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Sexual signalling and viability in a wolf spider (*Hygrolycosa rubrofasciata*): measurements under laboratory and field conditions

Abstract This study examined the crucial prediction of the conditional-handicap theory, the relationship between male sexual trait size and male viability, in the wolf spider *Hygrolycosa rubrofasciata*. In this species, males court females by drumming dry leaves with their abdomen, and males with the highest drumming rate enjoy highest mating success. We determined male drumming rate, body mass, and mobility, which reflects mate-searching activity, in relation to male survival. Because it is often difficult to know how results obtained from laboratory studies reflect the natural world, particularly when the measured variable is survival, we repeated our study in both laboratory and field conditions. Males drumming at the highest rate survived better than males drumming at a lower rate in both laboratory and field conditions. These results are in accordance with the predictions of conditional-handicap models of sexual selection. Survival was independent of male body mass and there was no significant correlation between male drumming activity and body mass. However, large males moved further than smaller males, and males moving longer distances lost less mass than those moving shorter distances. These results suggest that, moving, and consequently mate-searching activity, may be a condition-dependent trait and that there may be a advantage for large males in mate searching.

Key words Conditional handicap · *Hygrolycosa rubrofasciata* · Laboratory versus field study · Mate choice · Sexual selection · Viability

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Introduction

Conditional handicap models (Zahavi 1975, 1977; Nur and Hasson 1984; Andersson 1986; Pomiankowski 1987; Grafen 1990a, 1990b; Iwasa et al. 1991; Johnstone and Grafen 1992) suggest that sexual trait size or display activity should be largest in the most viable males and, consequently, secondary sexual traits may serve as honest signals of male quality for choosy females. For a trait to serve as an honest signal of quality, three underlying assumptions need to be fulfilled. First, the production or maintenance of sexual traits must cause significant costs that reduce one component of the fitness of the bearer. Second, sexual traits must be condition dependent and, third, the marginal costs of sexual traits must be less for males in good condition than for males in poor condition. When these assumptions are met, a positive correlation between sexual trait size and viability is predicted (Grafen 1990a; Johnstone and Grafen 1992).

There are many different indirect measures of male quality (e.g. nutritional status, body mass, residuals from body mass vs some other size measure, fat content, various blood parameters, endurance of physical stress, fluctuating asymmetry; see e.g. Andersson 1994; Jakob et al. 1996), and it is often hard to know how a measure of a quality is related to individual fitness. Viability, measured as survival over time, is a direct component of individual fitness and, therefore, may be used as a more reliable measure of quality. Empirical evidence for a correlation between sexual trait size or male attractiveness and viability exists but is far from abundant (e.g. Butlin and Day 1985; Göransson et al. 1990; Alatalo et al. 1991; Møller 1991; Kempenaers et al. 1992; Kotiaho et al. 1996; Mappes et al. 1996; Hoikkala et al. 1998).

Hygrolycosa rubrofasciata (Ohlert) is a wolf spider (Lycosidae) which inhabits open, moist meadows and bogs. Males moult into adulthood during the autumn and overwinter as adults; thus there are unlikely to be

any significant age differences when the mating season starts in the spring. In southern Finland, most matings take place during the few days immediately following the snow melt in late April or early May, but males will court until the beginning of June. Each adult male cohort reproduces during only one mating season and males die during or immediately after it. However, we have observed individually marked females surviving until the next mating season.

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 1984, 1996). The drumming is clearly audible from several metres and has been demonstrated to be under directional sexual selection through female choice (Kotiaho et al. 1996, 1998a; Parri et al. 1997). Male body mass varies from 9 to 25 mg (male body length is 5–6 mm; Kronestedt 1984). However, even though larger males are able to repel smaller males in fights (Kotiaho et al. 1997), there are no obvious mating advantages for larger males (Kotiaho et al. 1996). Body mass is not correlated with drumming rate and generally there is no relationship between body mass and survival (Kotiaho et al. 1996; Mappes et al. 1996). This suggests that, in this species, body mass may be only of minor importance in sexual selection. However, under very stressful conditions, body mass has been observed to be weakly but positively correlated with survival (Mappes et al. 1996), indicating that in some circumstances, mass may play a role and, therefore, more detailed studies on its importance are needed.

In an earlier laboratory experiment with *H. rubrofasciata*, males experimentally manipulated to increase their drumming activity suffered increased mortality (Mappes et al. 1996). However, within the manipulation group, the most actively drumming males survived better than less actively drumming males. Accordingly, in another laboratory experiment, where male survival was observed over a 1-month period at a fixed low temperature, we found a positive relationship between male drumming activity and survival (Kotiaho et al. 1996). However, it is possible that there are interactions between the trait and the environment (e.g. Roff 1992, 1997; De Jong 1995) and therefore it is often difficult to know how results obtained from highly controlled laboratory studies reflect the natural world. This is particularly true for studies in which the measured variable is survival. For this reason, work that combines results from both controlled laboratory studies and less controlled field studies are greatly needed.

Here we present results from a combined laboratory and field examination of the survival, sexual signalling rate, body mass and mate-searching activity of the wolf spider *H. rubrofasciata* during four mating seasons. Our two main objectives were to determine whether male survival is related to drumming rate under laboratory, and in particular, under field conditions, and to determine if body mass could potentially be a factor in sexual selection in this species.

Methods

Laboratory study

Specimens ($n = 30$) for the laboratory study were collected from a bog at Sipoo in southern Finland (60°16′N and 25°14′E) in April 1995. Spiders were housed individually in plastic jars (diameter 40 mm) filled with *Sphagnum* spp. at 6 °C in darkness to prevent males becoming sexually active until the measurements began. In addition to small arthropods naturally present in the *Sphagnum*, spiders were given *Drosophila melanogaster* fruitflies ad libitum and the jars were moistened regularly. On 1 June, males were taken out of the fridge into a naturally fluctuating temperature and light regime. From this date, males were taken into the laboratory approximately every 3rd day during a 2-month observation period for mass and drumming-rate measurements. Body mass was measured to the nearest 0.1 mg and the mass change was calculated by comparing each measurement to the first measurement. For drumming-activity measurements, males were individually placed in plastic arenas of 10×15 cm with some dry birch leaves. During each observation period, the number of drums was counted three times for 2 min. A previous study showed considerable repeatability in male drumming rate (61.6%; $F_{16,51} = 3.51$, $P < 0.001$) (Kotiaho et al. 1996). Survival was measured as the number of days males survived from the beginning of the experiment.

Field studies

Field studies were conducted during 1993, 1994 and 1996, on two populations at Sipoo. They began immediately after snow melt in late April and continued until late May–early June after which most of the females were already mated and had started to produce eggsacs.

Mate-searching activity in the field

Mate-searching activity was studied during 1993 and 1994 with the mark-and-recapture method. Between 11 and 13 May 1993, within an area of 7×7 m, males were captured using pitfall traps, marked individually by placing a small dot of paint on the dorsal surface of the prosoma, ophistosoma or both, and released immediately to the capture site. Pitfall traps were constructed from a clear plastic sheet (200×150 mm) and two plastic cups (diameter 65 mm). Traps were dug into the ground so that the plastic sheet was between the cups and functioned as a fence that directed spiders towards the cups. These spiders are unable to climb out of the plastic cups. Pitfall traps were situated in the centre of each 1×1 m square such that the fence between the cups was alternately oriented north-south and east-west. All males captured during the day were taken to the laboratory for body mass measurement. Between 28 April and 15 May 1994, the mark-and-recapture study was conducted in another area (10×10 m) of the same bog in a similar manner as described for 1993, but males were weighed to the nearest 0.1 mg each time they were recaptured. In both years, male mobility was estimated as the distance between the two successive capture sites.

Survival and drumming activity in the field

Drumming activity and survival of individual males were studied during 1996 with another mark-and-recapture study on a different population (distance between populations was ca 1 km) within a closed area of 7×7 m. The area was closed with sequential long pitfalls ($800 \times 20 \times 20$ mm) deposited at a small angle such that the outside wall prevented arthropods coming in from the outside, while the inside wall allowed them to fall in from the inside. These pitfalls could also be closed by depositing a cloth on the inside wall and base such that arthropods could walk in and out of them.

The gaps between long pitfalls were blocked by a plastic fence preventing any non-flying arthropods escaping from or entering into the area. Simple pitfall traps (diameter 65 mm) were dug every 25 cm in the study area.

Before the mating season started, we captured 100 males outside but close to the enclosure and housed them for 10 days in the fridge. Prior to starting the study, we measured male drumming activity, mobility and body mass. Drumming activity and mobility was measured simultaneously in the plastic arenas described above. For the mobility measurement, we divided the plastic arena into four equal parts and counted how many times a male entered a new section of the arena. This number was used as a mobility index. Drumming activity and mobility measurements were made three times for 2 min and the procedure was repeated on 3 consecutive days. Male body mass was measured to the nearest 0.1 mg and males were marked individually as described earlier. Before releasing these males to the enclosure, 100 males were removed from the enclosure to maintain the natural density.

Pitfalls inside the area were opened every observation day at noon and emptied and closed at 3.00 p.m. All captured individuals were identified and their body mass immediately measured under constant laboratory conditions after which they were returned to the study area. The long pitfalls around the area were opened in the evening prior to the observation day and checked four times: in the morning, at noon, at 3.00 p.m. and in the evening when they were closed. All other arthropods in the pitfalls were returned to the study area in order to maintain its general faunal composition. The study was terminated on 1 June because most males drowned accidentally in pitfalls due to a heavy rainfall. However, by then, the mating season was already nearly over, and this premature ending is thus unlikely to distort the results.

Statistical tests

To test the relationships between drumming activity, mobility index, survival and body mass, we used the mean of the first three drumming activity, mobility index and body mass measurements, since they represent the initial situation. When testing the change of individual male drumming activity and body mass over time in the laboratory with repeated-measures ANOVA, we had to perform two separate tests in order not to lose relevant data due to the death of some males during the study. Repeatability analyses are completed following the methods outlined by Lessells and Boag (1987). Parametric statistics were used when assumptions were met either before or following transformation. If assumptions were not met, we used non-parametric statistics. All the probabilities reported are for two-tailed tests.

Results

Change in body mass

In the laboratory, male body mass did not change with time (repeated-measures ANOVA for the first ten and for the next ten measurements $F_{9,5} = 2.15$, $P > 0.2$ and $F_{9,7} = 2.54$, $P > 0.1$, respectively; for details see Methods; Fig. 1A). Variance of male body mass was much greater between than within individuals (ANOVA, $F_{29,396} = 124.45$, $P < 0.001$) and repeatability of male body mass was 0.90 (95% confidence interval: 0.84–0.94) (for methods see Sokal and Rohlf 1969; Lessells and Boag 1987; Krebs 1989).

In the field, however, male body mass decreased as the season progressed both in 1994 and in 1996 (re-
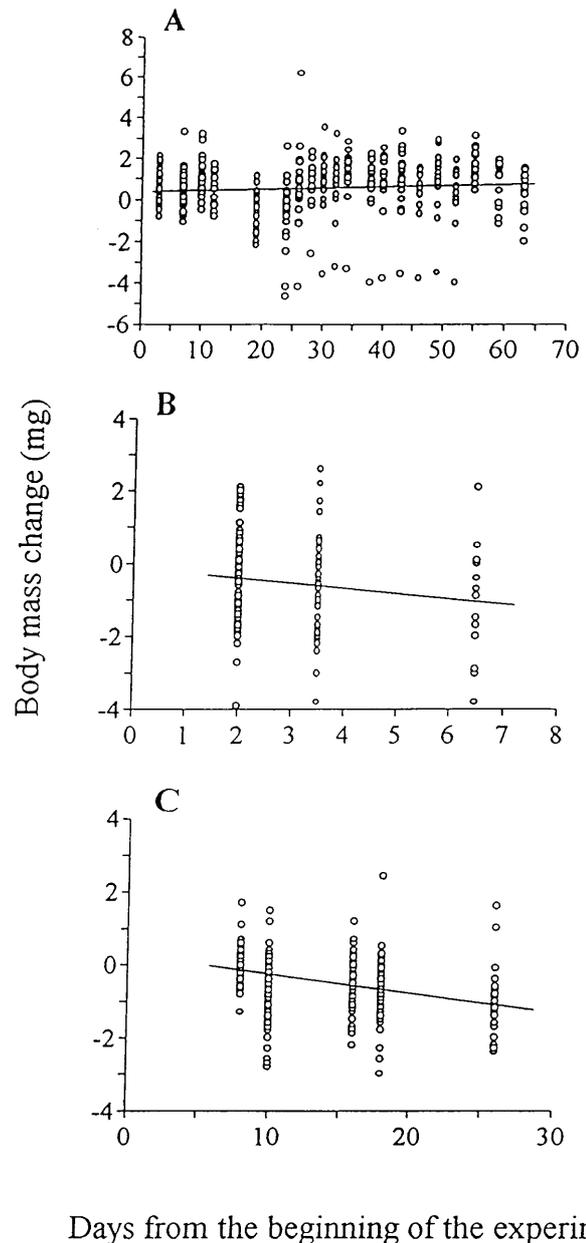

Fig. 1 **A** Relationship between male body mass change and date in the laboratory, 1995. **B** Relationship between male body mass change and date in the field, 1994. **C** Relationship between male body mass change and date in the field, 1996

peated-measures ANOVA $F_{2,48} = 4.15$, $P = 0.022$ and $F_{5,16} = 10.51$, $P < 0.001$, respectively; (Fig. 1B,C). Despite the decline in body mass, the repeatability was as high as 0.82 (0.75–0.87) (ANOVA, $F_{102,167} = 13.10$, $P < 0.001$) in 1994 and 0.94 (0.92–0.96) (ANOVA, $F_{100,315} = 64.74$, $P < 0.001$) in 1996.

Mate-searching activity

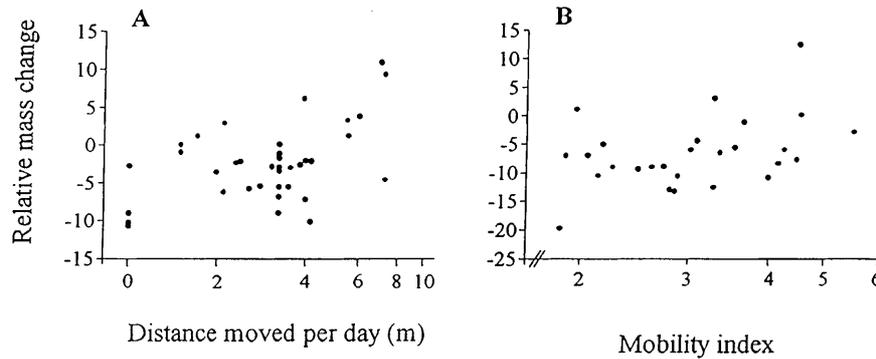During the mating season, males may be moving considerably long distances within a single day (observed

Fig. 2 A Relationship between the relative mass change (%) per day and the distance moved per day. Time between recaptures is 2 days maximum. Partial correlation between mass change and distance moved controlled for the mean temperature between 11.00 a.m. and 1.00 p.m. of the day: $r = 0.51$, $n = 38$, $P = 0.001$. Distance is ln-transformed. **B** Relationship between relative mass change (%) from the beginning to the end of the study and mobility index (see Methods) (Pearson's $r = 0.40$, $n = 27$, $P = 0.042$). Mobility index is ln-transformed

maximum > 30 m; mean $\pm$ SD 1993 $= 2.02 \pm 0.94$ m; 1994 $= 1.95 \pm 1.45$ m). There was also some repeatability in male mobility per day: in 1994 it was 0.48 (0.19–0.72) (ANOVA, $F_{24,35} = 3.25$, $P < 0.001$) and in 1996, 0.46 (0.25–0.81) (ANOVA, $F_{6,532} = 65.10$, $P < 0.001$). Male mobility in the field was positively correlated with male body mass in 1993 and 1994 (Pearson's $r = 0.49$, $n = 25$, $P = 0.014$ and $r = 0.20$, $n = 109$, $P = 0.036$, respectively; both mobilities are ln-transformed). Similarly in 1996, there was a positive correlation between male mobility index and body mass (Pearson's $r = 0.23$, $n = 100$, $P = 0.022$; mobility index is ln-transformed).

In 1994, males that lost more weight moved shorter distances. In fact some males moving long distances even gained weight (Fig. 2A). In 1996 also, there was a positive correlation between male weight change and mobility index (Fig. 2B). Mobility index was also positively correlated with male drumming rate (Spearman's $r = 0.37$, $n = 100$, $P < 0.001$), but there was no significant relationship between mobility index and male survival (Spearman's $r = 0.17$, $n = 100$, $P = 0.093$).

Drumming rate

In the laboratory, individual male drumming rate decreased with time (repeated-measures ANOVA for the first 10 measurements and for the next 11 measurements: $F_{9,10} = 11.46$, $P < 0.001$ and $F_{10,4} = 10.44$, $P = 0.019$, respectively; for details see Methods). The mean drumming rate at the beginning of the period was 2.1 drums per minute and in the end of the period 0.4. There was no significant correlation between male drumming rate and body mass in the laboratory (Spearman's $r = 0.31$, $n = 30$, $P = 0.100$) or in the field (Spearman's $r = 0.13$, $n = 100$, $P = 0.187$).

Survival

In the laboratory, males that in the initial phase of the experiment drummed most actively were most likely to survive the longest (Fig. 3A). Indeed, all the males with a drumming rate less than one per minute died very
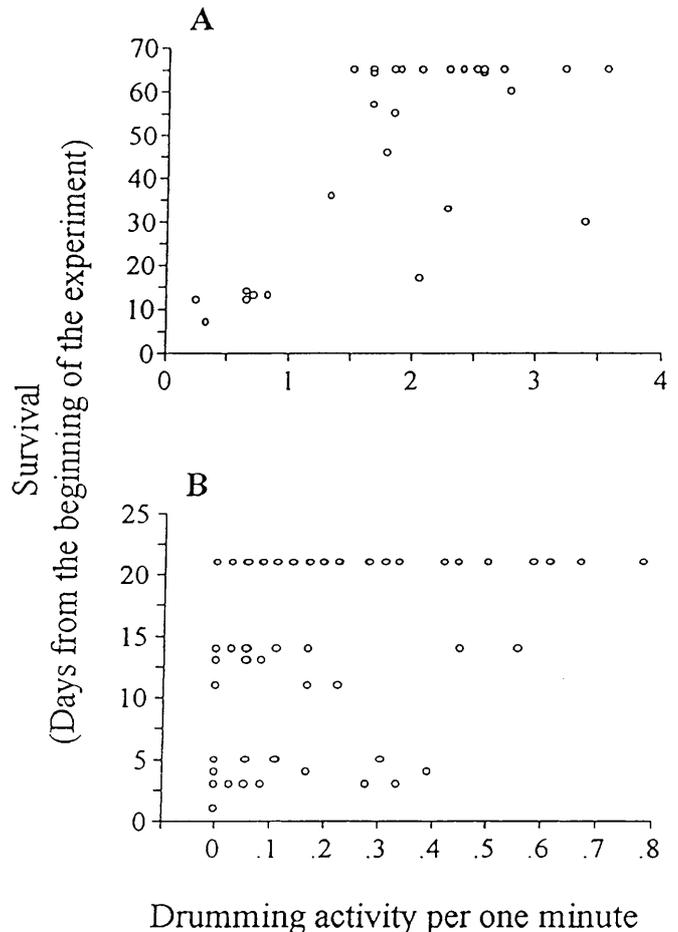

Fig. 3 A Correlation between male drumming activity per minute and survival in the laboratory (Spearman's $r = 0.61$, $n = 28$, $P < 0.001$). Survival is measured until the day a male was found dead. Drumming activity is the mean of the first three measurements of drumming activity. **B** Correlation between male drumming activity per minute and survival in the field (Spearman's $r = 0.26$, $n = 100$, $P = 0.010$). Survival is measured as the day the male was captured for the last time. Drumming activity is the mean of the first three measurements of drumming activity

soon, while many males with higher drumming rates survived until the end of the experiment. Male survival was independent of body mass (Spearman's $r = 0.17$, $n = 28$, $P = 0.376$). In the field, males that at the beginning of the experiment drummed most actively also survived for longer (Fig. 3B). Again, male survival was not correlated with male body mass (Spearman's $r = 0.02$, $n = 100$, $P = 0.867$).

Discussion

The most important finding of the present study was that male drumming rate was positively related to male survival in both field and laboratory conditions, suggesting that male drumming activity may be a reliable indicator of male viability. It may seem that if a trait is costly, trait size and viability should be negatively correlated. However, if the expression of the trait is dependent on the phenotypic condition of the bearer such that the costs of the trait are less for individuals in good condition than for individuals in poor condition, a positive correlation between trait size and viability is expected (Nur and Hasson 1984; Zeh and Zeh 1988; Grafen 1990a; Johnstone and Grafen 1992).

Male drumming rate was positively correlated with male survival while neither was correlated with male body mass. Because there is female preference for high drumming rate but not for greater body mass (Kotiaho et al. 1996), it appears that the body mass of an individual may play only a minor role in sexual selection in this species. However, three lines of evidence suggest that the picture may not be so simple. First, there is large variation in male body mass (Kotiaho et al. 1996); second, heavier males win more intermale encounters (Kotiaho et al. 1997), and third, heavier males survive slightly better under stressful conditions (Mappes et al. 1996). In addition to drumming rate, male mobility significantly influences male mating success: males moving more have an increased probability of encountering a receptive female (Kotiaho et al. 1998a). Therefore, before ruling out mass as a factor, the relationship between mobility and mass has to be considered.

In the laboratory and in the field, male mobility was positively correlated with male body mass, suggesting that large individuals may have an advantage in finding females (see Kotiaho et al. 1998a). This advantage may arise if it is simply easier for larger males to move around the complex three-dimensional leaf litter habitat. Another possibility is that larger males are in better condition or have more resources to invest in mate searching; the better condition of larger males might arise because environmental conditions during growth have a strong effect on adult size (J. Mappes, R.V. Alatalo, J.S. Kotiaho, S. Parri, unpublished data).

The positive correlation between the distance moved and the relative mass change (Fig. 2) was somewhat more surprising. Because moving is energetically demanding (Kotiaho et al. 1998b), the anticipated result would have been a negative correlation: males moving more should be spending more energy and consequently lose more mass. However, if moving is a condition-dependent trait, such that with the same costs, males in good condition can move more than males in poor condition, then a positive correlation may result. Since male drumming rate is a condition-dependent trait (Mappes et al. 1996; J.S. Kotiaho, unpublished data), and there was a positive relationship between male drumming rate and mobility, it follows that mobility may also be a condition-dependent trait. This would explain the observed positive correlations.

To conclude, large males moved more, suggesting that size may have a role in sexual selection in this species, but experiments are needed to determine the relative importance of mass-independent drumming rate and mass-related mobility. Male drumming rate was positively correlated with male viability in both the laboratory and field, suggesting that drumming may be a reliable indicator of male quality. Earlier work on this same system (Kotiaho et al. 1996, 1998a, 1998b; Mappes et al. 1996; Parri et al. 1997; Alatalo et al. 1998) has shown that drumming rate is a condition-dependent sexually selected trait that imposes significant mortality costs on males. Taken together with the present data, these results provide stark empirical evidence for viability indicator models of sexual selection.

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