Male courtship song frequency as an indicator of male genetic quality in an insect species, *Drosophila montana*

Anneli Hoikkala, Jouni Aspi and Leena Suvanto[*]

Department of Biology, University of Oulu, 90570 Oulu, Finland

Most theoretical models on evolution of male secondary sexual characters and female preferences for these characters suggest that the male characters evolve in response to female preferences that may themselves evolve in response to direct or indirect benefits of choice. In *Drosophila montana* (a species of the *D. virilis* group), females use male song in their mate choice, preferring males that produce songs with short sound pulses and a high carrier frequency. We demonstrate here that the females get indirect benefits from their choice: in our data the frequency of the male song correlated with the survival rate of the male's progeny from egg to adulthood (indirect benefit for the female), but not with the fecundity of his mating partner (no direct benefit for the female). Male wing centroid asymmetry did not correlate with male wing song characters, nor with female egg production nor the fitness of her progeny, suggesting that fluctuating asymmetry in male wings does not play a major role in sexual signalling. The fact that the male song gives the female information on the male's condition/genetic quality in *D. montana* suggests that in this species the evolution of female preferences for male song characters could have evolved through condition-dependent viability selection presented in some 'good genes' models.

Keywords: asymmetry; good genes; indirect benefit; sexual selection; sexual signalling

1. INTRODUCTION

It has been demonstrated in several bird species that the females choose mates on the basis of specific secondary sexual trait(s) of the male (Andersson 1982; Möller 1988; von Schantz *et al.* 1989; Hill 1991; Norris 1993; Petrie 1994; Hassenquist *et al.* 1996). In some cases it has also been shown that the females gain direct or indirect benefit from their choice (von Schantz *et al.* 1989; Hill 1991; Norris 1993; Petrie 1994; Hassenquist *et al.* 1996). The male's secondary sexual traits give information to the female on the male's condition (for a review, see Johnstone 1995). Among insect species where the males only deliver sperm for the females, females of *Drosophila melanogaster* fruitflies (Partridge 1980), *Colias* butterflies (Watt *et al.* 1986), *Coelopa frigida* seaweed flies (Crocker & Day 1987) and *Nauphoeta cinerea* cockroaches (Moore 1994), have been shown to exercise mate choice and to gain direct and/or indirect benefit from their choice. In most of these cases, the target of the female choice (the way the females recognize good quality males) is, however, unknown (but see Crocker & Day 1987). In *D. montana* and *D. littoralis*, it has been shown that the females use male courtship song in their mate choice in the wild, preferring males that produce short and dense sound pulses, a combination which leads to a high carrier frequency (Aspi & Hoikkala 1995). Female preference for high-frequency songs has also been verified in the laboratory (Hoikkala & Suvanto 1998), and by using playback

songs (Ritchie *et al.* 1998). In the absence of males producing good-quality songs, the females may also accept males producing inferior songs, as long as the songs are within the range of acceptable cues (Hoikkala & Aspi 1993).

Conditional viability variants of the 'good genes' model require that the expression of the male character depends on male phenotypic condition (e.g. Andersson 1986; Zeh & Zeh 1988). Repeatability provides an indication of the potential utility of the signal as a reliable indicator of competitive ability of the males (Clark & Moore 1995). Pulse characters of the song of *D. montana* (PL, CN and FRE, see figure 1) are highly repeatable among wild-caught males during the mating season of the flies in spring. These characters reflect the condition of the males as changes in male songs take place during overwintering (Hoikkala & Isoherranen 1997). In addition, fluctuating asymmetry (FA) of male morphological characters has repeatedly been suggested to be an indicator of male quality. It has been proposed that developmental stability, measured in terms of FA, reflects the overall ability of individuals to cope with genetic and environmental stress (see, for example, Palmer & Strobeck 1986; Hoffman & Parsons 1991).

In this paper, we have analysed the songs of wild-caught *D. montana* males and studied possible asymmetries in their wing size and shape. Also, we have mated these males with virgin females reared in the laboratory and studied whether the male song traits or possible wing asymmetries have an effect on female progeny production or on fitness of her progeny. This kind of information is of great
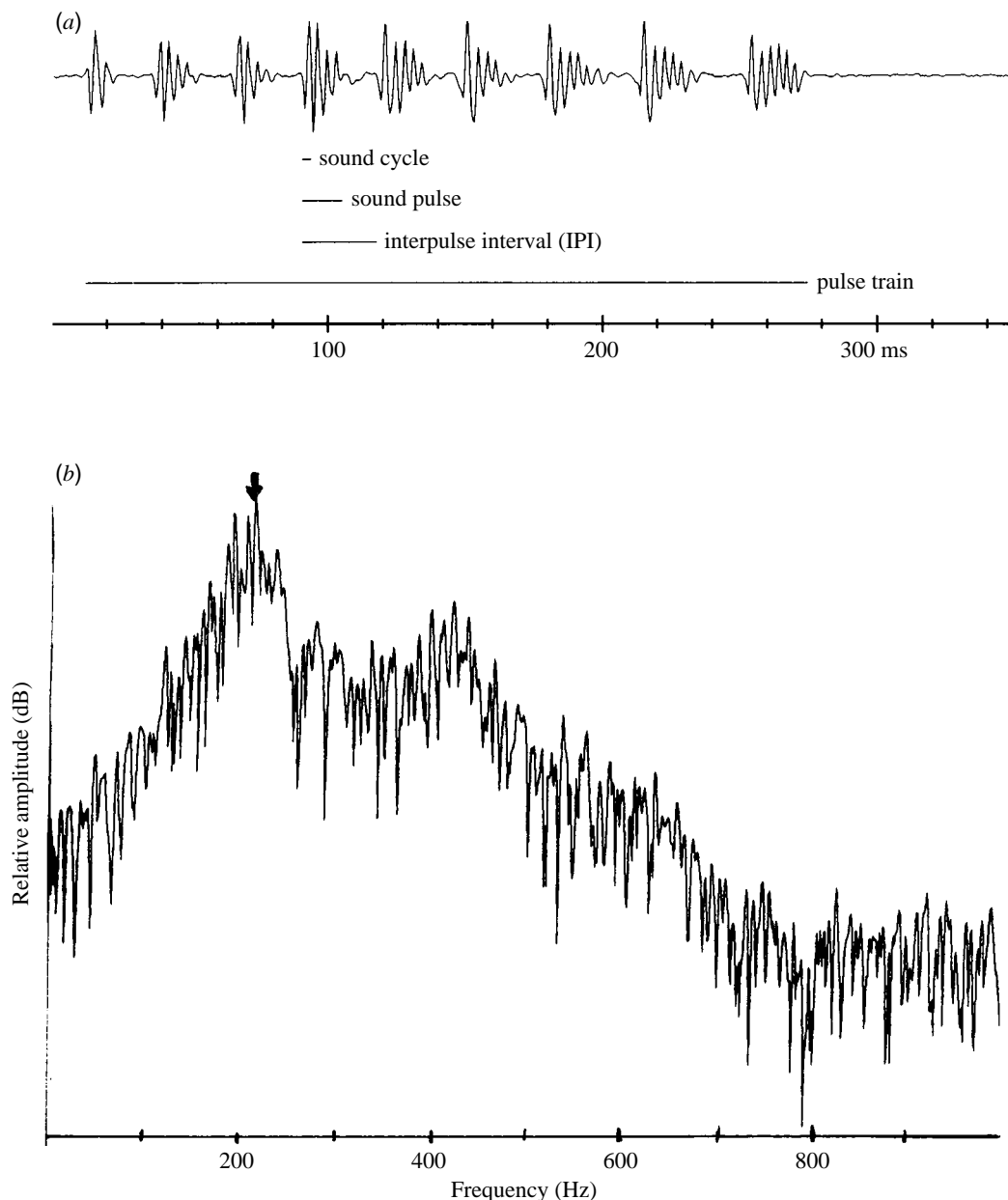
Figure 1. (*a*) Oscillogram and (*b*) Fourier spectrum of one approximately 300 ms long pulse train of the courtship song of a wild-caught *D. montana* male. The arrow in (*b*) represents the carrier frequency.

importance when studying evolution of sexual signalling in insect species.

2. METHODS

(a) *General methods*

We collected 100 overwintered *D. montana* males from malt baits in Kemi, northern Finland, during the mating season of the flies, which is in May (Aspi *et al.* 1993). Courtship songs of the males were recorded in single-pair courtships, and the males were mated individually to mature virgin females (one female per male) of a *D. montana* multifemale stock maintained in the laboratory for three years prior to the experiment. As soon as the flies had mated, the female was placed in a Petri dish (diameter 5.5 cm, depth 1.3 cm) which had a 5 mm layer of malt medium on the floor. The Petri dish was covered with a net (to

enable the transfer of the female) and a plastic cover. The females were left to oviposit in Petri dishes for three days, after which they were moved into fresh dishes. The number of eggs on the first set of Petri dishes was counted, and after one week the first-instar larvae (and the remaining food) were transferred from Petri dishes to culturing bottles with an additional 5 cm of food medium on the floor. The bottles were kept in continuous light at 19 °C, and the number of flies emerging from these bottles was counted. The second set of Petri dishes was kept in order to check the existence of male sperm in female spermathecae; only the females that also produced offspring on these dishes (88/100 females) were taken into account when measuring the females' egg production and the survival rate of their progeny from egg to adult on the first set of Petri dishes. Aspi (1992) has previously reported that *D. montana* females produce progeny for about six days after insemination.

(b) *Song analysis*

The courtship song of *D. montana* males consists of trains of polycyclic sound pulses (figure 1). The song of each male was recorded with a JVC-condenser microphone and a Sony TC-FX 33 cassette recorder. As the songs have been shown to be highly repeatable within males (Hoikkala & Isoherranen 1997), we analysed song characters from an oscillogram of only one pulse train per male. We measured the length of the pulse train (PTL) and counted the number of pulses in the train (PN). We also counted the number of cycles in the fourth pulse of the train (CN), and measured the length of this pulse (PL) and the distance from the beginning of this pulse to the beginning of the next pulse (IPI). Finally we measured the carrier frequency (shown with an arrow in figure 1*b*) of the pulse train from Fourier spectra. Song analysis was carried out using the Signal Sound Analysis System (Engineering Design).

(c) *Measurements on fluctuating asymmetry (FA)*

The wings of the wild-caught males (fathers) were mounted between two glass slides and measured to detect possible asymmetries in wing size and shape. Definition of size is quite arbitrary in traditional morphometrics. Instead of simple length and width measures, we used landmark-based morphometrics (for an unabridged review, see Bookstein 1991), and centroid size as the size variable. Centroid size, which is the only size variable in landmark morphometrics, can be defined as the square of the sum of all possible distances between landmarks. Some of the wings were partly broken, and centroid size and asymmetry for those individuals could not be estimated. Nine landmarks for the rest of the wings (figure 2) were digitized with a dissecting microscope, camera lucida and Genius HiSketch 1212 digitizing tablet by using the DS-Digit software (Slice 1994). Digitized coordinates were aligned and the centroid size calculated case by case (Bookstein 1991). The level of FA for individual flies was measured as the unsigned right-minus-left $(R-L)$ centroid value (Palmer & Strobeck 1986; Palmer 1994).

The two centroids were measured and their asymmetries estimated twice, on different days, for 79 individuals (with unbroken wings). The repeatability (Falconer 1981) of the centroids was very high $(R=0.97;\ F=46.40;\ \text{d.f.}=157,\ 158;\ p<0.001)$. The repeatability of the asymmetry was much lower $(R=0.60;\ F=4.01;\ \text{d.f.}=78,\ 79;\ p<0.001)$, which seems to be a common feature in asymmetry measurements (Merilä & Björklund 1995). Analysis of within and among individual variances (Falconer 1981; Bailey & Byrnes 1990) suggested that remeasuring asymmetry three times would give adequately small confidence intervals of the mean. Thus, to reduce the effect of measurement error each wing was measured the third time, and the mean for the three measurements was used as a measure of asymmetry.

Directional asymmetry or antisymmetry of a morphological character may make up a sizeable fraction of the between-sides variance in a sample. To analyse whether directional asymmetry in centroid size exists, we performed a two-way ANOVA where sides were the fixed factors and individuals the random factor (Palmer & Strobeck 1986; Merilä & Björklund 1995). This analysis suggested that there was no directional asymmetry in centroid size as there was no significant side-effect $(F=0.70;\ \text{d.f.}=1,\ 78;\ p=0.40)$. Centroid size did not demonstrate antisymmetry either, as the frequency distribution of signed right-minus-left character values did not deviate significantly from a normal distribution (Wilk–Shapiro tests; $p>0.05$). Analysis of plots of right-minus-left values $(R-L)$ versus size $((R+L)/2)$, and regression analysis of unsigned right-minus-left values
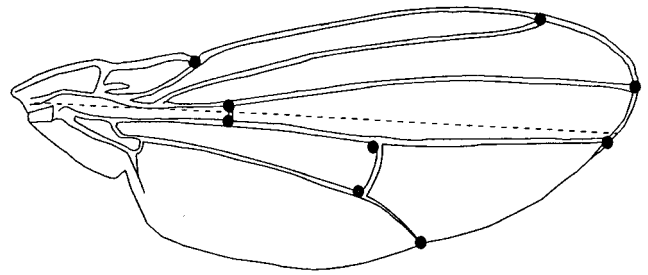

Figure 2. Wing of *D. montana* male: the nine landmarks and the boundary (dotted line) between anterior and posterior compartments.

$(|R-L|)$ against size suggested that there was a slight dependence in fluctuating asymmetry on centroid size $(t=2.51;\ \text{d.f.}=77;\ p=0.01)$. After the asymmetry values were divided by size this dependency disappeared $(t=1.73;\ \text{d.f.}=77;\ p>0.05)$. Therefore, relative FA values were used in the analysis of the effects of male size and asymmetry on female fecundity and offspring survival.

(d) *Statistical analysis*

The statistical analysis of connections between male song and wing characters and female egg production and survival rate of her progeny from eggs to adults involved calculations of two selection coefficients which allow an estimation of directional phenotypic selection and selection for correlated characters (Lande & Arnold 1983; Arnold & Wade 1984*a,b*). Selection differentials are the differences between the mean value or variance of a trait before and after selection representing the total effect of selection. Selection gradients measure the direct effects of selection on each trait. This measure is independent of any indirect effects caused by selection on the traits with which this trait is correlated. Accordingly, it shows the target and the direction of selection and allows a comparison of the magnitude of selection among several different traits.

Because the untransformed song characters were not normally distributed, they were Box–Cox transformed (e.g. Sokal & Rohlf 1981) for statistical analysis. The absolute fitness values (number of eggs laid, proportion of eggs surviving from egg to adult) were transformed to relative fitness values by dividing each absolute measure by the mean absolute fitness (Lande & Arnold 1983) to allow comparison across characters. Selection differentials were calculated as a covariance between male song characters and relative female fecundity or the relative survival rate of her offspring. Significance of these differentials was studied using Spearman's rank correlations and Bonferroni correction (Rice 1989). Selection gradients were estimated from the slopes of linear multiple regressions between different song characters and the fecundity or relative survival rate values. Student's *t*-test was used to test the significance of selection gradients.

3. RESULTS

In *D. montana*, the females gain indirect benefit when mating with males producing high-frequency songs. Selection differentials and selection gradients calculated for male song characters and female progeny production or progeny fitness showed that the carrier frequency of the male's song is correlated with the fitness of his progeny. Male wing centroid asymmetry was not found to correlate with male song characters nor female progeny production nor the fitness of her progeny.

Table 1. *Standardized directional selection differentials* (s′) *and gradients* (β′ ± s.e.) *for male song characters in relation to female fecundity and to offspring survival* (*given in units of phenotypic standard deviations*)

Trait	female fecundity		offspring survival	
	s'	β'	s'	β'
PTL	0.036	0.030 ± 0.010	−0.008	0.056 ± 0.129
PN	−0.044	−0.013 ± 0.011	−0.022	0.051 ± 0.136
PL	−0.020	−0.015 ± 0.078	0.007	0.114 ± 0.097
IPI	−0.019	−0.007 ± 0.057	−0.048	−0.050 ± 0.071
CN	−0.000	0.000 ± 0.088	−0.046	−0.146 ± 0.109
FRE	0.036	0.039 ± 0.061	0.173[a]	0.240[b] ± 0.075

[a] Statistical significance at level $p = 0.012$ (Spearman's rank correlation).
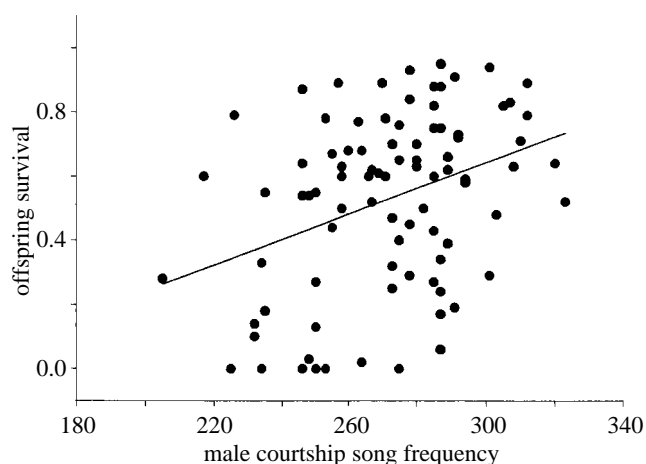[b] Statistical significance at level $p < 0.01$ (Student's t-test).

Figure 3. Non-parametric fitness function (solid line) for male offspring survival as a function of courtship song frequency. Offspring survival was estimated as a proportion of offspring emerging from the eggs oviposited within the three first days after copulation. The fitness function was estimated using the cubic-spline approach (Schluter 1988), which provides an univariate non-parametric estimate of fitness probabilities across the range of considered characters.

The mean number of eggs produced by the females during the three days' experiment was 56.6 (s.d. = 20.7). We could not find evidence of any direct benefit the females could have gained by choosing a male with the preferred song characters. All the selection coefficients of male song characters with the relative fecundity of his mate were non-significant (see table 1), which indicates that male song characters had no influence on female fecundity.

The mean proportion of offspring surviving from egg to adulthood was 0.52 (s.d. = 0.27). Here we found strong evidence for the effects of female mate choice (affecting the genotype of the egg) on the survival rate of the female's offspring. Selection differentials suggested that the offspring of the males having a high courtship song frequency (i.e. combination of short PL and high CN, preferred by females in the field), also had better progeny survival than the males producing song with a lower carrier frequency. The selection differential for the male song frequency was significant at the level of $p = 0.012$, even after a sequential Bonferroni correction (Rice 1989). Selection based on offspring viability would increase the

male courtship song frequency by about 0.17 phenotypic units. Selection gradients suggested that the male courtship song frequency was also the target of the selection. By choosing a male with courtship song frequency one standard deviation higher than average in the population, a female could increase the viability of her offspring by about 24%. The fitness function of male song frequency was monotonically increasing in the whole range of the character (figure 3). This indicates that no variance selection was present and directional selection coefficients could be interpreted as reliable ones (Mitchell-Olds & Shaw 1987; Schluter 1988).

During the development of adult *Drosophila* flies, the posterior and anterior parts of the wing develop from two different compartments (figure 2; Lawrence 1995). Accordingly, the asymmetry analysis was made for the whole wing and the two compartments separately. For the whole wing, average relative FA appeared to be very low, only 2.5% (s.d. = 1.6%) of centroid size. Analysis of different areas gave similar results to the whole wing, and are not reported here. There was no correlation between male wing centroid asymmetry, song characters, female fecundity, or offspring viability ($p > 0.05$ in all cases).

4. DISCUSSION

The results of the present paper show that in *D. montana*, the frequency of the male song correlates with the survival rate of the male's progeny from egg to adulthood (indirect benefit for the female), but not with the fecundity of his mating partner (no direct benefit for the female). This trait is one of the pulse characters that have earlier been shown to be targets of female choice (Aspi & Hoikkala 1995; Hoikkala & Suvanto 1998). Carrier frequency of the song has also been shown to be sensitive to environmental factors (Hoikkala & Isoherranen 1997) and to reflect male sexual activity (Hoikkala & Suvanto 1998). It is therefore a good candidate for a sexual trait that has evolved through a viability indicator process (Zahavi 1975; Kodric-Brown & Brown 1984; Pomiankowski 1987; Andersson 1986; Iwasa *et al.* 1991).

Kirkpatrick & Barton (1997) have suggested that direct selection on preference genes may often be more important than indirect selection. We did not find evidence of any direct benefit the females could have gained by choosing a male with the preferred song characters. This

is consistent with previous results, since Aspi (1992) has shown that *D. montana* females do not obtain extra resources from males for female nourishment or egg production as the females of some other *Drosophila* species do (Markow & Ankney 1984; Steele 1986). In *D. melanogaster*, female egg production is almost entirely maternally determined, whereas traits like egg-to-adult survival are determined by both maternal and non-maternal effects (Chapco & Ebisuzaki 1978). The situation in *D. montana* may be similar. Even though paternal effects are responsible for only part of the variation in egg-to-adult survival rate, their effects seem to be pronounced. As Kirkpatrick (1996) has suggested, if direct selection for preference genes is weak or absent, then indirect selection on preferences caused by good genes can have important evolutionary effects on preferences and hence also on sexually selected male traits.

Fluctuating asymmetry has been suggested to reflect male quality, because it results from the inability of the individuals to undergo identical development of the trait on both sides of the body, and because it thus represents a measure of the sensitivity of development to environmental stress. Möller & Pomiankowski (1993) have reported that secondary sexual characters show much higher levels of fluctuating asymmetry than other morphological traits. Also, Markow & Ricker (1992) have suggested that in *Drosophila pseudoobscura* wing symmetry may be important in the ability to deliver some signals to other males or females. We did not find any correlation between male wing centroid asymmetry, song characters, female fecundity or offspring viability ($p > 0.05$ in all cases). This might, however, be because, in this case, FA is not a very good measure of developmental stability or is 'a very small signal easily lost in a tumultuous sea of entropic force' (Palmer & Strobeck 1986). In addition, Rowe *et al.* (1997) have suggested that current discussions and conclusions about the role of FA in the evolution of signalling systems should be reconsidered.

The costs of mate choice may be rather small for *D. montana* females. In the wild, the flies mate on food resources (Aspi *et al.* 1993). The females mate repeatedly, and they may lay eggs for about six days after a single mating (Aspi 1992). High mating success of the males producing high-frequency songs may be due to both passive and active mate choice. Males caught in copula in the wild have been shown to have shorter sound pulses with a high number of cycles in a pulse (a combination that leads to a high carrier frequency; Aspi & Hoikkala 1995). At least in the laboratory, males with a high-frequency song are more active to begin courtship and they also achieve more matings in a choice situation (Hoikkala & Suvanto 1998).

Heritabilities of the pulse characters of the male courtship song have been found to be rather low in *D. montana* in the wild Kemi population, even though the respective heritabilities (especially for PL) are quite high when measured between fathers and sons reared in the laboratory (Aspi & Hoikkala 1993). The main reason for the low heritabilities in the wild is probably the sensitivity of the preferred song characters to environmental factors (Hoikkala & Isoherranen 1977). This sensitivity also offers the females an advantage: during the mating season of the flies in spring the male song can give the

female information on the condition of the male after severe winter conditions. Conditional variants of the 'good genes' model do not require high heritabilities, if variation between males is strengthened by environmental factors (Andersson 1986). In addition, female preference may persist despite minimal variation in a male trait, if it has little or no cost (Reynolds & Gross 1990).

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