

THE STUDY OF INTERSEXUAL SELECTION USING QUANTITATIVE GENETICS

by

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Summary

In this review, I stress the importance of incorporating Quantitative Genetics (QG) in the study of sexual selection through female mate choice. A short overview of QG principles and methods of estimating genetic variance and covariance is given. The state of knowledge is summarized as to two QG assumptions (genetic variance in female mating preferences and male sexual traits) and one QG prediction (genetic covariance between preferences and preferred traits) of models of sexual selection. A review is given of studies of repeatability of mating preferences because of recent accumulation of data. The general conclusion is that sexual traits and mating preferences show large genetic variation and are genetically correlated. The extensive genetic variation asks for an explanation that goes beyond the usual explanations of the maintenance of genetic variation in fitness traits. Two models that explain the high genetic variance in sexual traits are treated in detail: modifier selection and condition dependence. There are many unexplored areas of QG research that could stimulate further research in sexual selection like the study of genetic covariance between mating preferences and good genes, of genetic variances and covariances of multiple male traits and multiple females preferences, of genetic variance in condition, and of condition dependence of mating preferences.

Keywords: sexual selection, genetic variance, genetic covariance, female preference, sexual traits, quantitative genetics.

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What is the use of Quantitative Genetics in the study of intersexual selection?

During the past decades evidence has accumulated that female mating preferences are very powerful selective forces in shaping secondary sexual traits in males (Andersson, 1994). The majority of these studies of sexual selection through female mate choice or intersexual selection are phenotypic studies without knowing whether and to what extent the variation in the traits of interest (*i.e.* preferences and secondary sexual traits) is caused by genetic variation. Traits involved in sexual selection are often quantitative traits, that is, traits that have a continuous distribution. Such traits usually show multifactorial or polygenic inheritance. The discrete phenotypic distribution of traits controlled by few major genes, which is studied in Population Genetics, is converted into a continuous phenotypic distribution when traits are influenced by many genes, each with a small effect on the phenotype, and environmental variables. The effects of single genes can then not be traced any more. The study of the genetics of quantitative traits is therefore in essence a statistical description of phenotypic variance in terms of its net causal components. The evolution of quantitative traits is studied in Quantitative Genetics (abbreviated as QG hereafter). QG can be defined as a statistical description of the evolution of phenotypes (Pigliucci & Schlichting, 1997). For almost a century QG is successfully used for both the description and prediction of evolutionary change. Much of its theory originates from animal and plant breeding.

Many aspects of sexual selection can be addressed with phenotypic studies. The phenotypic approach is most suited in studying the targets of sexual selection, the nature and form of mating preferences, the intensity of selection that acts on sexual traits and preferences, and the mechanisms of sexual selection. The study of sexual selection can profit in several ways by the integration of QG. Knowledge of the extent of genetic variation and covariation of traits involved in sexual selection is essential to understanding the potential of and constraints in the evolution of these traits. Most theoretical models of sexual selection by female mate choice are based on QG assumptions (Andersson, 1994): the presence of genetic variance in male traits and female preferences, and the resulting genetic covariance between them. Recent reviews show that these assumptions are empirically supported to a large extent (Bakker & Pomiankowski, 1995; Pomiankowski & Møller, 1995; see below).

Intimately connected to the evolution of mating preferences and preferred sexual traits is the signal value of sexual traits: which kind of information is signalled by sexual traits, and consequently what are the benefits for females that base their mate choice on these signals? This is a frequently studied and debated issue in sexual selection. Because females may choose particular mates for the genetic benefits that the father will transmit to their offspring, it is evident that QG is needed to show such benefits. Models of intersexual selection highlight three possible benefits of choice: choosy females are rewarded by direct fitness benefits, or the offspring of choosy females benefit from the genetic make-up of their father by inheriting either genes for attractiveness or genes for viability (Kirkpatrick & Ryan, 1991; Andersson, 1994). It is often believed that the effects of direct benefits outweigh those of indirect benefits in the evolution of mating preferences (*e.g.* Kirkpatrick & Ryan, 1991; Johnstone, 1995a; Ryan, 1997); “In resource-based mating systems, direct selection on preferences is expected to be the rule rather than the exception. When under direct selection, we expect the female preference to evolve to an optimum that maximizes her fecundity...” (Ryan, 1997, p. 184-185). Recent work by Kirkpatrick & Barton (1997) about the impact of good genes preferences on the evolution of mating preferences nicely illustrates how the application of QG leads to a better understanding of sexual selection. Their estimations suggest that preferences for good genes work, but when competing with direct selection they do not work very well. In order to arrive at this conclusion, estimates of QG parameters like the heritabilities of female mate preferences and preferred male traits, are essential.

Kirkpatrick & Barton (1997) derived the following formula for the strength of indirect selection on female mating preferences:

$$I_I \approx 0.5\rho_{PT}r_{TW}h_T h_p^2 \sqrt{G_W}$$

where I_I is the change in the mean preference across one generation, measured in units of the preference's phenotypic standard deviation; ρ_{PT} is the phenotypic correlation between the preference and the sexual trait; r_{TW} is the genetic correlation between the male trait and total fitness; h_T is the square root of the heritability of the male trait; h_p^2 is the heritability of the preference; $\sqrt{G_W}$ is the genetic coefficient of variation for fitness. Thus, the fitness advantage that preference genes gain by indirect selection is proportional to the coefficient of variation of male quality, $\sqrt{G_W}$, and the

accuracy with which preference genes can associate themselves with fitness genes (the remainder of the above equation). The median estimate for h_T is 0.7 (Pomiankowski & Møller, 1995), for h_P^2 0.4 (Bakker & Pomiankowski, 1995), and for $\sqrt{G_W}$ 0.25 (Charlesworth, 1987; Burt, 1995). If we assume the most favourable conditions, *i.e.* a signal that indicates breeding value for fitness with complete fidelity ($r_{TW} = 1$), and a perfect correlation between the preference and the sexual trait among mated pairs ($\rho_{PT} = 1$), then the upper bound for I_I is 0.035. Even then, indirect selection changes the mean preference by only 3.5% of the preference's standard deviation per generation. It is likely that this figure will be much smaller. Direct selection can cause changes that are a factor of magnitude larger (Kirkpatrick & Barton, 1997). This is, however, based on changes caused by direct selection on characters other than mating preferences. No such data are available for mating preferences. It seems thus likely that direct selection on preference genes overwhelm indirect selection. But even weak indirect selection will be important if preference genes are free of direct selection.

Some basics of Quantitative Genetics: additive genetic variance and covariance

QG is basically concerned with the quantification of the various causal factors for phenotypic variation. I will give here a simplified treatment of some basics of QG with the purpose to elucidate the quantification of the amount of genetic variation that is transmitted to the offspring. This is of course only one aspect of QG. For more balanced overview and more detailed treatment of principles and methods, the reader is referred to the textbooks of Falconer (1989), Roff (1997) and Lynch & Walsh (1998).

The basic equation in QG divides the phenotypic variance of a trait (V_P) into a part due to genetic causes (V_G , the genetic variance) and a part due to environmental causes (V_E , the environmental variance):

$$V_P = V_G + V_E$$

The genetic component can be further subdivided into a part that is transmitted to the offspring (V_A , the additive genetic variance) and a part that is not directly transmittable (V_D , the dominance variance):

$$V_P = V_A + V_D + V_E$$

The additive genetic variance is caused by genetic differences that show their effect on the phenotype more or less independent of the rest of the genome. Additive means that the average effects of those genes simply add up to the value of the phenotype. The proportion of the phenotypic variance that is due to additive genetic variance is called heritability in the narrow sense or simply heritability (h^2):

$$h^2 = V_A / V_P$$

It is of interest because heritability predicts the response of a phenotype to short-term selection, and it measures the degree of resemblance between relatives. A low heritability may however be due to low additive genetic variance or high residual variance (that is phenotypic variance minus additive genetic variance, and thus includes non-additive genetic and environmental effects). For comparative purposes Houle (1992) argued that the coefficient of additive genetic variance (CV_A) is a more appropriate measure of genetic variation. It standardizes the additive genetic variance with respect to the mean value of the trait (\bar{X}):

$$CV_A = \frac{100\sqrt{V_A}}{\bar{X}}$$

But also this measure has to be applied critically because it is scale dependent (Roff, 1997).

Another QG parameter of interest here is the genetic correlation (r_A) which measures the genetic coupling between traits. It is actually the correlation between the additive genetic effects of two sets of overlapping genes. Like the phenotypic variance of one trait can the phenotypic correlation between two traits X and Y (r_P) be split up in an additive genetic component (r_A) and an environmental component (r_E) which also includes non-additive genetic effects:

$$r_P = r_A \sqrt{h_X^2 h_Y^2} + r_E \sqrt{(1 - h_X^2)(1 - h_Y^2)}$$

The causal correlations are weighted by the relative importance of heritable and nonheritable effects.

Heritabilities and genetic correlations can be calculated from the resemblance between related individuals (Table 1). The easiest but least accurate way is to compare individuals with themselves, that is to take repeated measures of the same trait on individuals. In this way only phenotypic variance

TABLE 1. *Phenotypic resemblance between relatives*

Comparison	Regression or correlation
Repeated measures on individuals	$(V_A + V_D + V_{Eg})/V_P$
Offspring and one parent	$0.5V_A/V_P$
Offspring and mid-parent	V_A/V_P
Half sibs	$0.25V_A/V_P$
Full sibs	$(0.5V_A + 0.25V_D + V_{Ec})/V_P$
Selected generations	V_A/V_P

V_P is the phenotypic variance; V_A is the additive genetic variance; V_D is the dominance variance; V_{Ec} is the common environmental variance; V_{Eg} is the general environmental variance.

due to temporary circumstances (the so-called special environmental variance) can be separated from other causes of variation (genetic, that is additive and non-additive genetic, and general environmental causes arising from permanent circumstances). The resulting measure is thus a very crude estimate of the heritability, it merely sets an upper limit to it. The most frequently used comparisons that give reliable heritability estimates are parent-offspring involving one or both parents (in the latter case an average value, the mid-parent value is used), full sibs (which however also resemble each other due to dominance effects and common environmental effects) and half sibs. Parent-offspring comparisons can be augmented by artificial selection experiments. It must be realized that QG studies in general need much larger sample sizes than phenotypic studies (*e.g.* Roff, 1997).

Genetic variance of secondary sexual traits

Pomiankowski & Møller (1995) recently reviewed QG studies of sexual traits. Heritabilities of traits known or assumed to be under sexual selection were till then published for 30 species, 60% of which were invertebrates. In their analysis, estimates for more than one trait in a single species were averaged so that one estimate per species was obtained. The heritabilities of sexually selected traits averaged (\pm SD) 0.58 ± 0.26 (Fig. 1). This figure is unexpectedly high for traits that are closely connected to fitness. The average

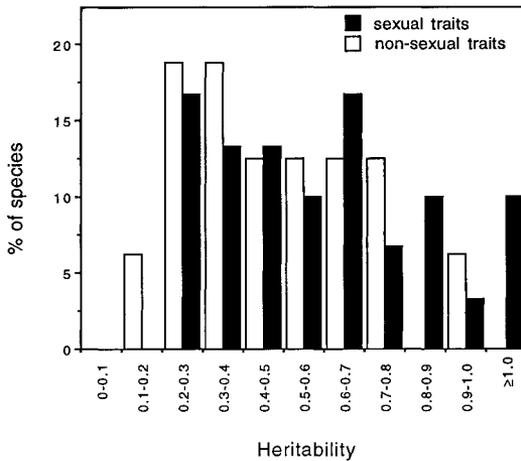


Fig. 1. Frequency distributions of heritability estimates of sexual traits (closed bars, 30 species) and non-sexual traits (open bars, 16 species). Multiple estimates per species were averaged. Non-sexual traits were comparable to the sexual traits and in most cases from the same species. Data from Pomiankowski & Møller, 1995. Note that Pomiankowski & Møller (1995) used non-sexual traits of 19 species in their analyses but the data for some species were missing in the data-set that they provided.

heritability of non-sexual traits was 0.46 ± 0.21 (Fig. 1) which is significantly lower than that of sexual traits in the paired comparison (16 species) but not so in the unpaired comparison (Pomiankowski & Møller, 1995).

Even more pronounced were the differences in the coefficients of additive genetic variance between sexual and non-sexual traits: 15.98 ± 20.38 (30 species) *versus* 4.77 ± 3.62 (16 species), respectively (Fig. 2). Similar differences were established in the paired comparison (16 species) and in a paired comparison involving only species in which sexual and non-sexual traits were of the same kind (*i.e.* all morphological traits, 10 species) (Pomiankowski & Møller, 1995). Contrary to expectation, sexual traits are more genetically variable than comparable non-sexual traits. This enhanced genetic variability of sexual traits asks for an explanation which goes beyond the usual explanations for the maintenance of genetic variation in fitness, such as frequency-dependent selection, mutation-selection balance, temporal variation in fitness, the Red Queen, and selection on the environmental component of a trait (*e.g.* Møller, 1994a). In the next section, two explanations are offered (see also Houle, 1998).

Heritability seems to be a rather poor predictor of additive genetic variance: the correlation between the two parameters was less than 0.4

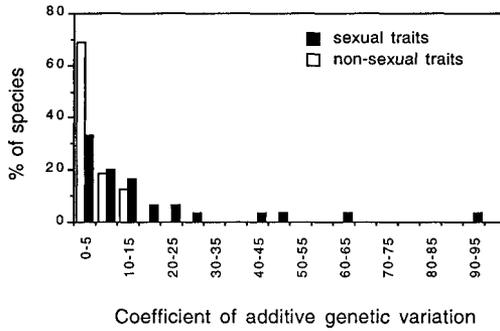


Fig. 2. Frequency distributions of coefficients of additive genetic variation of sexual traits (closed bars) and non-sexual traits (open bars). Same data set as in Fig. 1.

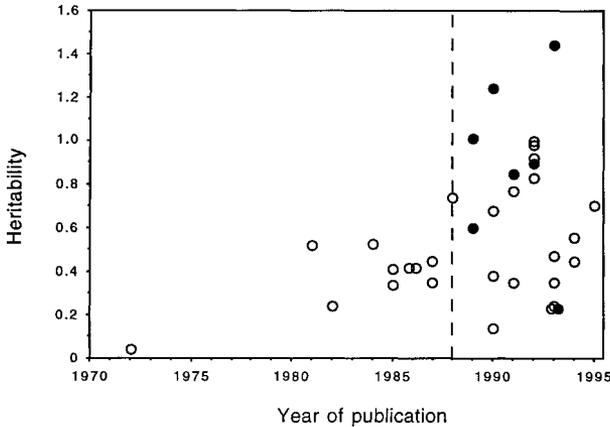


Fig. 3. Heritability of sexual traits as a function of the year of publication. Filled symbols are estimates from studies with relatively small sample sizes (offspring from less than 20 fathers). The line marks the year 1988. After Alatalo *et al.* (1997), data from Pomiankowski & Møller, 1995.

in Pomiankowski & Møller's (1995) review, and 0.06 in Houle's (1992) literature review of 400 estimates. This and other data suggest that there are parallels between the processes shaping environmental and genetic variances (Houle, 1992).

A cautionary note is here in place. If we plot the heritabilities of sexual traits against their year of publication, then since 1988 heritabilities have significantly higher values and show higher variance than those published before 1988 (Alatalo *et al.*, 1997; Fig. 3). No significant changes were evident in estimates of the heritability of non-sexual traits and in the

coefficient of additive genetic variance of sexual traits. The year 1988 was the turning point in the theoretical acceptance of good genes sexual selection (Pomiankowski, 1988). In earlier years Zahavi's ideas (1975, 1977) were rejected on theoretical grounds (*e.g.* Kirkpatrick, 1986). The difference in mean heritability (until 1987, 0.37 ± 0.14 , $N = 10$; since 1988, 0.67 ± 0.34 , $N = 24$; Alatalo *et al.*, 1997) suggests a publication bias. After the theoretical acceptance of the good genes model 7 studies were published that were based on relatively few data (Fig. 3). The heritabilities of these studies are significantly greater than those of the remaining 27 studies.

How can there so much genetic variance in sexual traits be maintained?

The realization that secondary sexual traits display high levels of additive genetic variance seems to have resolved a long-lasting debate known as the lek paradox. In lek species where males provide no parental care or resources the benefits of female mate choice are assumed to be indirect: females gain genetic benefits for their offspring. The strong sexual selection pressure exerted by females was expected to deplete the genetic variation in the preferred male traits leading to small indirect benefits of female choice. A depletion of additive genetic variance would be predicted by Fisher's Fundamental Theorem of Natural Selection (1930): "the change in fitness caused by natural selection is equal to the additive variance in fitness". Traits that are closely related to fitness like life-history traits do indeed seem to follow this prediction: they have low heritabilities compared to traits that are subject to less strong selection (Gustafsson, 1986; Mousseau & Roff, 1987; Roff & Mousseau, 1987; Houle, 1992; Roff, 1997). However, this is not due to low additive genetic variance: in fact, fitness traits have higher standardized genetic variability (Houle, 1992). At the same time, fitness traits have proportionately extremely large residual variability relative to morphological traits (Houle, 1992). This may be the consequence of the larger number of loci, the wider range of environmental variables, and more interactions among them that affect fitness traits. Fitness traits tend to integrate variability over the lifetime of the organism, and result from all the selective forces acting on other characters (Price & Schluter, 1991; Fig. 4).

Like life-history traits, secondary sexual traits have high standardized additive genetic variance compared to non-sexual (mainly morphological)

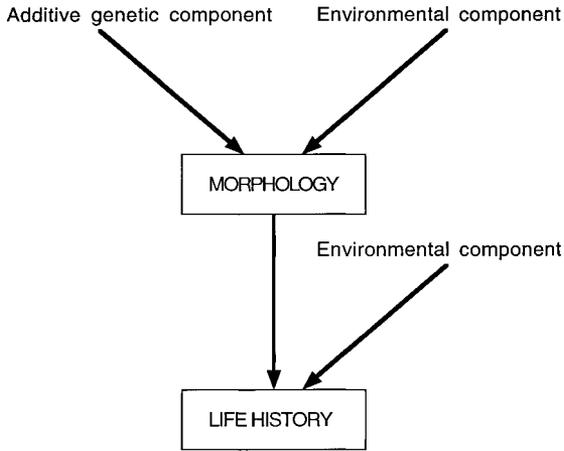


Fig. 4. Causal relationship between a morphological trait and a life-history trait. Arrows connect independent variables to dependent variables. Life-history traits have lower heritabilities than morphological traits because they are subject to additional environmental variation that does not influence morphological traits. After Price & Schluter, 1991.

traits (Houle, 1992; Pomiankowski & Møller, 1995). Unlike life-history traits, sexual traits tend to have higher heritabilities than non-sexual traits (Houle, 1992; Pomiankowski & Møller, 1995; Roff, 1997). Whether this is a fundamental difference between life-history traits and sexual traits is unclear. In Pomiankowski & Møller's (1995) analysis sexual traits were lumped irrespective of their signal function. How closely sexual traits relate to fitness may depend on their signal function: Fisherian traits will be less closely connected to fitness than good-genes traits or traits that signal direct benefits. In Pomiankowski & Møller's (1995) analysis standardized additive genetic variances and heritabilities are inflated by maternal and common environmental effects because estimates were in part based on full sib correlations or on resemblance between relatives in the wild.

How is the high genetic variability in sexual traits explained? Pomiankowski & Møller (1995) suggested that the high genetic variability results from persistent directional selection which is greater than linear, that is individuals with greater than average trait values have disproportionately higher fitness. Such a selection regime would favour increased phenotypic variance (Lande, 1980). This could be achieved by favouring modifiers that increase phenotypic variation, either by increasing the number of genes or by increas-

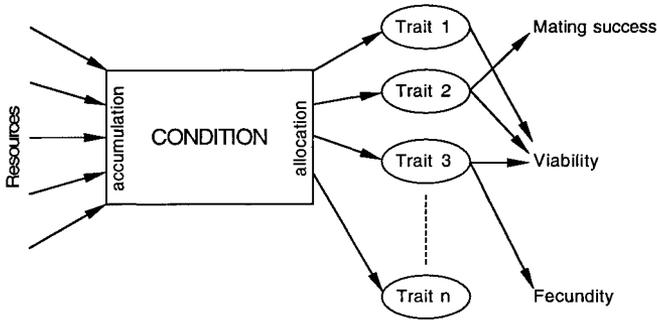
ing the average effect of each locus on sexual traits (Pomiankowski & Møller, 1995).

An alternative explanation was offered by Rowe & Houle (1996). They criticized the concave upwards fitness function of greater sexual trait exaggeration that Pomiankowski & Møller (1995) assumed. They argue that trait exaggeration will eventually stop when the costs of further exaggeration balances the gains from mating success. Thus at equilibrium, sexually selected traits are expected to be under conflicting, that is net stabilizing, selection rather than directional selection. Under such conditions, high genetic variability in sexual traits can be explained when we assume condition dependence of sexually selected traits and high genetic variance in condition. During the evolution of sexual traits genetic variance in overall condition is converted into genetic variance in the male trait. Rowe & Houle (1996) call this process genic (which means additive genetic) capture. How does that work?

Rowe & Houle (1996) define condition as follows: "We imagine the life history as a process of accumulating resources that are then allocated to the production or maintenance of traits that enhance fitness. We will refer to the pool from which resources are allocated as Condition . . .". During the transition of a trait from stabilizing natural selection to directional sexual selection, it will become more costly because with increasing exaggeration of the trait more resources are allocated to the trait at the expense of other fitness enhancing traits (Fig. 5). The exaggeration will stop when the benefits of exaggeration are balanced by the costs. Once a trait becomes costly, it is expected to evolve condition dependence because individuals in higher condition are better able to pay higher marginal costs of further exaggeration than those in lower condition. A crucial assumption in Rowe & Houle's (1996) explanation is that there exists high genetic variance in condition. They expect that a large proportion of the genome affects condition because condition is a complex summary of many processes (Price & Schluter, 1991). It is difficult to imagine metric traits that do not contribute in some way to condition. Thus the mutational target size for condition is large (Houle, 1998). Rowe & Houle (1996) derived the following QG justification of their hypothesis. Let us assume that a metric trait T is a linear function of condition C

$$T = a + Cb$$

A. BEFORE (natural selection on Trait 1)



B. AFTER (natural and sexual selection on Trait 1)

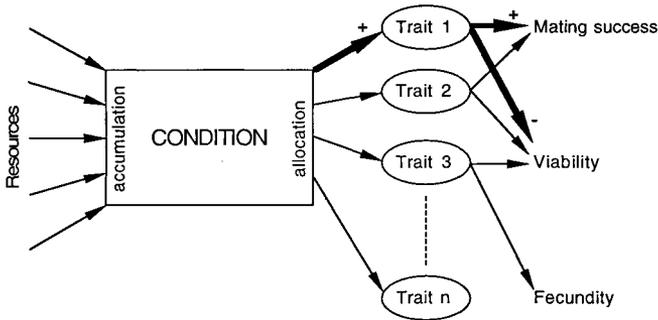


Fig. 5. Path diagram of the relationships between condition, various traits (trait 1 — trait n), and fitness components before (a) and after (b) sexual selection on trait 1. Thickness of the path indicates amount of resource flow to the traits. Before sexual selection, trait 1 is assumed to be under stabilizing viability selection with little or no correlation between condition and trait 1. After some period of sexual selection on trait 1, there is conflicting selection on trait 1 indicated by the opposite signs of the relationships with mating success and viability. Trait 1 becomes then correlated with condition (condition dependence). There is a dramatic increase in allocation of resources to trait 1 at the cost of allocation of resources to one or all of the other traits. After Rowe & Houle, 1996.

where a is the condition-independent level of expression of T , and b the rate at which expression increases with condition. Selection for condition dependence of a trait will select for greater b . The genetic variance of T , G_T , is approximately

$$G_T \approx G_a + \bar{b}^2 G_C + \bar{C}^2 G_b$$

Sexual selection is expected to both minimize G_a and G_b and increase b but leaves G_C largely unaffected. If condition dependence becomes strong, this will then likely result in increased genetic variance of T compared to the situation in which T was only subject to natural selection. This increase is due to the contribution of the large genetic variance in condition which is scaled by b squared. Thus traits that evolve condition dependence will capture some of the genetic variance in condition. Rowe & Houle (1996) point to similarities of sexually selected traits and life-history traits in this respect. Recently, data of stalk-eyed flies strongly supported Rowe & Houle's model (Wilkinson & Taper, 1999).

Pomiankowski & Møller (1995) suggested that their model also would work when the proposed modifier locus is substituted by a locus that influences condition dependence of the sexual trait. In that respect their explanation is similar to that of Rowe & Houle (1996). The difference between the two alternatives is that the latter does not have to assume directional selection which is more than linear acting on sexual traits. One has to realize that one of the assumptions of the models contrasts with the general (but unfounded) belief that condition is environmental in origin (see references in Rowe & Houle, 1996). There is an obvious gap in our knowledge here.

Genetic variance of mating preferences

Measuring repeatabilities is a relatively easy way to get an impression of genetic variance in mating preferences. In species where breeding under controlled laboratory conditions is difficult or impossible, but where it is possible to keep track of individuals under field conditions, it may be the only way to estimate genetic variation. Remember that the repeatability is a very rough measure of the narrow sense heritability, it merely sets an upper limit to the heritability. Table 2 summarizes laboratory and field studies of repeatabilities in mating preferences (and mate choice). It illustrates some of the problems that may be encountered in estimating repeatabilities of behavioural traits.

Six of the 21 studies that have seriously tried to measure repeatabilities of mating preferences failed for various reasons (see below) to find significant consistency (Boake, 1989; Banbura, 1992; Ritchie, 1992; Poulin, 1994;

TABLE 2. *Repeatabilities of mating preferences*

Organism	Preferred trait	Test situation	Repeatability \pm SE	Reference
Red flour beetle <i>Tribolium castaneum</i>	pheromone	preference (binary scale) in lab	0 (NS)	Boake, 1989
Cockroach <i>Nauphoeta cinerea</i>	pheromone	preference (binary scale) in lab	no estimate (*)	Moore, 1989
Bush cricket <i>Ephippiger ephippiger</i>	calling song	preference (binary scale) in lab	no estimate (NS)	Ritchie, 1992
Pine engraver <i>Ips pini</i>	pheromone	preference (cont. scale) in lab	lower estimate: 0.23 ± 0.15 (NS); upper estimate: 0.86 ± 0.06 (*)	Hager & Teale, 1994
Field cricket <i>Gryllus integer</i>	calling song	preference (cont. scale) in lab	lower estimate: -0.02 ± 0.24 (NS); upper estimate: 0.59 ± 0.16 (*)	Wagner <i>et al.</i> , 1995 ¹⁾
Stalk-eyed fly <i>Cyrtodiopsis whitei</i>	eye stalk length	choice (mean of at least 5 binary) in lab	0.59 ± 0.14 (*)	Wilkinson <i>et al.</i> , 1998
Stalk-eyed fly <i>Cyrtodiopsis dalmani</i>	eye stalk length	choice (mean of at least 5 binary) in lab	0.33 ± 0.17 (*)	Wilkinson <i>et al.</i> , 1998
Fruitfly <i>Drosophila virilis</i>	calling song	preference (binary scale) in lab	0.33 ± 0.24 (*)	Isomerranen <i>et al.</i> , 1999
Australian frog <i>Uperoleia rugosa</i>	unknown	choice in field	no estimate (*)	Robertson, 1986

TABLE 2. (Continued)

Organism	Preferred trait	Test situation	Repeatability \pm SE	Reference
African painted reed frog <i>Hyperolius marmoratus</i>	calling song	preference (binary scale) in lab	no estimates (NS and *)	Jennions <i>et al.</i> , 1995
American toad <i>Bufo americanus</i>	body size	choice in field	lower estimate: 0.08 \pm 0.07 (NS); upper estimate: 0.25 \pm 0.30 (NS)	Howard & Young, 1998
American toad <i>B. americanus</i>	calling song	preference (binary scale) in lab	lower estimate: - 0.13 \pm 0.15 (NS); upper estimate: 0.42 \pm 0.20 (*)	Howard & Palmer, 1995; Howard & Young, 1998
Guppy <i>Poecilia reticulata</i>	coloration	preference (cont. scale) in lab	lower estimate: 0.05 \pm 0.09 (NS); upper estimate: 0.47 \pm 0.11 (*)	Kodric-Brown & Nicoletto, 1997
Guppy <i>P. reticulata</i>	coloration	preference (cont. scale) in lab	0.58 \pm 0.11 (*)	Godin & Dugatkin, 1995
Three-spined stickleback <i>Gasterosteus aculeatus</i>	coloration	preference (cont. scale) in lab	0.65 \pm 0.14 (*)	Bakker, 1993
Upland bully <i>Gobiomorphus beviceps</i>	body size	preference (binary scale) in lab	no estimate (NS)	Poulin, 1994

TABLE 2. (Continued)

Organism	Preferred trait	Test situation	Repeatability \pm SE	Reference
Japanese medaka <i>Oryzias latipes</i>	body size	choice (binary) in lab	0.18 \pm 0.11 (*)	Howard <i>et al.</i> , 1998
Barn swallow <i>Hirundo rustica</i>	tail length (abs.)	choice in field	0.15 \pm 0.23 (NS)	Banbura, 1992
Barn swallow <i>H. rustica</i>	tail length (abs.) tail length (rank)	choice in field	0.18 \pm 0.16 (NS) 0.57 \pm 0.11 (*)	Møller, 1994b
Red jungle fowl <i>Gallus gallus</i>	comb & feathers	choice (binary) in lab	no estimates (NS)	Ligon & Zwartjes, 1995
Red jungle fowl <i>G. gallus</i>	comb & feathers	choice (binary) in lab	lower estimate: -0.12 \pm 0.10 (NS); upper estimate: 0.19 \pm 0.10 (*)	Johnsen & Zuk, 1996

* = $p < 0.05$; NS = $p > 0.05$; ¹⁾ SE calculated according to Becker (1994) from data in Wagner *et al.* (1995).

Ligon & Zwartjes, 1995; Howard & Young, 1998). When repeatability of mating preference is not significantly different from zero, one has to be cautious in concluding that there is a lack of genetic variance. In such cases, there is a need to investigate other ways of measuring preference. For example, in a laboratory study of flour beetles, *Tribolium castaneum*, females significantly preferred male pheromone over blanks in choice tests. In repeated choices, however, females were highly variable in their responses, with no consistent patterns leading to zero repeatability of female preference for male pheromone (Boake, 1989). Some factors that influence female response to male pheromone were investigated with pine engravers, *Ips pini* (Hager & Teale, 1994). Repeatability of response to male pheromone in this beetle was a function of pheromone dosage and the number of measurements used to determine a female's response phenotype. Repeatability was greater for higher dosage, but females appeared to become less choosy after successive exposures to the pheromone. Repeatability values varied in this way from non-significant to 0.86 ± 0.06 .

Standardization of preference tests can much improve repeatabilities of mating preferences. In a study of visual preference for the amount of orange area in guppies, *Poecilia reticulata*, Kodric-Brown & Nicoletto (1997) analysed repeatability with three methods. In the first test design, females could visually interact with two males that differed in the amount of orange area, in the second and third design this was prevented by placing one-way mirrors between the female and the male, and by presenting video movies of the two males instead of live males, respectively. Although female responses were highest in the interactive test, the repeatability of female preference for orange area was lowest in this test (0.05 ± 0.09 ; one-way glass: 0.40 ± 0.11 ; video: 0.47 ± 0.11). One can even go a step further in the standardization of preference tests by letting females choose between two virtual males displaying on a computer monitor which differ only in the trait(s) of interest (Künzler & Bakker, 1998). This method has recently been successfully applied in measuring mating preferences (Künzler & Bakker, 1998). When applied to suitable organisms, it offers a unique tool for the study of preferences because single visual (morphological and behavioural) traits and combinations of traits can be manipulated.

Studies with barn swallows, *Hirundo rustica*, showed the importance of considering the right choice criterion when estimating repeatabilities. It is clear that one would not expect consistency of mate choice for male

traits that are not subject to female choice. Thus, repeatabilities of female barn swallow's choice between years for such traits were not significantly different from zero (wing length: 0.13 ± 0.13 ; length of central tail feathers: 0.09 ± 0.13 ; tarsus length: 0.15 ± 0.13 ; Møller, 1994b). Because female barn swallows prefer to mate with males with long outermost tail feathers (Møller, 1994a), one should expect consistency of choice for this trait. But Banbura (1992) and Møller (1994b) did not find a significant repeatability of choice for absolute male tail length between years in different populations of barn swallows. Obviously, this was not the criterion of mate choice that female barn swallows apply. If differences in the availability of potential mates were taken into account by taking the rank of the tail length of the chosen male relative to all males available in the breeding colony, then female mate choice was repeatable in the Danish colony (Møller, 1994b). The repeatabilities of the non-sexually selected traits mentioned above did not change when treated as ranks. Møller (1994b) raised the possibility that consistency of choice need not be due to genetic differences: it could arise through environmental differences between females, *e.g.* caused by consistent differences in female condition. However, such differences may also be genetic in origin (see above).

Like the studies in barn swallows, several other studies measured the repeatability of mate choice instead of the repeatability of mating preference (Table 2). Preferences do not necessarily translate into choice: for instance, with a given preference ecological variables influence mate choice (*e.g.* Milinski & Bakker, 1992), and strategic decisions whether to mate repeatedly with the same male may come into play. For instance, in mate choice trials using two non-interacting, tethered red jungle fowl, *Gallus gallus* which differed in comb size, females clearly preferred to copulate with the large-combed male in the first choice trial (Ligon & Zwartjes, 1995). Females were then repeatedly tested with the same two males at intervals of 48 h until each had copulated five times. Although overall more copulations were with large-combed males, only 3 of the 15 females were consistent in their choice and mated five times with the large-combed male. The authors favoured the genetic diversity hypothesis in interpreting their data.

A comparable experiment was conducted in the field with the Australian frog, *Uperoleia rugosa* (Robertson, 1986). Males found in amplexus had a larger than average male body size. Amplectant pairs were separated (and thus copulation interrupted) and the male placed in a chorus of males. Once

the male resumed calling, the female was released in the chorus so that she was about the same distance from her original mate and 4-5 other males. This was repeated 3-4 times per pair with different positions of the male in the chorus. Nearly all females always returned to their original males. In this species, females initiate pairing. In a similar study with American toads, *Bufo americanus*, males found in amplexus were also larger than average. In repeated mate choice trials in the field, females did however not make consistent choices: only 22% of the pairings involved females that mated with the same male more than once (Howard & Young, 1998). Repeatability of choice for male body size was low and not significant (Table 2). In contrast to the Australian frog, more than half of the pairings in the American toad were male initiated. When only pairings that were observed to be initiated by the female were considered, repeatability improved but remained not significant due to low sample size (Table 2).

In preference or choice tests, responses are often scored as binary traits (1 for the choice of one male or trait and 0 for the alternative choice) (Table 2). It is quite surprising that in the literature on sexual selection such binary responses are not treated as threshold traits which they typical are. When a trait is dichotomous (yes/no), the threshold model assumes that the determination of this variation is a consequence of some underlying continuous trait (liability: Falconer, 1989). Individuals in which the liability exceeds some threshold value show a particular phenotype, whereas those below the threshold show the alternative. Because the liability is continuously distributed, it can be treated using the usual QG approach. Thus, when calculating repeatabilities for binary choices, we first compute the repeatability measured on the 0,1 choice scale, and then convert this to the repeatability of the mating preference by the formula (Lush *et al.*, 1948; Dempster & Lerner, 1950):

$$r = r_{0,1}p(1 - p)/z^2$$

where r is the repeatability measured on the underlying scale, $r_{0,1}$ is the repeatability measured on the 0,1 scale, p is the mean proportion in the population, and z is the ordinate on the standardized normal curve which corresponds to a probability p . The opportunity to detect genetic variation is at greatest at intermediate frequencies of the binary trait. The repeatability (and heritability) of binary traits on the 0,1 scale depends therefore on the frequency of the trait, being greatest at intermediate frequencies and

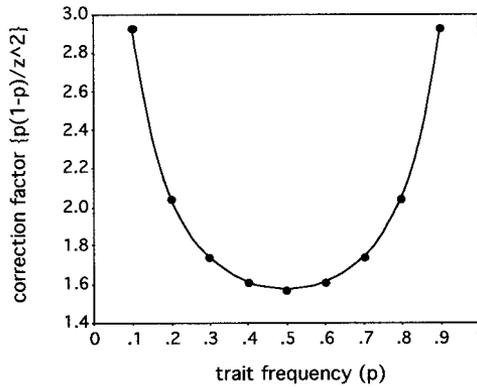


Fig. 6. Correction factor for heritability estimates of threshold traits as a function of trait frequency.

declining as one of the alternatives becomes more frequent. The repeatability (and heritability) of the underlying liability will not be frequency dependent. The factor by which $r_{0,1}$ has to be multiplied compensates for the frequency dependence of $r_{0,1}$; it is lowest (*i.e.* 1.57) for intermediate frequencies ($p = 0.5$), and increases as the binary trait becomes more biased in one or the other direction, *e.g.* 2.92 when $p = 0.1$ (Fig. 6; Dempster & Lerner, 1950). The above formula slightly overestimates the real repeatability (and heritability) (*e.g.* Dempster & Lerner, 1950; Garcia & Toro, 1989).

Illustrative for the binary scorings of female mating preferences are the recent studies of Howard and co-workers on mate choice for male body size in Japanese medaka, *Oryzias latipes* (Howard *et al.*, 1998), and on mating preferences for male vocal properties in American toads, *Bufo americanus* (Howard & Young, 1998). In both studies, most repeatability estimates were low because most females unanimously preferred one type of male (or trait), and not because females had weak preferences. However, the studies did not correct for the high chances to detect consistency of choice when the alternative choice is made infrequently in the whole population. The repeatability estimates therefore underestimate genetic variation of mating preference.

Consistency of mating preference and mate choice was investigated in 20 studies on 17 species (Table 2). Repeatability estimates were made for 12 species. In addition to estimate repeatabilities, additive genetic variance in mating preference were (and more reliably) estimated by various other

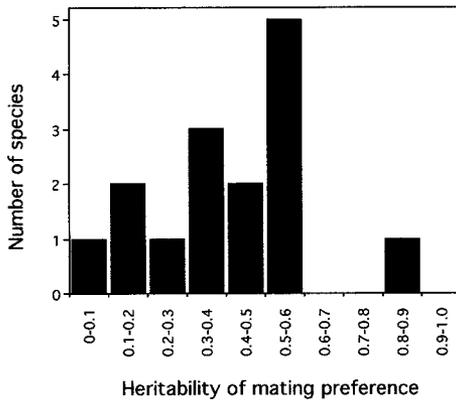


Fig. 7. Frequency distribution of heritability estimates of female mating preferences (15 species). Data from Bakker & Pomiankowski (1995) supplemented with new data.

methods. These included artificial selection for the preference or the preferred trait, resemblance of relatives, and differences between lines (Bakker & Pomiankowski, 1995). A total of 18 such QG studies were listed in Bakker & Pomiankowski (1995). Since then no further studies based on methods other than repeatability have been published. In only 3 of the 28 independent studies (species) no significant genetic variance in mating preference was measured (*i.e.* Boake, 1989; Ritchie, 1992; Poulin, 1994). In only 15 species heritability estimates of mating preference were made (Fig. 7). The mean estimate \pm SD was 0.41 ± 0.21 which is high for behavioural traits (*e.g.* Mousseau & Roff, 1987) but significantly lower than the high average heritability of sexually selected male traits ($t = 2.19$, $df = 43$, $p < 0.04$). It is at the moment unclear whether 0.41 is a biased estimate due to an overestimation of narrow sense heritability by calculating repeatabilities (11 of the 15 estimates) or due to an underestimation by not treating binary scored preferences as threshold traits.

Clearly more QG studies of mating preferences are needed to get a better and more reliable picture of the level of heritability and additive genetic variance. The estimates made so far suggest high heritabilities. One may speculate about the origin and maintenance of genetic variation in mating preferences. Can it be explained by condition dependence like Rowe & Houle (1996) and Pomiankowski & Møller (1995) suggested for male sexual traits? Their models would also apply to female mating preferences under the assumption that it is costly to be choosy. Costs could involve physiological

costs but also costs of mate choice. In males, condition dependence of sexual traits is well established (see above). There is also evidence for condition dependence of mate choice (see below), but there is a lack of studies about condition dependence of mating preferences. The problem with condition-dependent mate choice is that strategic decisions may come into play while mating preference need not be condition dependent. What is the evidence so far on condition-dependent mate choice and preference?

Only females in good condition can afford to mate according to their preferences when there are high costs of choice. In barn swallows, *Hirundo rustica*, for instance, attractive males mate with females with higher condition than less attractive males (Møller, 1994a). Similarly, mated female grasshoppers, *Eyprepocnemis plorans*, had a higher physical condition than unmated females (Martin-Alganza *et al.*, 1997). Such patterns may however be due to reasons other than actual female choice. Effects of search costs on mate choice have been documented in several species. For instance, in sticklebacks, *Gasterosteus aculeatus*, an experimental increase in the costs of choice like energetic costs increased the choice for less attractive males in a sequential choice situation (Milinski & Bakker, 1992). Thus with costs of choice, condition-dependent female mate choice is expected. In several insect species food (quantity or quality) affects mate choice (*e.g.* Gwynne & Simmons, 1990; Sih & Krupa, 1992; Schatral, 1993; Brown, 1997; Clark *et al.*, 1997; Kvarnemo & Simmons, 1998). Often these mating systems involve material benefits of choice.

Further suggestive data in the extensive literature on sexual selection relate female mating preferences to infection status in females. Poulin (1994) studied female preference for male body size in the upland bully, *Gobiomorphus breviceps*, in relation to infection of the females with the trematode *Telogaster opisthorchis*, a parasite that correlated negatively with physical condition. Females were scored for mating preferences in two successive simultaneous preference tests. Female preference correlated with parasite intensity: the higher the parasite load of the females the more they preferred the less attractive (smaller) males. Although overall consistency of preference between the two tests was low (Table 2), the data suggest that females with extreme parasite loads were more consistent: females with few parasites preferred the large male, and those with many parasites the small male. In brook sticklebacks, *Culaea inconstans*, females that were heavily infected by the helminths *Bunodera inconstans* and *Neoechinorhynchus*

rutili, courted for a longer period of time and more intense to an enclosed male than females with low infection levels suggesting that the former were more willing to accept a mate (McLennan & Shires, 1995). Studies of Kavaliers and co-workers (e.g. Kavaliers *et al.*, 1998) suggested that non-pathological infections (with the nematode parasite *Heligmosomoides polygyrus* or the protozoan parasite *Eimeria vermiformis*) can affect females' mice responses to male odours. A further suggestion of condition-dependent female mating preferences is female's body-size dependent preference in the African painted reed frog *Hyperolius marmoratus* (Jennions *et al.*, 1995). Recently, Bakker *et al.* (1999) assessed condition-related mate preferences in sticklebacks using computer animations.

The above-mentioned examples suggest at best that female mating preferences may be condition dependent, but direct tests are lacking.

Genetic correlations between preferences and preferred traits

QG is also needed to study another parameter of interest in sexual selection: the genetic correlation between female mating preference and preferred male trait. Given that there is genetic variation in preference and preferred trait, and that females mate according to their preferences, theoretically a genetic correlation between preference and preferred trait is built up due to linkage disequilibrium. Females' preference genes become genetically but not physically associated with the corresponding preferred sexual trait genes due to nonrandom mating; they are consequently transmitted together to the next generation. It is in this respect unimportant what the genetic benefits of female choice are: a genetic correlation is predicted when females mate with particular males both because of attractiveness genes for their male offspring (Fisherian sexual selection) or because of viability genes for their offspring that are revealed by attractiveness genes (good genes sexual selection). In the latter case, additionally a genetic correlation between the female's mating preference and male's viability are predicted (Iwasa *et al.*, 1991; Fig. 8).

The genetic correlation due to linkage disequilibrium is not a permanent association but only exists by virtue of nonrandom mating. When females are not able any more to mate with preferred mates, the genetic correlation is broken down again due to recombination. Alternatively, permanent associations between preferences and preferred traits may exist due to pleiotropic

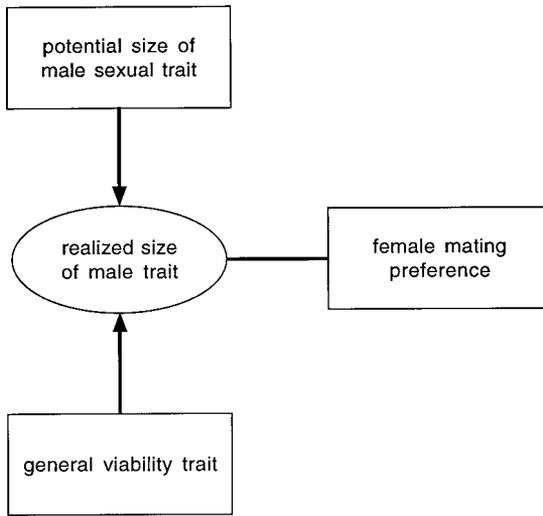


Fig. 8. Path diagram showing correlations between traits in the conditional or revealing handicap model. Females choose males through the realized size of the males' sexual trait. Females with stronger preferences prefer males with more pronounced traits, so there is a positive genetic correlation between preference and trait size. The realized size of the male trait depends on both the potential size of the male trait and the general viability trait. It is assumed that females can make a better assessment of the general viability trait as the potential size of the male trait increases. So there will be a positive correlation between female preference and both the potential size of the male trait and the general viability trait arising directly from female mate choice. After Iwasa *et al.*, 1991.

gene action, that is variation in mating preferences and preferred traits are (entirely or partly) influenced by the same genes. It has been proposed that signal production and reception may be controlled by similar neural mechanisms. There is however little evidence of this concept termed genetic coupling (reviewed by: Butlin & Ritchie, 1989; Boake, 1991). A probably more plausible common genetic control of preferences and sexual traits may occur via condition. Many sexual traits are condition dependent, and there is some evidence of condition-dependent expression of mating preferences as well (see above).

What is the evidence of the predicted genetic correlation between mating preferences and preferred sexual traits? Bakker & Pomiankowski (1995) recently reviewed the evidence from 11 studies in 10 species, 8 of which were insects. Since then no new cases have been published. Only in sticklebacks an estimate of the genetic correlation was made (0.75 ± 0.31 : Bakker, 1993). Bakker & Pomiankowski (1995) concluded: "Our survey shows that

a number of recent studies demonstrate the presence of genetic correlation in redbanded leafrollers, cockroaches, sticklebacks, stalk-eyed flies, guppies and seaweed flies. . . with some weaker evidence in fruitflies, pink bollworms and planthoppers. . .”. In four cases genetic covariance could not be demonstrated which could be the result of the loss of linkage disequilibrium due to recombination during the breeding experiments (Bakker & Pomiankowski, 1995). The theoretical prediction of a genetic correlation between preferences and sexual traits seems thus to be validated. Unclear in most but two cases is the nature of the genetic correlation. The decay of the genetic correlation in the course of a selection experiment on male coloration in guppies *Poecilia reticulata* (Houde, 1994) suggests linkage disequilibrium as a cause for the correlation, the more so as colour is Y-linked. In the seaweed fly *Coelopa frigida* both mating preference and sexual trait are in large part determined by inversion karyotype (no recombination occurs within the inversion) (Gilburn & Day, 1994). Here is physical linkage thus the cause of the correlation.

What next?

There are many possible routes for future QG studies of sexual selection. I have listed a few possibilities.

- (1) It is evident from the above review of QG data of sexual selection that more data are needed of genetic variation in mating preferences and genetic covariation between preferences and preferred traits. Assessment of the shape of female mating preferences (*e.g.* Schluter, 1988; Ritchie, 1997) would be an improvement compared to the usual two-way mate choices. The inclusion of characteristics of the shape of female mating preferences in QG studies is promising because they are more accurate measures of mating preferences.
- (2) More research should be focussed on condition dependence of mating preferences in order to test the condition-dependence hypothesis as an explanation for high genetic variance and genetic covariance with condition-dependent male traits (see above). Condition-dependent and condition-independent traits could be compared for QG parameters as a first test of the Rowe & Houle (1996) hypothesis. The study of genetic variance in condition is a topic that urgently needs more attention.

- (3) For the sake of independency of the data points in comparative statistical analyses, QG data of different male traits and female preferences have been averaged per species (see above). This may be adequate for statistical purposes, but there is no *a priori* reason why multiple traits and multiple preferences would have similar genetic variances. Within-species studies are needed that explore the QG of multiple sexual traits and multiple mating preferences. Recently, theoreticians have begun to explore the evolution of multiple ornaments (Pomiankowski & Iwasa, 1993; Schluter & Price, 1993; Iwasa & Pomiankowski, 1994; Johnstone, 1995b, 1996). No data are currently available about the genetic variances and covariances within and between the sexes of multiple traits and multiple preferences.
- (4) Good genes models of sexual selection predict a genetic correlation between female mating preference and male good genes like resistance genes or genes that promote immunocompetence (Iwasa *et al.*, 1991; Fig. 8). The establishment of this genetic correlation would be an ultimate test of good genes sexual selection.

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