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Testing the assumptions of conditional handicap theory: costs and condition dependence of a sexually selected trait

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Abstract Conditional handicap models of sexual selection predict that sexual traits are reliable signals of male quality because they are (a) condition dependent and (b) costly to produce or maintain. In this study, my objective was to experimentally investigate whether the drumming of male *Hygrolycosa rubrofasciata* wolf spiders is a condition-dependent costly trait. Males court females by drumming dry leaves with their abdomen and females preferentially mate with males drumming at higher rates. I manipulated male phenotypic condition and drumming rate simultaneously by keeping males on three different food rations and either introducing or not introducing them to a female. Food ration treatment affected male condition, as males on a low food ration lost mass while males on a high food ration maintained their mass at a constant level. The manipulation of food ration affected male drumming rate: males on a low food ration had the lowest drumming rate while males on a high food ration drummed at the highest rate. Manipulation of drumming rate incurred significant fitness costs: males induced to drum at higher rates suffered higher mortality than other males. Furthermore, there was a significant female introduction by food ration by male size interaction on male survival. When induced to increase their drumming rate, large males manipulated to be in good condition survived better than large males manipulated to be in poor condition. There was no such difference in small males. When drumming rate was not increased, the slopes between males survival and size were homogeneous and weakly positive across each condition treatment. Despite the higher mortality when introduced to females, there was still a significant positive correlation between drumming rate and survival. My results demonstrate that sexual signalling in *H. rubrofasciata* is condition dependent

and costly, thus supporting conditional handicap models of sexual selection.

Key words Costs · Conditional handicap · Good genes · Phenotypic condition · Sexual selection

Introduction

Conditional handicap models (Zahavi 1977; Andersson 1982; Nur and Hasson 1984; Pomiankowski 1987; Grafen 1990a; Iwasa et al. 1991; Johnstone and Grafen 1992; Rowe and Houle 1996) suggest that secondary sexual traits may serve as honest signals of male quality for choosy females. Three important assumptions underlying these models are that (a) the expression of the sexual trait is dependent on male phenotypic condition, (b) traits are costly to produce or maintain and (c) for males in good phenotypic condition, the costs of increased trait size are smaller than for males in poor condition [Grafen 1990a; Johnstone and Grafen 1992; for an argument against assumption (c) see Getty 1998]. When these assumptions are met, a positive correlation between the degree of expression of the sexual trait and male quality is predicted. This positive correlation is the central basis of conditional handicap models. Females choosing mating partners on the basis of honest quality revealing sexual traits are expected to benefit either directly by choosing direct benefits for themselves (Price et al. 1993), or indirectly by choosing good genes for their offspring (Møller and Alatalo 1999).

Evidence supporting the positive condition dependence of sexual traits is accumulating (Milinski and Bakker 1990; Møller 1991; Frischknecht 1993; Hill and Montgomerie 1994; Johnstone 1995; Mappes et al. 1996; David et al. 1998; Griffith et al. 1999; Keyser and Hill 1999; for an interesting exception see Candolin 1999). Nutritional status is generally closely related to phenotypic condition and thus provides a relatively easy way of manipulating condition (Frischknecht 1993; Mappes et al. 1996; David et al. 1998; Candolin 1999). However,

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the second assumption, that secondary sexual characters are costly has not been as easy to demonstrate. In most theoretical models, costs have been explicitly described as having a negative influence on fitness, and in particular survival, of the trait bearer (Nur and Hasson 1984; Andersson 1986; Pomiankowski 1987; Grafen 1990a, 1990b; Iwasa et al. 1991). Therefore, if obtaining or maintaining a sexual trait does not have a negative influence on the possessor's fitness it cannot be inferred as causing evolutionarily significant costs. In fact, significant costs are too often inferred in recent literature, when there are actually no empirical grounds for doing so (J.S. Kotiaho, unpublished data). As an example, energy expenditure has often been assumed to reflect costs of sexual display, even though energy expenditure in itself cannot be viewed as an evolutionarily significant cost if it has not been shown to either increase the mortality or reduce the reproductive success of an individual. In the growing body of literature that is viewed as supporting the prediction that sexual traits are costly, very few studies have actually addressed evolutionarily meaningful costs (Cade 1975; Møller 1989; Møller and de Lope 1994; Mappes et al. 1996; Grether 1997; Zuk et al. 1998). Demonstrating that sexual traits are costly is difficult because animals are expected to optimise their level of signalling in each situation. Therefore, the trade-off between expression of the sexual trait and survival may not be revealed by correlational studies and, hence, the fact that all six studies mentioned above are experimental works is not a coincidence.

The third assumption, that individuals in good condition are better able to bear the costs of increased sexual trait size, has also proven difficult to establish. No studies have examined condition-dependent costs with simultaneous manipulation of condition and sexual trait. Ultimately, however, the third assumption can only be supported or rejected by such simultaneous manipulations. If simultaneous manipulation of condition and sexual trait has an interaction effect on survival, such that the difference in survival between individuals in good or poor condition is greater in individuals with a larger trait than in individuals with a smaller trait, strong evidence will have been provided that individuals in good condition are better able than those in poor condition to bear increased costs.

Hygrolycosa rubrofasciata (Ohlert) is a wolf spider (Lycosidae) which patchily inhabits open meadows and bogs through northern Europe. The body mass of males varies from 9 to 25 mg, while repeatability of body mass within individuals is high ($R=0.82-0.99$) (Kotiaho et al. 1996, 1999b). Male body length is 5–6 mm (Kronestedt 1996). Larger males are able to repel smaller males in fights (Kotiaho et al. 1997, 1999a), but we have not detected any mating advantages for larger males (Kotiaho et al. 1996). *H. rubrofasciata* males court females by drumming dry leaves with their abdomen. One drumming consists of 30–40 separate pulses and lasts about 1 s (Kronestedt 1996; Rivero et al., in press). The drumming is clearly audible from several metres and so can

be observed accurately. The drumming rate between males varies naturally from 0 to 5 drums per minute (mean ca 1.1 drums per minute) and the drumming rate of individual males is quite repeatable (61.6%) (Kotiaho et al. 1996). Earlier studies demonstrated that females base their mate choice on male drumming, preferentially mating with males that drum at higher rates (Kotiaho et al. 1996, 1998a; Parri et al. 1997). Mappes et al. (1996) studied the effect of food ration on male drumming rate and found that it was positively dependent on male nutritional status. With another experiment on a different set of males, Mappes et al. (1996) found that males kept in poor nutritional status and manipulated to drum more suffered increased mortality.

The aim of this study was to experimentally investigate the three main assumptions of the conditional handicap theory with a simultaneous, and therefore more realistic, manipulation of phenotypic condition and sexual display rate. In addition, I determined whether body mass was related to the display rate or survival. In our previous experiment on costs and condition dependence (Mappes et al. 1996), we manipulated male display rate only with males that were kept in a poor nutritional state, i.e. with males that were in poor condition. Therefore, the main result that males suffered increased mortality is valid only for males that are in poor condition and leaves open two major questions: do males in good condition suffer costs of increased display rate and, more important, are males in good condition better able to bear the costs of increased display rate than males in poor condition. The latter question can only be answered definitively by examining the interaction effect from simultaneous manipulation of both condition and display rate.

Methods

H. rubrofasciata was collected from a meadow in Sipoo, southern Finland by pitfall trapping on 14 May 1997. Spiders were housed in darkness in individual clear plastic jars with moss at 5°C. These housing conditions were used to prevent males from becoming sexually active before the experiment was initiated. On the 21 May, spiders were moved to a constant temperature of 20°C and naturally fluctuating light regime. The substrate in the jars was changed to soft cellulose paper that was moistened regularly. All males were fed ad libitum (*Drosophila melanogaster*) for a period of 7 days after which their "initial" body mass and drumming activity were quantified. Body mass was measured to the nearest 0.1 mg. Drumming rate was measured five times for 2 min in small (10×15 cm) plastic arenas containing a sheet of dry copy paper as a drumming substrate. Body mass and drumming rate measurements were repeated after 2 days.

After determining their initial body mass and drumming rate, males were assigned to one of six treatment groups assuring similar initial body mass and drumming rate. Treatments were low, medium or high food ration [one *D. melanogaster* every 6th day (low), one every 3rd day (medium) and one daily (high)] with or without daily introduction to a female. *H. rubrofasciata* males drum without the presence of females or female silk but will increase their drumming rate considerably in the presence of a female. Thus, the costs of male sexual signalling may be tested by manipulating not the trait itself, but the expected pay-off (probability of mating), thus avoiding manipulative artefacts that may arise by direct manipulation of the sexual trait (e.g. cutting, glu-

ing, painting). Sample size in each treatment group was designed to be 36. Unfortunately, due to escapes and accidents in handling the spiders, the final sample size varies between 30 and 36.

During the experiment, males were transported daily from their individual jars to small plastic arenas (10×15 cm) with a sheet of dry copy paper as a drumming substrate. For the female introduction group, a randomly chosen female was released into each of the arenas 30 min before starting the experiment. Females were released to the arena to lay down silk which induces greater male drumming. Prior to releasing males, females were captured in small (diameter 2 cm) cotton net cages in the centre of the arenas. Cages prohibit direct contact but allow auditory, vibratory and olfactory communication. Males in the no-female-introduction group were released into similar arenas with empty cages. Each day, males were left in the arenas for 3 h. Every 3rd day, male body mass and drumming rate (twice for 2 min each time) were quantified for each male. For the comparison of changes in body mass and drumming rate, I combined the data in 10-day periods. Male survival was recorded daily and the number of days the male survived from the beginning of the experiment was used as an estimate of male survival. The experiment was terminated after 49 days when only a few males were still alive.

I used parametric statistics when the assumption of these tests were fulfilled. In repeated-measures ANOVA, the sphericity assumption was always violated; to account for this violation, degrees of freedom were Greenhouse-Geisser adjusted. If assumptions were not met, non-parametric alternatives were applied. All reported probabilities are for two-tailed tests.

Results

Body mass

Prior to manipulation there were no differences in body mass of the males between the treatments (ANOVA $F_{5,197}=0.56$, $P=0.733$). However, as the experiment proceeded, male body mass changed significantly (repeated-measures ANOVA full model $F_{1,49,161.27}=76.16$, $P<0.001$; degrees of freedom are Greenhouse-Geisser adjusted to account for violation of the sphericity assumption). The three-way interaction between date, food ration and female, and the two-way interaction between date and female were not significant ($F_{2,99,161.27}=0.88$, $P=0.452$ and $F_{1,49,161.27}=1.91$, $P=0.162$, respectively). However, the two-way interaction between date and food ration was ($F_{2,99,161.27}=18.37$, $P<0.001$). This interaction resulted from males on a high food ration maintaining their mass while males on medium and low food rations lost mass during the course of the experiment (Fig. 1).

Drumming rate

Prior to manipulation, there were no differences in drumming rate between the treatments (ANOVA $F_{5,197}=0.04$, $P=0.999$). However, as the experiment proceeded, drumming rates changed significantly (repeated-measures ANOVA full model $F_{2,49,259.24}=17.80$, $P<0.001$; degrees of freedom are Greenhouse-Geisser adjusted to account for the violation of the sphericity assumption). The three-way interaction between date, food and female, and the two-way interaction between date and food were not significant ($F_{4,99,259.24}=0.97$, $P=0.438$ and $F_{4,99, 59.24}=1.46$, $P=0.203$, respectively). However, the

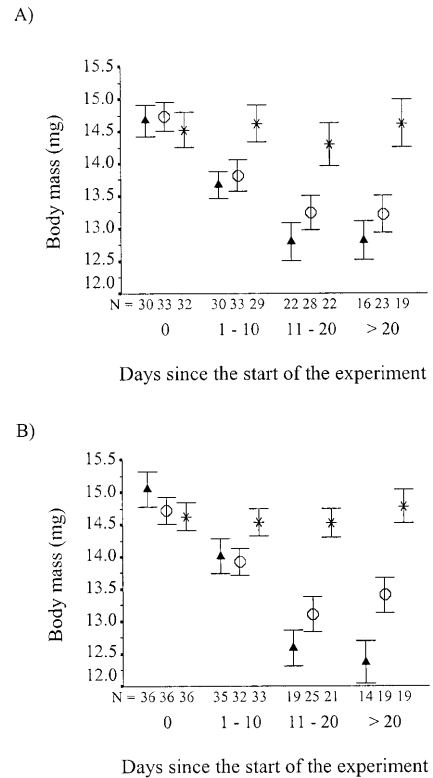


Fig. 1 Mean (± 1 SE) body mass (mg) of male spiders not introduced to the female (**A**) and introduced to the female (**B**) in different food ration regimes (stars high food ration, open circles medium food ration, closed triangles low food ration)

two-way interaction between date and female was ($F_{2,49,259.24}=24.85$, $P<0.001$), indicating that the within-individual drumming rate changed depending on the female treatment. This interaction resulted from a decrease in the drumming rate of males not introduced to females (Fig. 2A), and from an increase in the drumming rate of males that were introduced to females (Fig. 2B). Between subjects, there was a strong main effect of both female and food treatment on drumming rate ($F_{1,104}=106.34$, $P<0.001$ and $F_{2,104}=4.84$, $P=0.010$, respectively). However, these effects need careful examination as there was also a significant interaction between food and female treatment on drumming rate ($F_{2,104}=4.51$, $P=0.013$). Examination of Fig. 2 reveals that the effect of female introduction is very robust, as the drumming rate of males introduced to females is about ten times greater than that of males not introduced to females. The effect of food ration is also clear: after 10 days of experimentation, the highest and lowest drumming rate was associated with the highest and lowest food ration, respectively. The significant interaction results from the difference in the magnitude of the effects across the female treatments: in the no-female-introduction group, the effect of food ration on drumming rate is positive (Fig. 2A) but not as strongly positive as in the female introduction group (Fig. 2B).

There was no correlation between male drumming rate and body mass prior to manipulation (Spearman's

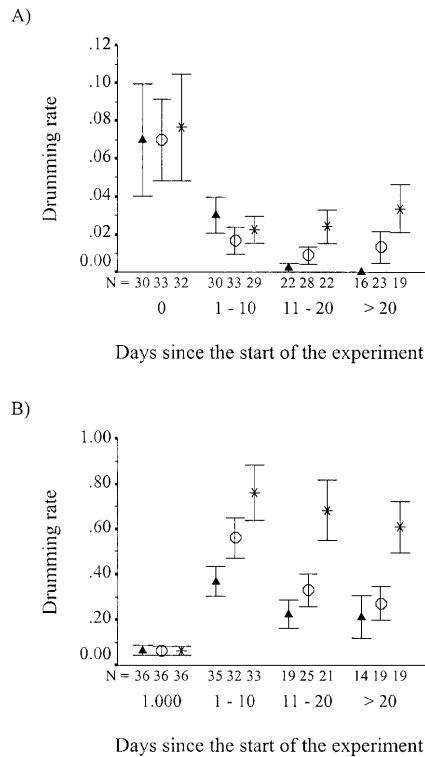


Fig. 2 Mean (± 1 SE) drumming rate per minute on different food rations in the no-female (A) and female (B) treatment (stars high food ration, open circles medium food ration, closed triangles low food ration). Note the different scales on the y-axis

$r = -0.092$, $n = 203$, $P = 0.194$). To examine the effect of food ration on this correlation, I included only males that were not introduced to females (because female introduction changes male drumming behaviour). After 20 days of experimentation, males on a low food ration had stopped drumming almost completely (21 out of 22) and thus correlations were not performed on these males. On the medium food ration, there was a negative correlation between initial body mass and drumming rate (Spearman's $r = -0.481$, $n = 28$, $P = 0.010$) while on the high food ration, the relationship remained flat (Spearman's $r = -0.056$, $n = 22$, $P = 0.804$).

Survival

I analysed survival with a fully saturated cox-regression (survival analysis) with food and female as categorical covariates and initial body mass and mean drumming rate as continuous covariates. The fully saturated model was significant ($\chi^2_{23} = 47.26$, $P = 0.002$). To determine the terms causing this significant effect, I used a stepwise removal of terms starting from the highest-order interactions. The four-way and all but one three-way interactions were not significant with an α -level > 0.5 , and the significant three-way interaction involved food ration, female introduction and initial body mass (Wald = 6.45, $df = 2$, $P = 0.040$). The overall model retaining the signifi-

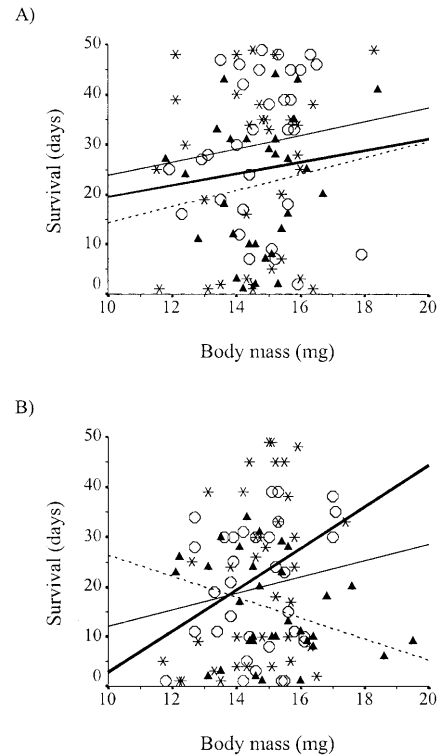


Fig. 3 Representation of the three-way interaction between initial body mass, food ration and female treatments on survival when males were not introduced to a female (A) and when males were introduced to a female (B) (stars/bold solid line high food ration, open circles/solid line medium diet, solid triangles/dashed line low food ration)

cant three-way interaction and all lower-level terms was highly significant ($\chi^2_{16} = 45.40$, $P < 0.001$). This interaction is best presented graphically (Fig. 3): when males were induced to spend more on drumming (Fig. 3B), large individuals in good condition (Figs. 3B, 4D, bold solid line) survived better than large individuals in poor condition (Figs. 3B, 4D, dashed line). However, the manipulation of condition had a much weaker effect on survival of small males (Figs. 3B, 4B). When males were not introduced to the female, survival was constantly and slightly positively related to male body mass across the three conditions (Fig. 3A).

The significant interaction constrains the interpretation of the main effects. However, compared with the interaction term, the main effects were relatively strong for both food ration and female introduction (Wald = 14.19, $df = 2$, $P < 0.001$ and Wald = 11.65, $df = 1$, $P < 0.001$, respectively). To examine these main effects more closely, I split the data into small ($<$ mean body mass) and large (\geq mean body mass) males (to account for the interaction with body mass) and constructed separate survival functions for food rations (Fig. 4) and for female treatments (Fig. 5). Food ration had a clear effect on male survival: males on a low food ration always had the lowest survival regardless of their size or female introduction treatment (Fig. 4). The effect of female introduction was

Fig. 4A–D Effect of food ration on male survival for small (<mean body mass) and large (\geq mean body mass) males separately and for female treatments (*bold line* high food ration, *thin line* medium food ration, *dashed line* low food ration). **A** Small males with no female introduction. **B** Small males with female introduction. **C** Large males with no female introduction. **D** Large males with female introduction

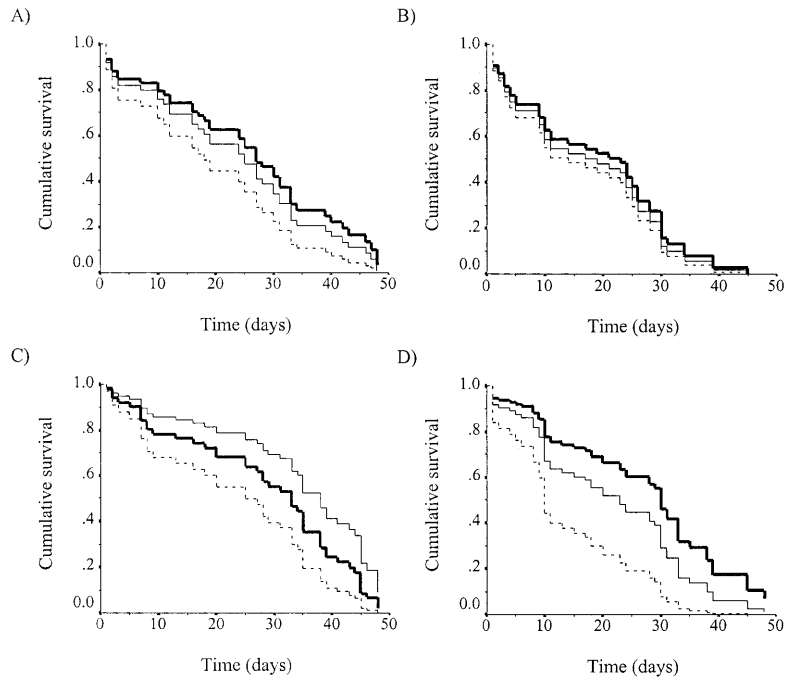
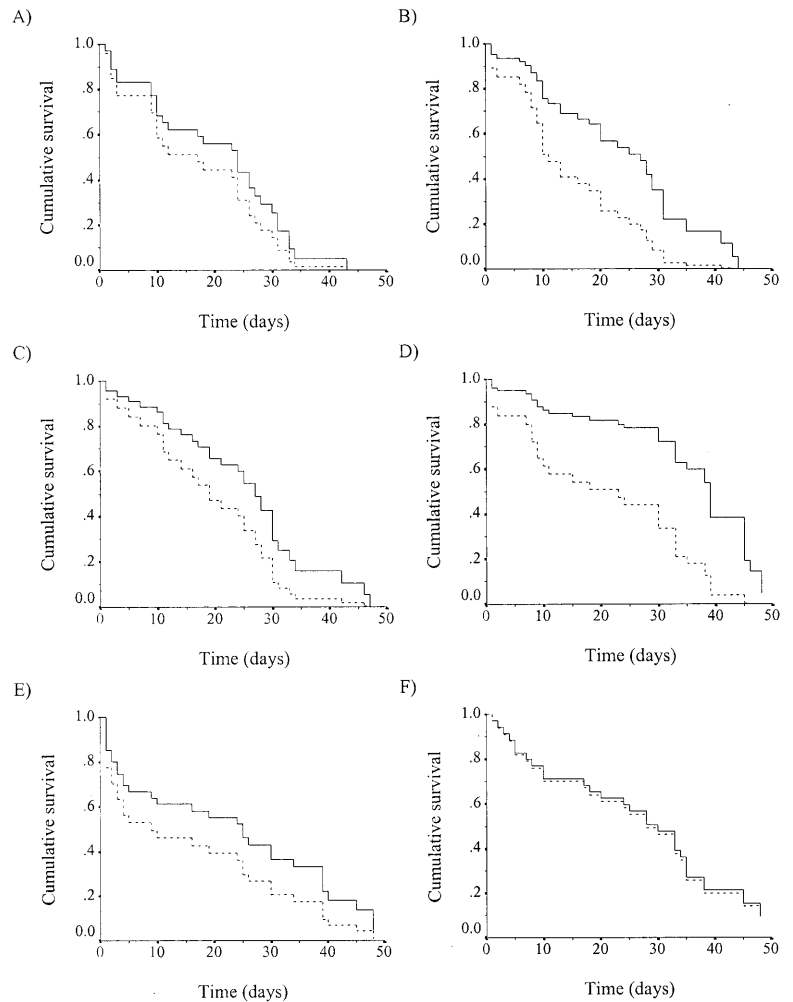


Fig. 5A–F The effect of female introduction on survival of the small and large males on different food rations (*solid line* no female introduction, *dashed line* female introduction). **A** Small males, low food ration. **B** Large males, low food ration. **C** Small males, medium food ration. **D** Large males, medium food ration. **E** Small males, high food ration. **F** Large males, high food ration



even clearer, as in all food ration treatments, regardless of male size, introduction to the females always reduced male survival (Fig. 5).

Overall there was no correlation between male survival and mean drumming rate (Spearman's $r=0.014$, $n=203$, $P=0.848$). However, when the female treatments were analysed separately, there was a significant positive correlation between mean drumming rate and survival in males that were introduced to the females but not in males that were not introduced to the females (Spearman's $r=0.236$, $n=108$, $P=0.014$ and $r=0.052$, $n=95$, $P=0.614$, respectively).

Discussion

If sexually selected traits are costly and expressed in proportion to the phenotypic condition of the possessor, larger and well developed traits should be reliable indicators of quality. These assumptions form the backbone of the conditional handicap theory of sexual selection (Zahavi 1977; Nur and Hasson 1984; Andersson 1986; Grafen 1990a; Johnstone and Grafen 1992).

In this study I found that food ration was effective in manipulating male condition: males on a low and medium food ration lost mass while males on a high food ration did not. Similarly, exposure to females effectively manipulated male drumming rate: males introduced to females drummed about ten times more than males that were not introduced to females. Drumming rate was condition dependent, as manipulation of condition affected the sexual signalling rate of males. Moreover, males induced to drum more suffered an increased mortality, providing evidence that there are significant fitness costs of sexual display. These two results accommodate two of the predictions of handicap models.

The third prediction of conditional handicap models is that males in good condition are better able to bear the costs of increased trait expression than males in poor condition. This prediction should lead to a positive correlation between trait expression and survival. Indeed, despite their reduced survival, there was still a significant positive correlation between drumming rate and survival in males that were induced to drum above their optimum level. To date, all support for the third assumption comes from these kinds of correlations (e.g. Møller 1989; Grether 1996; Kotiaho et al. 1996; Mappes et al. 1996). However, a positive correlation, or indeed a lack of negative correlation, between trait and survival is at best weak evidence for the prediction that males in good condition are better able to bear the costs of increased trait expression than males in poor condition. Ultimately, this prediction can only be supported or rejected by simultaneous manipulation of condition and the sexual trait.

The most important finding of this study was the significant three-way interaction between food ration, female introduction and initial body mass on male survival. This interaction means survival varies with male condition, display rate and body size. I will first consider

the males that were induced to increase their drumming rate (Fig. 3B). When males spent more on drumming, large individuals in good condition survived better than large individuals in poor condition. However, the manipulation of condition had no effect on the survival of small males. Comparing these results with those from males that were not induced to increase their drumming rate (Fig. 3A) demonstrates clearly that the effect of body mass on survival was constant and slightly positive across the three conditions. This interaction provides evidence for the third assumption of handicap models, but note that the effects are dependent on male size.

My conclusion, that males suffer viability costs due to increased sexual signalling, corroborates a key assumption of most models of sexual selection (e.g. Nur and Hasson 1984; Andersson 1986; Pomiankowski 1987; Grafen 1990a, 1990b; Iwasa et al. 1991). In the recent literature on the costs of sexual traits, the definition of cost as a negative influence on individual fitness has often been neglected and on many occasions, the evidence that traits cause evolutionarily significant fitness costs is at best circumstantial (J.S. Kotiaho, unpublished data). Evidence that sexual traits cause evolutionarily significant fitness costs is actually drawn from a very small number of experimental studies (Cade 1975; Møller 1989; Møller and de Lope 1994; Mappes et al. 1996; Wagner 1996; Grether 1997; Zuk et al. 1998).

Male body mass was not related to male drumming rate. In an earlier study on metabolic rates, Kotiaho et al. (1998b) found that larger males require significantly more energy per unit mass during drumming than smaller males. This relationship was somewhat counterintuitive, since metabolic rate generally decreases with body size (see e.g. Kleiber 1932; Reiss 1989). Due to the positive relationship between energy expenditure per unit mass and body mass, a negative relationship between body mass and drumming rate might be expected. However, such a negative correlation has never been found; rather, the relationship has always been flat or slightly positive (Kotiaho et al. 1996, 1998b, 1999b; Mappes et al. 1996). Heavier males seem, therefore, able to compensate for the higher energy demand of drumming. In the present study, male drumming rate was again not related to male body mass. However, after 20 days of experimentation, the drumming rate of males on the medium food ration was negatively correlated with body mass, while on a high food ration, the relationship was still flat. The difference between these two relationships supports the hypothesis that larger males are able to compensate for the increased energy requirement of drumming by increasing their energy input. In other words, when food input was experimentally restricted, larger males were not able to maintain their drumming activity at the same level as the smaller males, generating the negative relationship observed. Moreover, when large males were experimentally induced to drum at a higher rate and simultaneously kept on a low food ration, they suffered increased mortality, lending further support to the idea that large males need a higher energy input to

sustain the same levels of sexual signalling as small males.

In conclusion, my results provide evidence for the conditional handicap models of sexual selection. First, drumming rate was dependent on male phenotypic condition: males in better condition drummed at a higher rate than males in poorer condition. Second, increased sexual display rates caused significant mortality costs and, finally, these mortality costs were dependent on male condition and size. These results together with earlier studies (Kotiaho et al. 1996, 1998b, 1999b; Mappes et al. 1996; Alatalo et al. 1998) provide strong evidence that for *H. rubrofasciata*, drumming is an honest signal of male quality.

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