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Towards a resolution of the lek paradox

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Genetic benefits in the shape of 'good genes' have been invoked to explain costly female choice in the absence of direct fitness benefits¹⁻³. Little genetic variance in fitness traits is expected, however, because directional selection tends to drive beneficial alleles to fixation⁴⁻⁶. There seems to be little potential, therefore, for female choice to result in genetic benefits, giving rise to the 'lek paradox'⁷⁻⁹. Nevertheless, evidence shows that genetic variance persists despite directional selection^{10,11} and genetic benefits of female choice are frequently reported^{12,13}. A theoretical solution to the lek paradox has been proposed on the basis of two assumptions¹⁴: that traits are condition-dependent, and that condition shows high genetic variance. The observed genetic variability in sexual traits will be accounted for, because a proportion of the genetic variance in condition will be captured and expressed in the trait¹⁴. Here we report results from experiments showing that male courtship rate in the dung beetle *Onthophagus taurus* is a condition-dependent trait that is preferred by females. More importantly, male condition has high genetic variance and is genetically correlated with courtship rate. Our results thereby represent a significant step towards a resolution of the lek paradox.

High genetic variance in condition and condition-dependent expression of sexual traits are two critical assumptions underlying the condition capture model for the evolution of costly female preferences in the absence of direct benefits^{1,14}. When these predictions are empirically validated, the long-standing problem of sexual selection of good genes, the lek paradox, will be resolved^{7-9,14}. Although there is abundant evidence for condition-dependent expression of traits^{3,15-18}, direct empirical evidence for genetic variance in condition is rare¹⁹⁻²¹.

We used random mating trials to study female preference for male courtship rate in the dung beetle *O. taurus*. Males used in this experiment were derived from a half-sib breeding design^{5,6}, and females were laboratory-reared virgins selected at random from a large culture population. Male dung beetles cannot copulate unless they can persuade the female to open her genital tergite. To do this, a male will court a female by tapping her back with his head and forelegs in bouts lasting a few seconds. We excluded the possibility of male competition affecting our results by introducing only one male and one female into an artificial dung beetle tunnel. Courtship rate was calculated as the number of courtship bouts per unit time. We observed 232 pairs, of which 170 males were successful in

mating. The probability of mating was strongly affected by the male's courtship rate (logistic regression $\chi^2_1 = 79.76$, $n = 232$, $P < 0.0001$; effect size estimated as Pearson's correlation coefficient $r = 0.6$; Fig. 1). To ensure that this result was robust and not biased by measures derived from related males, we replicated the experiment using males collected from a field population: this replication confirmed the above result (logistic regression $\chi^2_1 = 43.30$, $n = 80$, $P < 0.0001$; effect size $r = 0.7$). The preference function shown in Fig. 1 resulted in moderate directional selection for higher courtship rate (intensity of directional selection (i) with 95% confidence intervals (CI) and significance test: $i = 0.331$, $CI_{lower} = 0.121$, $CI_{upper} = 0.491$; $t_{400} = 3.20$, $P = 0.0015$; methods as described^{22,23}).

We experimentally examined the condition-dependence of courtship rate by manipulating the condition of males through their nutritional state. We measured the initial courtship rate and body mass of 80 field-collected males and randomly allocated them to one of two food treatments (constant supply of food or no food). The mean and variance in initial courtship rate or body mass did not differ between the groups (means: analysis of variance (ANOVA) $F_{1,78} = 0.00$, $P = 0.9876$ and $F_{1,78} = 0.00$, $P = 0.9823$, respectively; variances: Levene's test, $F_{1,78} = 0.14$, $P = 0.7065$ and $F_{1,78} = 0.05$, $P = 0.8302$, respectively). After five days of food manipulation, the courtship rates and body masses were remeasured. The manipulation had a substantial effect on courtship rate: males with

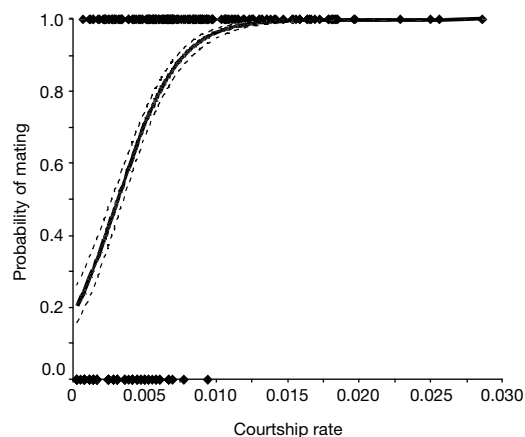


Figure 1 Probability of mating \pm s.e. as a function of courtship rate. Diamonds, original data. The function was estimated using cubic spline nonparametric regression with FORTRAN77 computer routines²³. Standard errors were derived from 1,000 bootstrap replications.

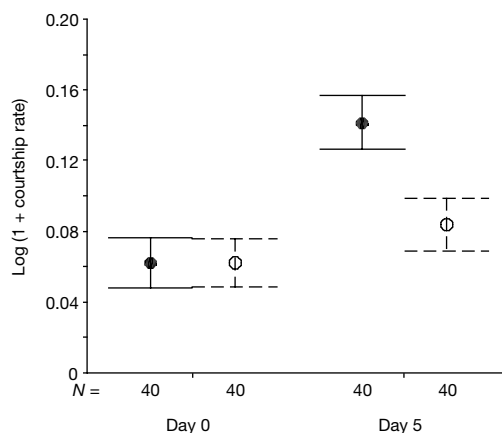


Figure 2 Condition dependence of courtship rate. Left, mean \pm s.e. of courtship rate per minute (log + 1 transformed); right, the same after five days of manipulation of food availability. Solid symbols, constant food treatment; open symbols, no food treatment.

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Table 1 Nested analysis of variance for courtship rate

Source	SS	d.f.	MS	F	P	Eta ^{2*}
Date†	1.28 × 10 ⁻⁴	1	1.28 × 10 ⁻⁴	0.21	0.6491	0.002
Sire	1.73 × 10 ⁻²	11	1.57 × 10 ^{-3‡}	2.16	0.0495	0.462
Dam (Sire)	1.77 × 10 ⁻²	24	7.38 × 10 ⁻⁴	1.20	0.2517	0.178
Error	8.17 × 10 ⁻²	133	6.14 × 10 ⁻⁴			

Courtship rate is square-root transformed. d.f., degrees of freedom. SS, sums of squares; MS, mean square; F, test statistics; P, probability.

*Eta² refers to the proportion of variance explained.

† Courtship rate tended to covary with the date of the observation. This is accounted for by using the date of observation as a covariate.

‡ To account for unequal sample sizes of offspring within sires, the error term for sires was calculated using Satterthwaite's approximation: 0.918 MS(Dam(Sire)) + 0.082 MS(Error) = 7.28 × 10⁻⁴.

constant food had significantly higher courtship rates than males with no food, indicating that, as predicted, courtship rate covaries positively with condition (repeated measures ANOVA $F_{1,78} = 6.15$, $P = 0.0153$; Fig. 2).

In addition to courtship rate, male body mass changed depending on the food treatment. Males with constant food increased in mass, whereas males with no food decreased in mass (repeated measures ANOVA $F_{1,78} = 160.37$, $P < 0.0001$). As there was no difference in the initial body mass between the treatments, our manipulation was effective in increasing and decreasing the body condition. Moreover, we estimated the relative condition of males within the two treatments as residual mass from linear regression between log (body mass) and log (pronotum width)^{24,25}, and found that the courtship rate of males with no food covaried positively with condition ($r = 0.35$, $n = 40$, $P = 0.0268$) whereas there was no such covariation with constant food ($r = -0.09$, $n = 40$, $P = 0.5808$). These two correlations are marginally different from each other ($Z = 1.93$, $P = 0.0536$). The difference is expected because sexual selection theory predicts that only individuals of high genetic quality are able to bear the costs of trait expression under harsh conditions, whereas under good conditions the costs of expressing a trait decrease, thereby reducing the difference in trait expression between males³.

We estimated the genetic variance in courtship rate and condition using a standard half-sib breeding design^{5,6}. The data were analysed with nested analyses of variance, having sire and dam as random factors with the latter nested within the former. The genetic correlation between courtship rate and condition was estimated from nested multivariate analysis of variance.

There was a significant sire effect, indicating that there is genetic variance in male courtship rate (Table 1). The heritability estimate h^2_{sire} (2 standard errors (s.e.))⁶ of courtship rate was moderate 0.337 (0.288) and corresponds well with heritability estimates generally reported for sexual traits under directional selection¹¹. What makes our results novel, however, is that we found a strong sire effect on condition itself (Table 2; Fig. 3). Our result shows that 67% of total

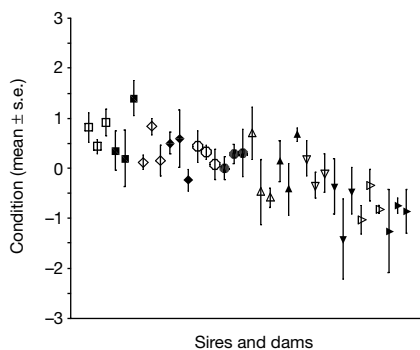


Figure 3 Genetic variation in condition. Condition is measured as the standardized residual mass from a linear regression of log body mass on log pronotum width. The different symbols represent the 12 sires. The three replications within each sire cluster represent the three dams for each sire. Sires are ranked according to the mean condition of their offspring.

Table 2 Nested analysis of variance for condition

Source	SS	d.f.	MS	F	P	Eta ^{2*}
Date†	6.01	1	6.01	8.37	0.0045	0.059
Sire	52.03	11	4.73‡	5.43	0.0001	0.684
Dam (Sire)	21.22	24	0.88	1.23	0.2269	0.182
Error	95.50	133	0.72			

*Eta² refers to the proportion of variance explained.

† Condition tended to covary with the date of the observation. This is accounted for by using the date of observation as a covariate.

‡ To account for unequal sample sizes of offspring within sires, the error term for sires was calculated using Satterthwaite's approximation: 0.918 MS(Dam(Sire)) + 0.082 MS(Error) = 0.87.

variation in condition was genetic in origin. Furthermore, the estimate of the genetic correlation r_{Asire} (2 s.e.)⁶ between male condition and courtship rate was positive and relatively high (0.709 (0.263)). To assess the levels of additive genetic variance (V_A) in courtship rate and in condition, we calculated the coefficient of variation for the additive genetic variances (CV_A) and compared these with published values of CV_A for sexually selected traits¹¹ and for two fitness components, fecundity and longevity¹⁰. The median value of CV_A for sexually selected traits was 8.2 (derived from Table 2 in ref. 11), and for fecundity and longevity 11.9 and 9.9, respectively¹⁰. Our estimate of CV_A (2 s.e.) for courtship rate was 8.57 (0.94) and for condition 27.05 (3.14). CV_A for courtship rate corresponds well with values previously reported for sexually selected traits. However, the CV_A for condition was more than twice those reported for fitness components. This comparison indicates that the level of additive genetic variance for condition is high, as predicted¹⁴.

Our comprehensive set of experimental tests provides empirical support for the condition capture model proposed to explain the maintenance of costly female choice on the basis of genetic benefits^{1,14}. As such, our study represents a step towards the resolution of the lek paradox. The condition capture model also predicts that over evolutionary time, the amount of genetic variation for sexual traits should increase as they become increasingly condition-dependent. Such an evolutionary association has recently been reported across species of stalk-eyed flies²⁶. Ultimately, the theory relies on the assumption that condition is influenced by a large number of loci, resulting in a relatively high frequency of mutations in genes coding for condition¹⁴. Thus, a complete resolution of the lek paradox will require that the frequency of mutations in genes that contribute to genetic variation in condition be quantified. □

Methods

Female choice

Artificial dung beetle tunnels were constructed from 60-mm-long clear rectangular plastic vials measuring 13 mm in width and 36 mm in depth. Vials were half filled with plaster of Paris to create a 60 mm long, 13 mm wide and 17 mm high tunnel. Tunnels were smeared with cow dung and dried. Before trials, tunnels were moistened with water. One randomly selected female and male were introduced into a tunnel and the courtship bouts of the males were observed constantly until mating occurred or for 60 min. No individual was used more than once. Before courtship and female choice observations, male offspring were housed individually in identical small sand-filled containers (7 × 7 × 5 cm³) with a constant supply of fresh dung.

Condition-dependence

At the start of the experiment we measured the initial body mass (to the nearest 0.01 mg), pronotum width (to the nearest 0.05 mm) and courtship rate of 80 males. Courtship rate was observed as described above. As some males mated during the observations, the time for courtship observations varies. Therefore, courtship rate per minute rather than total number of courtship bouts was used in the analysis.

After initial measurements, males were divided between two food ration treatments, with the two groups matched for mean and variance in morphological measures and initial courtship rates (see text). After measurements, beetles were housed individually in small plastic containers (7 × 7 × 5 cm³) two-thirds filled with moist sand. Constant food ration males were provided with a supply of fresh dung and no food ration males were provided with moist sand only. After five days of food manipulation, the measurements of male body mass and courtship rate were repeated as described above.

What is condition?

Rowe and Houle¹⁴ referred to condition as the pool of resources available for utilization. This definition of condition corresponds to residual reproductive value or state in life history models and accounts for a large proportion of fitness¹⁴. This definition means that condition cannot be measured directly. Therefore, we used the residual mass as an estimate of condition^{24,25}. Intuitively, residual mass approximates well the resources that should be available for utilization and there is likely to be a relationship between the two, but we acknowledge that this is not exactly the same as condition as used by Rowe and Houle¹⁴.

Genetic variances and correlation

To estimate the genetic variance in male courtship rate and in male condition we used a standard half-sib breeding design^{5,6}. We housed each of the 12 field-collected sires with three randomly selected F₁ laboratory-reared virgin dams. Dams did not differ in body size across sires. After five days, dams were set up individually to construct brood masses. As males of this species occasionally help in constructing the brood mass, non-genetic paternal effects may occur. This was taken into consideration in the experimental design by excluding males after mating so that females constructed brood masses alone. Thus, our experimental design excluded the possibility of non-genetic paternal effects.

It has also been suggested that females may differentially invest in their offspring depending on the attractiveness of the male^{27–29}. Differential investment based on male attractiveness could result in non-genetic similarities between the offspring of dams allocated to the same sire. If there is differential investment, apparent genetic sire effects may be confounded by non-genetic maternal effects. This problem of interpretation is inherent in all half-sib breeding designs where female investment has not been measured. In our experiments we took this possibility into account by measuring the female investment in offspring. There is variation in the weight of brood masses constructed by females, which is known to have a strong effect on offspring size and development. Thus, we measured the female investment as the brood mass weight. We found evidence for differential investment in brood mass weight translating into differential investment in offspring size (unpublished data), but brood mass weight did not influence offspring condition ($r = -0.042$, $n = 167$, $P = 0.596$) or courtship rate ($r = -0.053$, $n = 228$, $P = 0.427$). Therefore, our results do not arise from differential investment by females. However, we did not measure the size of the egg itself in the brood mass. Nevertheless, offspring growth and development in dung beetles is almost entirely dependent on maternal investment in brood mass³⁰ so that relatively subtle differences in the allocation of resources into eggs, if they existed, are unlikely to contribute to the sire effects reported here.

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Hyperacute directional hearing in a microscale auditory system

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The physics of sound propagation imposes fundamental constraints on sound localization: for a given frequency, the smaller the receiver, the smaller the available cues¹. Thus, the creation of nanoscale acoustic microphones with directional sensitivity is very difficult. The fly *Ormia ochracea* possesses an unusual 'ear' that largely overcomes these physical constraints^{2–5}; attempts to exploit principles derived from *O. ochracea* for improved hearing aids are now in progress⁶. Here we report that *O. ochracea* can behaviourally localize a salient sound source with a precision equal to that of humans⁷. Despite its small size and minuscule interaural cues, the fly localizes sound sources to within 2° azimuth. As the fly's eardrums are less than 0.5 mm apart, localization cues are around 50 ns. Directional information is represented in the auditory system by the relative timing of receptor responses in the two ears. Low-jitter, phasic receptor responses are pooled to achieve hyperacute timecoding^{8,9}. These results demonstrate that nanoscale/microscale directional microphones patterned after *O. ochracea* have the potential for highly accurate directional sensitivity, independent of their size. Notably, in the fly itself this performance is dependent on a newly discovered set of specific coding strategies employed by the nervous system.

Ormia ochracea (Diptera: Tachinidae) is a parasitoid fly^{10,11}. Gravid female flies locate their hosts, male crickets, by homing in on their loud, persistent songs. Because of its small body size, *O. ochracea* must deal with extremely small interaural difference cues to guide directional hearing³. The host cricket's calling song is an amplitude-modulated 5 kHz tone (6.8 cm wavelength); however, the fly measures less than 1 cm in any aspect and the distance

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