate was measured). The 'high sexual signalling group' was drumming more actively (drumming rate: 0.95 ± 0.04 bouts per minute, $n = 80$) than the 'low sexual signalling group' (drumming rate: 0.05 ± 0.003 bouts per minute, $n = 80$) (Mann-Whitney $Z = -10.97$, $P < 0.001$). The high sexual signalling group was also more mobile (mobility: 1.83 ± 0.09 line crossings per minute, $n = 80$) than the low signalling group (mobility: 0.63 ± 0.05 line crossings per minute, $n = 80$) ($Z = -9.19$, $P < 0.001$) but these two groups did not differ in their body mass (high: body mass: 15.89 ± 0.21 mg (mean \pm SE), $n = 80$; low: body mass: 16.00 ± 0.21 mg (mean \pm SE), $n = 80$; Mann-Whitney $Z = -0.69$, $P = 0.49$). Then, we created 40 quartets of size-matched males. Each quartet consisted of a pair of males from the low signalling rate group and a pair of males from the high signalling rate group. We also created ten extra quartets of males to be able to replace a quartet in case of death of a spider before the experiment.

Before the cost experiment half of the birds were randomly assigned as predators to either the 'high signalling' or to the 'low signalling' group. Because we simultaneously tested the predation pressure on the manipulated signalling rate, birds were always presented with a pair of spiders. Birds were allowed to eat only one spider in each trial and the same experiment was repeated a week later with the opposite signalling pair of spiders to ensure that the sample size for both of the signalling groups was the same (see below). Therefore this experiment simultaneously tests (i) predation pressure on the signalling rate and (ii) whether males' own signalling rate is related to the ability to escape predation attempts.

In the beginning of the cost experiment, we released a bird in the aviary, which had one perch inside. After the bird had landed on the perch, we switched off the lights. This was done to ensure that each predator started their predation attempts from a fixed position. From the pair of the spiders, one was placed in the high drumming container and the other in the low drumming container. We also placed two perches manually next to the containers (Fig. 2), before switching on the lights. We observed each predator-prey encounter through a one-way mirror, and we also filmed each encounter with digital video cameras (Sony DCR-TRV900E PAL, Tokyo, Japan) from above the containers (see Fig. 2). This was done to allow counting of the number of failed attacks by predators. After one week we repeated the experiment ($n = 29$, one bird refused to eat), but now the birds were given the other pair of the previously formed quartets. In other words, birds that had been given a pair of spiders with high sexual signalling rate were now presented with a pair of spiders with low sexual signalling rate and vice versa. The order of containers was reversed for each bird, but again the playback drumming was three or one bouts per minute.

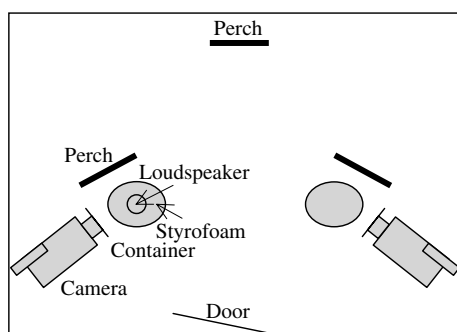


Fig. 2 The experimental setup in the cost experiment. We had two cameras each filming a container (bucket, which had a loudspeaker topped with a styrofoam) where the spider was placed. The room contained three perches on which the bird could sit indicated with black horizontal bars. Experimental aviary was $3.4 \times 3.9 \times 2.5 \text{ m}^3$ (height) in size. Observations of the bird behaviour were made through a door that had one-way mirror class. Thus the birds were unable to see the experimenter.

Escape ability experiment

In the above cost experiment, males had a limited chance to escape from predation regardless of their sexual signalling rate. In this other experiment, the possibility of the male to escape predation was greater. In this experiment, males ($n = 159$) were ranked according to their sexual signalling rate and two groups of males were formed, one from either end of the continuum. From these two groups we created pairs ($n = 51$) of males within which males did not differ in weight but did differ in their sexual signalling rate [high drumming rate group: $n = 51$, 0.67 ± 0.06 bouts per minute; mobility: 1.85 ± 0.10 line crossings per minute; body mass: 15.10 ± 0.30 mg (mean \pm SE); low drumming rate group: $n = 51$, 0.12 ± 0.01 bouts per minute; mobility: 0.68 ± 0.05 line crossings per minute, body mass: 15.12 ± 0.35 mg (mean \pm SE)]. There was a highly significant between-group (high vs. low sexual signalling rate) difference in the drumming rate (Mann–Whitney $Z = -7.29$, $P < 0.001$) and mobility ($Z = -7.93$, $P < 0.001$), but no difference in body mass ($Z = -0.41$, $P = 0.68$).

We simultaneously presented six spiders (three pairs) to each bird ($n = 12$), i.e. three males with high sexual signalling rate and three males with low sexual signalling rate. We placed spiders individually in six containers ($\phi = 30$ cm) that were placed in a circle around a perch in the same aviary as described above. Each container was covered with brown paper and six dry birch leaves, under which the spiders could escape. After the spiders were placed in the containers, we released the birds in the aviary. Then we recorded the order (1–6) in which the birds attacked and ate the spiders and tested whether highly active males were preferred by the predators. We also counted how many attacks the birds needed before capturing each spider. Overall, we performed 17 predation trials (a second trial with different spiders was repeated with five birds a week later), where we observed predation on 102 spiders. We used all of the spiders only once. We performed a binary logistic regression on the ability of each spider to escape the first predation attempt. In the model, a dependent variable was the probability of escape, either dead (zero) or escaped (one), and independent variables were the bird (as categorical) as well as the total drumming rate and the total movement of the spider measured before the experiment. Since the same bird was the predator for six spiders, bird ID was entered first in the model and it was also kept in the final model although it was not significant. Statistical analyses were performed using *SPSS* (Release 11.5.1).

Results

Cost experiment

Initially, the naïve birds attacked randomly on males manipulated to drum at different rates ($\chi^2_1 = 0.53$, $P =$

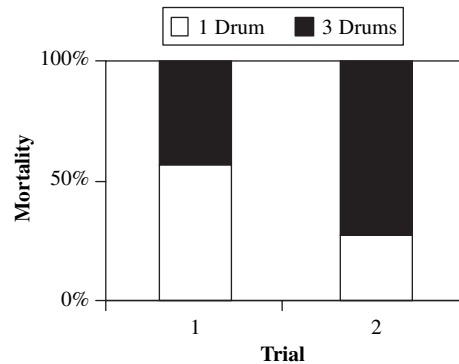


Fig. 3 The mortality rates of males that were manipulated to drum either one (a poor quality male; white area) or three bouts per minute (a good quality male; black area). Trials 1 and 2 represent repeated sequential experiments.

0.46) (Fig. 3), indicating that drumming was not used as a cue by the naïve predators. However, when we repeated the same experiment with the same set of birds a week later the birds' attack frequencies changed between trials (trial by attacked spider's signalling rate $\chi^2_1 = 5.11$, $P < 0.05$). Seventy-two per cent of the experienced birds attacked the males manipulated to drum at the higher rate, indicating that predation deviated from random ($\chi^2_1 = 5.83$, $P < 0.05$) (Fig. 3). This percentage did not deviate from that expected (75%) based on the three-fold difference in intensity (1 vs. 3 drummings per minute) ($\chi^2_1 = 0.10$, $P = 0.75$). In other words, birds preyed on the spiders in proportion to their signalling rate. Forty-two per cent of the spiders escaped the first predation attempt. However, spiders' own sexual signalling rate (low vs. high) was not related to their ability to escape attacks by predators counted as how many times birds missed the spider (the first trial: Mann–Whitney $U = 109.0$, $n_1 = n_2 = 15$, $P = 0.87$; the second trial: $U = 101.5$, $n_1 = 15$, $n_2 = 14$, $P = 0.86$).

Escape ability experiment

As their first choice, naïve birds randomly attacked males with low and high sexual signalling rate ($\chi^2_1 = 1.33$, $P = 0.25$). There was also no correlation between the order of attack and male sexual signalling rate ($r_s = 0.061$, $n = 102$, $P = 0.54$) or male mobility ($r_s = -0.142$, $n = 102$, $P = 0.15$). However, 46 of the 102 male spiders survived the predators' first attack. Therefore, we tested whether the male's ability to escape was related to its drumming rate or mobility. The interaction between drumming rate and mobility did not affect the escape ability (binary logistic regression, Wald₁ = 1.67, $P = 0.28$) and therefore it was deleted from the final model. Drumming rate alone had no effect on the likelihood of escaping the predation attempt (Binary logistic regression, Wald₁ = 1.07, $P = 0.30$). However, males with higher mobility

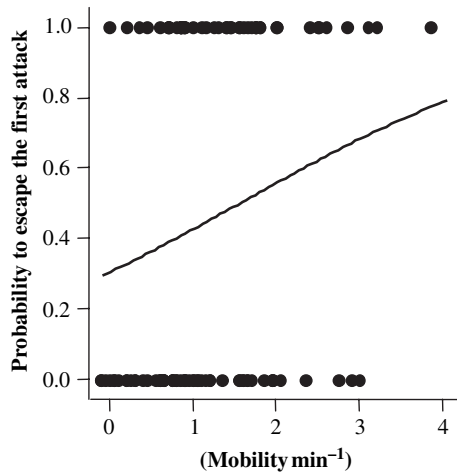


Fig. 4 Probability of escaping the first predation attempt as a function of the mean mobility of spiders. The function was estimated from the binary logistic regression by including only the mobility into the analysis.

were more likely to escape the predation than males with lower mobility ($\text{Wald}_1 = 4.71$, $P < 0.05$) (Fig. 4). There was no effect of the predator's identity on the likelihood of the spider to escape the predation attempt ($\text{Wald}_{11} = 12.84$, $P = 0.30$).

Discussion

The good genes models of sexual selection assume that traits are costly to produce and therefore with some additional assumptions they may act as honest indicators of heritable quality of males for the choosy females (e.g. Grafen, 1990; Johnstone & Grafen, 1992; Rowe & Houle, 1996; Tomkins *et al.*, 2004). Despite the importance of the costs for the theory, direct tests of e.g. predation costs have remained largely unexplored (cf. Kotiaho, 2001). In this study, we found that experienced flycatchers (*F. hypoleuca*) more frequently attacked males that were manipulated to signal at a high rate (Fig. 3.) indicating that predation risk is higher for males with high signalling rates (e.g. Zuk & Kolluru, 1998; Zuk *et al.*, 1998; Godin & McDonough, 2003). Therefore, in *H. rubrofasciata* natural selection seems to provoke costs on the trait that benefits males through sexual selection (see also Kotiaho *et al.*, 1998a; Ahtiainen *et al.*, 2005). However, it is important to note that the negative selection on the sexual signal was isometric as males were predated in proportion to the signalling rate. This suggests that the cost per signalling was the same for males signalling at a low vs. a high rate. Everything else being equal, this suggests that in this system predation alone cannot create different marginal costs for the signalling individuals. However, in *H. rubrofasciata* male drumming rate is condition dependent (Mappes *et al.*, 1996; Kotiaho, 2000), and female preference is positively allometric, i.e.

males with high drumming rate are preferred over the proportion to their drumming rate (Kotiaho *et al.*, 1996). Taken together, these results already suggest that the marginal costs of signalling may be lower for males in good condition, which would suggest that predation could act as an evolutionary cost enabling drumming to act as a honest indicator of male quality.

It may also be that males in good condition may be able to compensate for the increased costs of signalling. Some evidence exists that predation has shaped the evolution of sexual traits by turning males that live under heavy predation pressure to be less conspicuous (Endler, 1982; Winemiller *et al.*, 1990; Candolin, 1998), sing at a lower level (Ryan *et al.*, 1982; Zuk *et al.*, 1993) be smaller (Quinn *et al.*, 2001) or enhance endurance and escape abilities (Snell *et al.*, 1988; Miles *et al.*, 2001). It is also possible that males with high sexual signalling rates compensate behaviourally for their signalling activity. For example, in *H. rubrofasciata*, males decrease their drumming rate when they detect the presence of a predator (Kotiaho *et al.*, 1998b). Similarly, high signalling male crickets are more cautious when predators are present (Hedrick, 2000; Lewkiewicz & Zuk, 2004).

In our experiments male mobility was strongly positively related to their drumming rate (see Fig. 1, and see also Kotiaho *et al.*, 1998a; Ahtiainen *et al.*, 2003). In the escape ability experiment males with higher mobility were better able to escape predator attacks than males with lower mobility (Fig. 4). Provided that males with high signalling rate and high mobility are in good condition (Mappes *et al.*, 1996; Kotiaho, 2000), it seems that males in good condition bear the cost of signalling better than males in poor condition. Thus, the increased predation costs of males with high signalling rate may be balanced by males' ability to bear the cost by their increased escape ability (see also Godin & Dugatkin, 1996; Leal, 1999). Even though in this experiment we did not directly manipulate the condition of the males (see Kotiaho, 2001) our results imply that predation may function as a condition dependent cost promoting honest sexual signalling.

To conclude, we found that predation risk is higher for males signalling at high rate, but that the risk increases in proportion to the signalling rate. These results were observed only when the predators were experienced. Thus, in one sense it seems that predator behaviour does not fulfil the requirements of honest signalling where marginal costs are assumed to be different for males signalling at different rates (Grafen, 1990; Rowe & Houle, 1996; Tomkins *et al.*, 2004). However, our experiment also suggests that males with higher mobility were better at escaping the predation attempts. Since there is a strong positive correlation between drumming rate and mobility (see Fig. 1), it is likely that the predation costs are condition dependent, leading to the possibility that predation cost may be able to ensure honest signalling of heritable quality of males for the choosy females as suggested by the theoretical work.

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