creased microvascular permeability is also a regular feature of cellular immunity and neoplasia and is mediated by specific permeability factors secreted by activated lymphocytes (*14*) and tumor cells (*7*), respectively. We suggest, therefore, that increased vascular permeability, rather than special procoagulants associated with macrophages or tumor cells, also accounts for the substantial extravascular deposits of fibrin regularly found in cellular immunity and in solid tumors.

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8. Guinea pig fibrinogen was purified, labeled with $^{125}$I (*3*), and injected intravenously into each animal. Test and control substances were then administered. Twenty minutes later, guinea pigs received intravenously 0.5 ml of an anticoagulant-antifibrinolytic mixture containing heparin (1000 U), hirudin (100 U) or D-phenylalanyl-L-propyl-L-arginine chloromethyl ketone (250 μg), ε-aminocaproic acid (EACA) (25 mg), and Trasylol (700 U) in 0.15*M* NaCl. One minute later the animals were anesthetized with ether and exsanguinated. Blood samples were centrifuged (10,000*g* for 20 minutes) to prepare PPP for counting of radioactivity. Test and control tissues were dissected into tared tubes containing 2 ml of ice-cold 0.01*M* phosphate buffer (*p*H 7.5) supplemented with heparin (10 U/ml), hirudin (2 U/ml), EDTA (2 mg/ml), 0.1*M* EACA, 2 m*M* phenylmethylsulfonyl fluoride, 2 m*M* iodoacetate, and 2 m*M* *N*-ethylmaleimide (*3*). Test and control tissues were weighed wet. Tissue radioactivity (counts per minute per gram) was divided by that in PPP (counts per minute per microliter of plasma) to express accumulation of [$^{125}$I]GPF as microliters of PPP that entered each gram of test or control tissue. Microliters of PPP can be converted to fibrinogen equivalents (micrograms) by multiplying by 3.34 (*3*). To characterize the [$^{125}$I]GPF deposited, tissue samples were minced and extracted first with tissue buffer (to solubilize fibrinogen, fibrin monomer, and water-soluble fibrin degradation products) and then with 3*M* urea (to solubilize non–cross-linked fibrin) (*9*). Radioactivity remaining in the urea-insoluble residue, largely representing cross-linked fibrin, was counted to calculate cross-linked fibrin accumulation.
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## Genetic Consequences of Mate Choice: A Quantitative Genetic Method for Testing Sexual Selection Theory

Abstract. *To investigate whether female mate choice could be directed at male genetic quality, male chemical signals and progeny fitness were studied in the red flour beetle (*Tribolium castaneum*). Differences among males in the attractiveness of their pheromone to females were statistically significant. Developmental time of progeny was significantly heritable, indicating that some males have "good genes" for this trait. There was no statistically significant correlation between progeny fitness and male attractiveness. These results do not support the hypothesis that in this species the evolution of female preferences for male pheromone is adaptive.*

In species in which males provide neither resources nor parental care as part of reproduction, the evolution of sexual dimorphism as a result of female mate choice has been explained by two opposing models. The models are similar in that the evolution of conspicuous male displays is seen to result from selection due to female choice; they differ in their explanation of the evolution of female choice. Fisher and others (*1*) described a process in which extreme female mating preferences evolve as a correlated response to sexual selection on the male display, not as a consequence of increased fitness of discriminating females. This process originates when preference by some females for a particular trait in some males leads to a genetic covariance between the loci controlling the female trait (choice) and the male trait (display) as a result of assortative mating for these traits. A genetic covariance permits these traits to evolve because the male offspring of discriminating females bear a trait that makes them more attractive and female offspring bear a trait making them more discriminating.

Contrasting models emphasize the adaptive nature of female choice: females choose males because traits in the male display are correlated with components of male fitness that are under natural as opposed to sexual selection (*2*). That is, females mate with males possessing "good genes" and thereby produce progeny that are more viable than those sired by less conspicuous males. A crucial issue in these models is whether there are "good genes" that are correlated with traits detectable by females (*3*). I describe an experiment in which quantitative genetic techniques were used to measure progeny fitness of males that differ in their attractiveness to females.

First, male attractiveness is evaluated through behavioral tests with conspecific females. Second, the genetic quality of the same males is evaluated by quantitative genetic techniques. Males are considered to differ in genetic quality if components of fitness measured in their progeny have significant (narrow sense) heritability. Third, the extent to which females recognize and prefer males bearing good genes is evaluated by computing the correlation between attractiveness of sires to females and the fitness of progeny of these sires. This procedure is applied to an analysis of male attractiveness and genetic quality in the red flour beetle (*Tribolium castaneum*).

*Attractiveness of males to females.* Adult male flour beetles at low densities in high quality habitat emit a volatile pheromone that attracts conspecific females and males (*4*). These general attractant characteristics make the signal analogous to the advertisement calls and calling songs of anuran amphibians and crickets (*5*). The pheromone gives females an opportunity to make a general decision about which male to approach. Once near a male, a female apparently cannot exert mate choice: males attempt to copulate with any discontinuity in the flour, and the flour medium appears to be too soft for a female to dislodge a male.

The attractiveness of each of 16 males was determined empirically through behavioral tests of their pheromone in a two-choice pitfall trap apparatus (*6*) in which each male's pheromone was com-

pared to a blank control. Twenty randomly chosen virgin females were tested simultaneously in each apparatus. After a 30-minute test the number of females in each trap of the apparatus was counted. The proportion of females preferring the pheromonal stimulus to the control was averaged over two to four tests per male (*7*), and these averages were used to rank male attractiveness. Individual male attractiveness varied greatly between successive tests; however, there were statistically significant differences between males for the four tests combined [$F(15, 44) = 15$; $P < 0.02$] (*8*).

The fitness of the progeny of these males was determined by breeding each one with two randomly chosen females [a half-sib breeding design (*9*); these females had not participated in the behavioral tests]. The developmental time of F1 progeny and the representation of progeny of F1's in the F2 generation were measured as components of fitness.

*Developmental time of F1 progeny.* Developmental time can be regarded as a component of fitness because the rapidity with which individuals reach reproductive age affects the total number of progeny that they in turn can produce. Newly hatched larvae were collected from each female every 24 hours and housed individually in 1 g of medium (*10*). (Most females provided ten larvae, but in some cases fewer larvae were collected.) When the larvae had pupated, they were removed from the flour and observed once every 12 hours until they eclosed as adults. Developmental time was expressed as number of days after isolation and ranged from 20 to 29 days with a mean of 24.5 days (Fig. 1a). I used an analysis of variance to estimate the parental components of variance, which were then used for computing heritabilities (*9*). The observed components of variance due to sires and due to dams were of similar magnitude, indicating that the genetic variance was largely additive; the estimated heritability (narrow sense) was 1.02 ± 0.49 (standard error) (*11, 12*).

*Representation of F1 in F2 generation.* This experiment was designed to measure the inherited variation in the fitness of F1 progeny from different sires relative to a population of beetles. I examined the number of F2 progeny attributable to a given F1 parent. No mate choice by or of the F1 progeny is implied because, at the density of beetles in each vial, females cannot exercise mate choice. This experiment measures a combination of components of fitness: fertility and fecundity of F1 individuals, developmental time of F2 larvae, and F2 larval competitive ability (cannibalism is a major form of larval competition) (*13*). It may be as close to an estimate of total fitness of F1 individuals as can be obtained.

The background population and the F1 progeny were distinguishable by body color. All the F1 progeny from the "good genes" sires were homozygous wild type for body color, which is a reddish brown. Each of six adult F1 progeny from each of the 30 dams (two dams per sire and three F1 progeny of each sex) was placed in 8 g of medium with 15 homozygous black adults (*14*). Forty-eight days later the populations were sifted, killed by freezing, censused, and scored for genotype. All progeny of the F1 parent were heterozygous for body color, which is dark brown; thus they were distinguishable from both homozygotes.

Because the number of progeny produced by F1 females and by F1 males were not correlated ($r = 0.32$, $P = 0.09$), heritabilities were computed for each group separately. The estimated heritability of progeny production was not statistically significant, 0.08 ± 1.07 for F1 females and 0.68 ± 1.04 for F1 males (*11*).

In summary, overall fitness as approximated by the number of F2 progeny was not significantly heritable, but developmental time had a significant additive genetic component in this study. The adaptive interpretation of these results is that some males do possess "good genes" that affect at least certain components of the fitness of their progeny, and detection of such males by females should be favored by evolution. However, none of the correlation between mean attractiveness scores of the sires and the fitness of their progeny was significantly positive (Fig. 1). Thus, the phenotypic correlation between male attractiveness and progeny fitness predicted by the "good genes" model was not observed.

It is conceivable that this lack of a statistically significant correlation is a result of my having chosen the "wrong" trait as a measure of male attractiveness. It is worth noting that the pheromone is available for female choice, and females have not exploited it as an indicator of

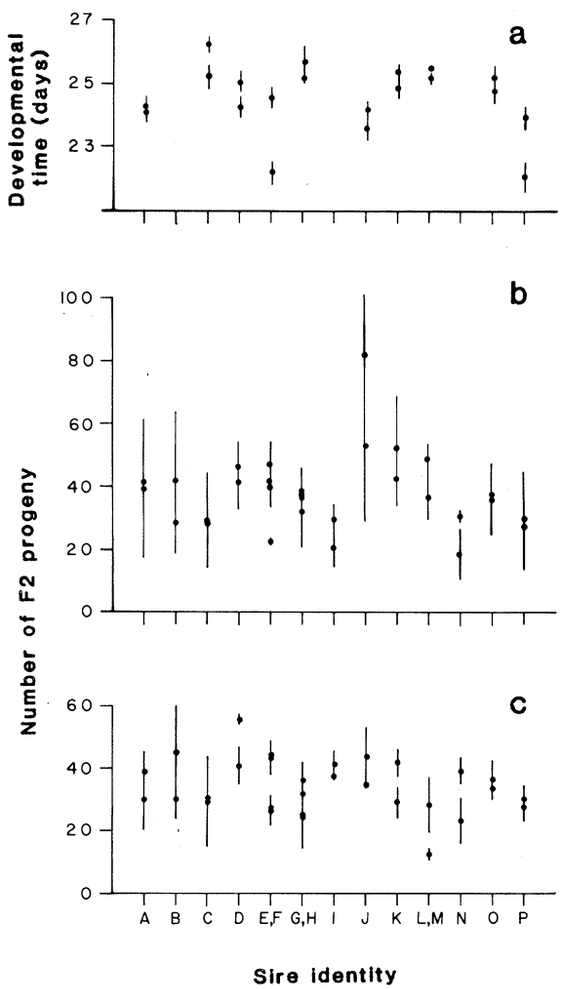


Fig. 1. Relation between components of fitness and sire identity (sires are arranged by rank of attractiveness score with the least attractive on the left). The progeny of two dams per sire were examined in each experiment and their means (± 1 standard error) are presented separately. Nine sires were common to both analyses; three pairs of sires, E and F, G and H, and L and M, shared attractiveness scores. None of the correlations between sire attractiveness and progeny fitness was statistically significant. (a) Developmental time in days. Pearson product-moment correlation between developmental time of progeny and attractiveness of sires: $r = -0.34$, $P = 0.33$. (b) Number of F2 progeny produced by F1 males. Correlation between number of progeny and sire attractiveness: $r = -0.10$, $P = 0.72$. (c) Number of F2 progeny produced by F1 females. Correlation between number of progeny and sire attractiveness: $r = -0.32$, $P = 0.25$.

male genetic quality, at least as it relates to these measures of fitness.

The quantitative genetic techniques used here are applicable to any organisms in which the attractiveness of males is measurable in the field, if those males can be brought into the laboratory to breed with randomly chosen females, subject to certain constraints. First, a knowledge of the variance in attractiveness of individual males is essential for interpreting the genetic results appropriately; a knowledge of the variance in female response to males would also be useful. In other words, a single test of each male's attractiveness is insufficient. Second, large numbers of families are necessary for the reliable estimation of heritability of components of fitness (*9, 11*).

In most organisms components of male mating displays are likely to be under polygenic control, as is fitness. Thus, "good genes" arguments can be seen as falsifiable hypotheses, subject to the type of tests that I have described.

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7. Two males died before they could be tested more than twice.
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## Visual Flow and Direction of Locomotion

Regan and Beverley (*1*) simulated the optic array of a moving observer looking to one side while approaching a line of static objects, such as fence posts. From their data they concluded that, in judging the direction of locomotion, the point of maximum rate of magnification may be sufficient, but the optical focus of expansion is not. The latter conclusion may be warranted (*2, 3*), but the former seems not.

First, within 10° of the direction of the point of impact, the normal optic flow of objects is well approximated by a power function with exponent $n = 1.0$ (Fig. 1A). Beyond 10° or with other exponents, however, it becomes seriously discrepant, simulating either the view through a zooming photographic lens, or an unstable, nonrigid world that continuously bends. Neither situation is natural for any organism.

Second, in the real world, the point of maximum rate of magnification is surrounded by other points with rates nearly as great. The function is not highly articulated until the observer is near the point of impact on a flat plane (Fig. 1B).

Third, their display presented a visual array of 20° by 16°, vastly reduced from the roughly 180° by 100° available in normal vision. Visual flow is greatest, and perhaps most useful, outside the parafoveal region. Since their display excluded more than 97 percent of the solid visual angle of the optic array, it is not clear that information in optic flow was given a fair test.

As an example, consider a situation in which one cannot look in the direction of motion and yet it is essential to be able to judge its direction—the landing of a single-engine, propeller-driven aircraft, particularly one with a radial engine. On final approach to landing, in nose-up attitude, the pilot is obliged to look out to one side because the direction of motion is completely obscured by the engine and its housing. The point of maximum rate of change of magnification lies halfway between the point of impact and that point on the ground nearest the pilot [note 6 in (*1*)] and is simply unavailable. The pilot must know and maintain direction without ever seeing that point, and the cost of error is high. Yet pilots routinely make such judgments with accuracy, despite the implications of Regan and Beverley (*1*).

Finally, their analysis assumes no vi-

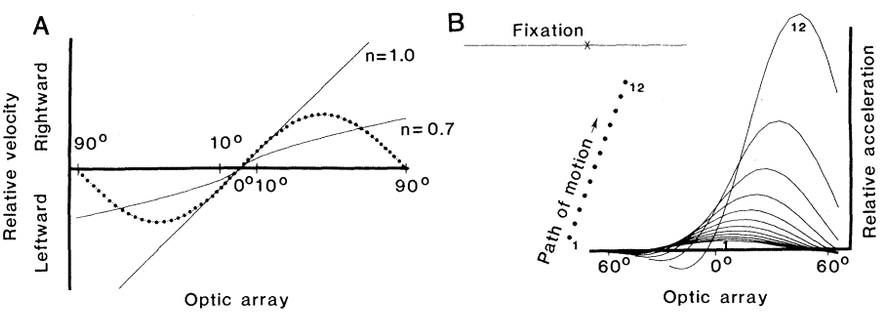


Fig. 1. (A) Relative velocities for two exponential flows used by Regan and Beverley (*1*) in their simulations, and the flow (dotted line) for actual orthogonal approach to a plane [$d\theta/dD = -x \sin\alpha(D^2 - 2Dx\cos\alpha + x^2)$, where $\theta$ is the angle of gaze with respect to motion, $\alpha$ the angle of approach to the plane, $D$ the distance of the observer from the plane along the path of motion, and $x$ the distance along the plane to the observed texture element from the point of impact]. Within ±10°, true flow is well approximated by $n = 1.0$; it is not for $n = 0.7$. (B) Nonorthogonal approach to a plane, with a maintained fixation point off to the left. Relative accelerations of textures are measured, with 0° the fixation point. Peaks in the functions correspond to the points of maximum rate of change of magnification. When an observer is relatively distant from the plane, functions are flat and this point is surrounded by neighbors of similar expansion rates. The function generated is $d^2\theta/dDdx = -\sin\alpha(x^2 - D^2)/(D^2 - 2Dx\cos\alpha + x^2)^2$.