Mate choice for offspring performance: major benefits or minor costs?

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There is considerable disagreement over whether or not gaining viability benefits to offspring could be substantial enough to overcome the costs of female choosiness. A recent review suggested that the 'lek paradox' might be resolved by large indirect benefits as indicated by highly heritable ornamental traits. We selected males of a wolf spider *Hygrolycosa rubrofasciata* in relation to their sexual signalling rate (audible drumming). The estimated correlated response in offspring viability was rather small (0.12 s.d.). However, it may be large enough if the costs of being choosy are small. In fact, females mate with better-than-average males just by responding passively to a random drumming signal, and the active choice by females seemed to increase this benefit only slightly. In many mating systems, females obtain better-than-average males as a consequence of intense male–male competition or because of the extraordinary variance in male signalling. The costs of any additional choice may be so minor that female choice for honestly signalling males may evolve even with minute benefits in offspring viability. This may be the general solution to the lek paradox, as most studies report no apparent fitness benefits. Publication bias favouring statistically significant results may have led to an overemphasis on the few studies with large effects.

Keywords: sexual selection; good genes; female choice; wolf spider

1. INTRODUCTION

The origin of male sexual ornaments through female choice has been a major theoretical puzzle (Zahavi 1977; Lande 1981; Iwasa *et al.* 1991; Pomiankowski *et al.* 1991; Andersson 1994). The classical 'lek paradox' (Taylor & Williams 1982) states that inherited fitness benefits for the offspring cannot be large enough to allow costly female choice. A review of current studies (Pomiankowski & Møller 1995) indicated that ornamental traits were highly heritable and thus indirect benefits might be relatively large, when there would be no paradox at all (Rowe & Houle 1996). However, the published data may be biased towards the high heritability estimates, as illustrated in a reanalysis of the same data (Alatalo *et al.* 1997). Furthermore, a more definitive answer requires an estimate of the indirect benefits enhancing offspring fitness (Turner 1995; Ritchie 1996), which should be compared with the costs of choice (Reynolds & Gross 1990).

Indirect benefits might arise from the inheritance of 'good genes' enhancing offspring viability (Zahavi 1977; Iwasa *et al.* 1991) or from the inheritance of sexual attractiveness alone (Lande 1981; Pomiankowski *et al.* 1991). In the former case, the sexually selected male traits can be viewed as honestly signalling handicaps and, in the latter case, as arbitrary Fisherian traits. However, we need to obtain information about the costs of choice for females in the same populations to unravel the crucial relationship between costs and benefits.

Males of the wolf spider *Hygrolycosa rubrofasciata* have a drumming signal (*ca*. 1-s long) as a sexually selected trait preferred by females (Kotiaho *et al.* 1996, 1998; Parri *et al.* 1997). In southern Finland, matings take place in the first warm days of the spring in late April/early May. Males patrol around the habitat (bog or abandoned field) and, after a female responds by shaking her body, a mating takes place and lasts typically 30–60 min (see also Kronestedt 1996). Males seemingly only provide the sperm from their pedipalps and only very occasionally does the female eat the male after copulation (authors' personal observations). Males vary greatly in their drumming performance and there is considerable repeatability in signalling rates. Our experiments have indicated that drumming activity is costly and therefore honestly indicates viability for females (Kotiaho *et al.* 1996; Mappes *et al.* 1996; Parri *et al.* 1997). Here, we have explored the level of indirect fitness benefits, and we relate them with the costs of female choosiness. Finally, we review the current sexual selection studies that have estimated the indirect consequences for the offspring of choosy females.

2. METHODS

We collected male and female *Hygrolycosa rubrofasciata* from a population (area 50 m × 20 m) in a small bog at Sipoo, southern Finland, just after the snow had melted between 21 April and 5 May 1995. We kept spiders in a cool temperature until the start of experimentation in late May. Males ($n = 423$) were tested for their drumming rates in a standardized manner. In our previous study (Kotiaho *et al.* 1996), the repeatability of male drumming rate turned out to be relatively high from day to day

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(>60%). Males produce drums singly, but there may be some temporal autocorrelation with periods of higher and lower activity. Thus, males were observed during 2 h over two days for five 2-min periods each time in a small plastic arena with a few dry leaves as the drumming substrate. Males were allowed to habituate to the room temperature for 1 h before testing. They were arranged in groups of six males each in their own arena, so that the observer could record the drumming of six males at the same time during each 2-min period.

To obtain a powerful test we used only the top and bottom quarters as the high and low lines for matings (figure 1a). To approximate normality, drumming rates had to be ln-transformed and the strength of selection can thus be described as the difference between the means for the high and low lines (being up to 2.7 s.d. units). We stopped collecting females from the field once drumming activity started, thereby ensuring that most of the sampled females had not previously mated. The collected females were first used in playback experiments, and they were thus kept several days in warm conditions. During that time, females that had mated in the field would have produced an egg sac with proper eggs. We could therefore exclude the few females (ca. 10%) that produced egg sacs before any matings in the laboratory, which ensured that those used in the following experiment were virgin.

We mated 80 high-line males and 73 low-line males to randomly chosen females. The randomly chosen females were placed together with a low- or a high-line male, and matings were observed. As females had been in warm conditions for several days they were very willing to mate with any male. Matings typically started within 2 h, but in some cases the procedure had to be repeated next day for mating to take place. After mating, females were kept singly in small plastic jars until the spiderlings emerged from the egg sac. Because early-instar spiderlings of small wolf spider species are not easy to raise, we kept each brood initially together in a glass jar with moistened moss and provided them with a variety of food (laboratory-raised collembolans and wingless fruit flies with a mixture of field-collected aphids, leaf-hoppers and small soil arthropods).

The survival of the offspring was followed starting from the age of 45 d, when each spiderling was placed in its own plastic vial (diameter 2.8 cm, height 6.7 cm). The spiderlings were kept in a room at ca. 20 °C with continuous light, and humidity was provided through a cotton tube in the bottom of the vial, which was moistened daily. At the age of 185 d, all the offspring could be sexed and there were 121 female and 96 male offspring. At this age, offspring size equals the size of the adult males, which makes it a reasonable cut-off point for studying offspring performance. We continued to follow the spiderlings until the age of 290 d; by that time, all of the surviving spiderlings had moulted to adulthood.

Although laboratory conditions can never perfectly reflect natural conditions, we managed to raise the offspring to similar sizes as their parents (mean male body mass in the parent sample from the field = 17.10 mg, s.d. = 2.40, $n = 72$; mean size of offspring males at maturation in the laboratory = 17.48 mg, s.d. = 2.26, $n = 44$; for means, $t = 0.85$, $p = 0.40$; for variances, $F = 1.13$, $p = 0.34$). However, offspring mortality was high (figure 1b) and thus the raising conditions were by no means unrealistically favourable.

3. RESULTS

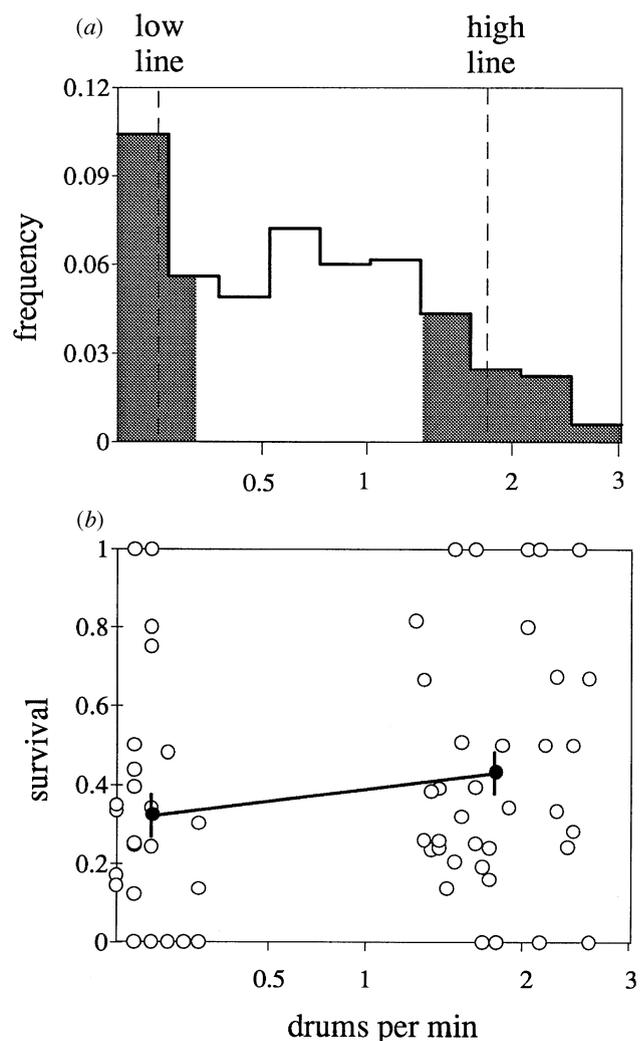There was a slight tendency for the offspring of the high-line males to survive with a higher probability

Figure 1. Selected drumming lines with effects on offspring survival. (a) The distribution of drumming rates among males ($n = 423$) and the selected low and high lines (shaded areas) with their means (broken lines). The difference between means corresponds to 2.68 s.d. units of the ln-scaled male sexual trait. (b) The proportion of offspring surviving from the age of 45 d to the age of 185 d against the drumming rate of their father. The open circles refer to each family mean, and the averages (filled circles) with standard errors are indicated for the low lines (mean = 0.33, s.d. = 0.35, $n = 35$) and high lines (mean = 0.44, s.d. = 0.31, $n = 36$; Mann–Whitney rank test, $z = 1.71$, two-tailed $p = 0.09$).

(44%) until the age of 185 days than the offspring of the low-line males (33%) (figure 1b). Although the difference is not quite significant using a two-tailed test ($p = 0.09$), a more powerful test comparing differences in the average family lifespans of the offspring provides more confidence for a positive effect (low-line mean = 172.3 d, s.e. = 9.5, $n = 35$; high-line mean = 200.2 d, s.e. = 7.6, $n = 36$; Mann–Whitney rank test, $z = 2.31$, two-tailed $p = 0.03$). However, it is more important that the correlated response in offspring viability due to the selection of the male sexual activity can be estimated to be relatively slight in magnitude. To illustrate the response in a standardized way, we have normalized both of the traits (figure 2), and thus the correlated response can be estimated to be +0.12 s.d. units. The benefit cannot be
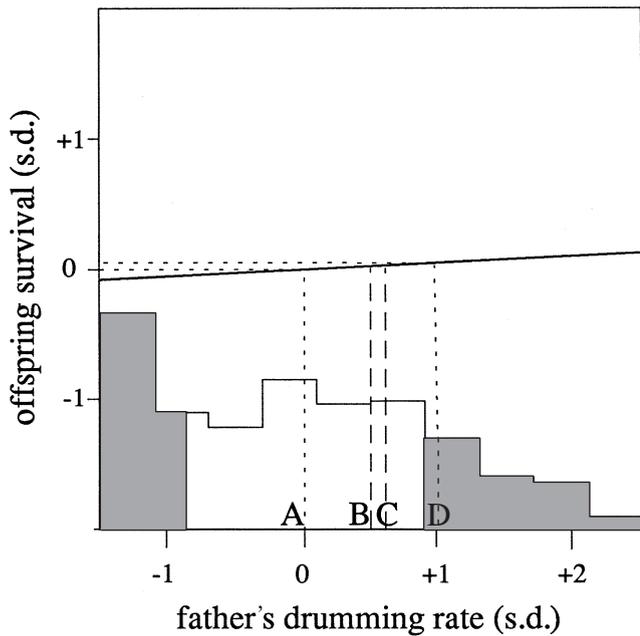
Figure 2. Estimated offspring survival against father's drumming rate according to the selection experiment that revealed a correlated response of 0.12 s.d. On the background, the male distribution of drumming is presented with the selected lines indicated by shading. If females mated with an average male (stippled line A projected to vertical axis) they would not gain any benefit in offspring survival, which corresponds to the expectation of offspring survival among females mated randomly to any male irrespective of his drumming activity. In another experiment (Kotiaho *et al.* 1996), we presented three males to females and, in that case, if females would have just passively responded after any male signal (line B), the gain would have been 0.06 s.d. (which corresponds to an increase in offspring survival of 5.8% compared with offspring of average males). However, females exhibited some preference (line C), increasing the benefit to 0.07 s.d. (or 6.8%). If females had been allowed to respond merely passively to any male of the present selected population (stippled line D projected to vertical axis) the benefit would have increased to 0.12 s.d. (or 10.7% in offspring survival).

very large, as confidence intervals indicate that at the 5% risk level the true estimate is below +0.26 s.d. units.

The small benefit can now be compared with the costs of female choosiness. In this species, and very many others, male activity affects directly the likelihood of encountering females. Once a female is willing to mate she responds by shaking her abdomen within a few seconds after a single drumming bout (Kotiaho *et al.* 1996; Parri *et al.* 1997). Thus, a female taking no costs and responding to the first signal would not mate randomly, as illustrated in figure 2. Indeed, she mated with a male that was +0.53 s.d. units above the average when three randomly chosen males were presented to her in a small test arena (using previous data in Kotiaho *et al.* (1996)). Active female preferences were significant in that test situation, but they increased the signalling quality of the male only slightly to +0.63 s.d. units. The three males in each test situation were randomly chosen by us with no weighting by male activity, and thus these averages are likely to underestimate qualities of mating males in the

field situation, where many more males are available to females. Indeed, if we pick up random signals from the population of the males used in the present selection experiment, they would on average represent a male that is up to +0.98 s.d. units above the average male in respect to his drumming rate.

Thus, even if correlated responses may have slopes that are close to zero, they may have significant evolutionary consequences. The correlated response by merely random female choice within the population gave an estimate of a 0.12 s.d. increase in offspring survival, which corresponds to an estimate of 10.7% higher offspring survival compared with females that would have mated with a male of average drumming performance. Active female preferences (Kotiaho *et al.* 1996; Parri *et al.* 1997) may slightly add to these benefits and allow selection for female choosiness. There are ample possibilities for females to be selective in the field, as we have estimated that females are visited, on average, by one male each hour. Our mark−recapture studies have confirmed that males move around and females are much more local (authors' unpublished data). To study mating possibilities in the field we placed females in small enclosures (3 cm × 3 cm) on the middle of a cardboard plate (30 cm × 30 cm) covered with dry leaves as the drumming substrate. In total, we followed 29 different females (2−4 h each during 13−16 May 1997) for the number of males drumming close by and for the cases when females accepted the males. Altogether there were 86 visits by males drumming within 15 cm distance of the female. In total, females responded to 27 males (which were removed instantly after female response), of which 89% were within 15 cm from the female. Thus, the average rate of male visitation was 1.00 (s.d.=0.74, n=29) per hour and the average number of drumming events within 15 cm was 2.28 (s.d.=1.71, n=29) per hour.

4. DISCUSSION

In this and many other species, much of the selection could also be attributed to male−male competition and passive female choice (Parker 1983). In many mating systems, males compete directly for access to females, and in these cases females are unlikely to take on any major costs of choice. Male−male competition alone may guarantee that females mate with a better-than-average male. In addition, in many species, males possess condition-dependent ornaments with typically high variance between males (Pomiankowski & Møller 1995; Rowe & Houle 1996), which in essence is another form of male−male competition. The extraordinary variation in ornaments allows females to choose between males with minor costs of comparison.

It is possible that a general solution to the lek paradox is the small costs of choice rather than any major benefits. Indeed, a recent model suggests that the extravagant ornaments could not evolve if costs of choice are substantial (Kirkpatrick 1996). We compiled studies that assess the possible indirect fitness benefits as a consequence of sexual selection. In addition, we included a few studies where male−male competition might be the main agent of sexual selection rather than female preference, because, as illustrated by this study, these two processes may act in

concert to benefit females. It is practically impossible to tell how much of sexual selection is due to intrasexual and intersexual selection if both of the processes favour the females for the same reason of enhanced offspring viability.

We found seven studies (Reynolds & Gross 1992; Norris 1993; Petrie 1994; Møller 1994; von Schantz et al. 1994; Hasselquist et al. 1996; Sheldon et al. 1997) that report very high indirect benefits corresponding to correlated responses above 0.30 (conforming to s.d. unit estimates used in this paper and reflecting genetic correlations above 0.60, see also Kirkpatrick (1996)), whereas another six studies report smaller benefits (Partridge 1980; Crocker & Day 1987; Woodward 1987; Moore 1994; Hoikkala et al. 1998; this study). Finally, given that in general only 8.6% of ecological papers report non-significant results for their main hypothesis (Csada et al. 1996), there were surprisingly many (43%) studies that had not found significant offspring benefits in the survival traits (Schaeffer et al. 1984; Boake 1985; Howard et al. 1994; Semlitsch 1994; Nicoletto 1995; Whittier et al. 1995), even if some of them had positive effects in offspring maturation or growth (Woodward 1986; Simmons 1987; Woodward et al. 1988; Mitchell 1990). Taking the probable publication bias (Alatalo et al. 1997) into account (none of the studies with high benefits has sample sizes large enough to detect small benefits), it seems that in general the viability benefits to offspring may be rather small. This would agree with the view that heritabilities of fitness are rather small and probably do not exceed 0.10 (Gustafsson 1986; Charlesworth 1987; Burt 1995; Houle et al. 1996), which would allow correlated responses of less than 0.5.

There is a clear pattern that among three major animal groups (endothermic vertebrates, ectothermic vertebrates and arthropods), it is mainly the endothermic vertebrates (represented by six studies on birds) that have been reported to have high indirect benefits (Kruskal–Wallis test, $H=13.21$, $p<0.001$ with pairwise comparisons confirming the significant ($p<0.02$) difference between endothermic vertebrates and the other two groups). It remains to be seen whether these differences represent true taxonomic biases or whether they arise from biases in publication (Alatalo et al. 1997) or in the design of studies (Tregenza & Wedell 1997). In any case, it may be that even minor benefits are sufficient for the evolution of female preferences for male ornamentation.

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