

## Genetic Variation Underlying Sexual Behavior and Reproduction<sup>1</sup>

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**SYNOPSIS.** Selection depletes additive genetic variation underlying traits important in fitness. Intense mating competition and female choice may result in negligible heritability in males. Females often appear to choose mates, however, suggesting genetic variation in males which is important to females. Evidence is reviewed on allelic substitutions, karyotypic variation, and especially the heritable variation of continuous traits involved in sexual behavior and reproduction. Phenotypic variation in male mating speed and courtship intensity, female mating and oviposition behavior, egg size and number, body size, parthenogenesis, and the sex ratio generally have heritable variation. The maintenance of genetic variation, and the meaning of heritability estimates for natural populations is considered.

### INTRODUCTION

Some biologists have proposed that most traits affecting fitness are characterized by negligible genetic variation. In many cases, however, these predictions do not agree with results from direct measurements of genetic variation. I here review the relationship between genetic variation and selection with special reference to intraspecific variation in traits important in sexual behavior and reproduction. I consider the techniques used to measure heritable variation, the empirical results from selected examples of genetic variation underlying reproductive traits, the meaning and consequences of genetic variation, and the maintenance of genetic variation in natural populations. Heritability of traits of possible importance in fitness is an extensive subject. Grant and Price (1981) reviewed genetic variation underlying ecologically important traits, and Istock (1978, 1981) considered the heritability of insect development (see also Dingle and Hegmann, 1982).

### SELECTION AND GENETIC VARIATION

The rate of fitness increase in a population is proportional to the additive genetic variance for fitness (Fisher, 1958). Natural selection increases the frequency of alleles

advantageous to reproduction and survival, simultaneously depleting the underlying additive genetic variance. Population genetic models predict a reduction in additive genetic variance in response to selection, and that the intensity of selection and rate of depletion are correlated (Fisher, 1958; Turner, 1969; Crow and Kimura, 1970). Models of reduced additive variation under selection have underlying assumptions, but traits most important in reproduction and survival should have a lower amount of genetic variation than less important traits (Falconer, 1960; Futuyma, 1979).

### *The paradox of female choice*

Williams (1975), Howard (1978), Maynard Smith (1978), Harpending (1979), and Thornhill (1980a) predicted that female mating preferences would deplete genetic variation underlying traits important to male reproduction and survival. If so, female discrimination of mates will not result in further genetic advantages compared to females who mate at random. West-Eberhard (1979) also proposed that genetic models of female choice required unrealistic levels of heritable variation in males, and that competition for any limiting resource such as mates, oviposition or nesting sites, food, and shelter would largely involve non-heritable traits. Females of many species appear to choose mates from an array of males, however, suggesting that males differ in the heritability of traits important to females. Unless males

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provide resources to females, female choice is paradoxical if predictions regarding negligible heritable variation are correct (Borgia, 1979).

*Alternative reproductive modes and genetic variation*

Reduced genetic variation has important implications for alternative reproductive behavior. Variations in male behavior often involve signaling to attract and stimulate females, or silently intercepting females attracted to signaling males (Howard, 1978; Cade, 1979; and references in this volume). If female choice and male-male competition reduce heritable variation in male traits to negligible levels, then intraspecific variation in sexual behavior should not reflect additive genetic variation.

Males often change their signaling behavior in response to conditions such as density, aggression, and individual age. To some, flexibility in behavior and genetic variation are antithetical: "selection under strong local intraspecific competition should favor a facultative (rather than genetic) switch," since individuals able to change their behavior maximize fitness under various conditions (West-Eberhard, 1979; see also Rubenstein, 1980; Thornhill, 1980a; and Waltz, 1982). Facultative alternatives and underlying genetic variation are not mutually exclusive possibilities, however, and individuals may differ in the tendency to change behavior under different conditions. Cade (1980), Dawkins (1980), and Dominey (1984) discussed facultative alternatives in terms of evolutionarily stable strategies.

GENETIC VARIATION AND  
REPRODUCTIVE TRAITS

Genetic variation associated with traits important in reproduction may be detected as allelic differences at one or many loci, and inversions and other variations in chromosome structure. In this section I first discuss the experimental techniques used to study heritable variation, and review examples from vertebrates and invertebrates on the heritability of behavioral and morphological traits associated with sexual behavior and reproduction. I then con-

sider the meaning of heritability estimates for natural populations, and the mechanisms maintaining additive genetic variation.

*Heritability and continuous variation*

Most traits important in fitness are continuously distributed and are probably under the influence of many loci (Falconer, 1960; Crow and Kimura, 1970). Some examples of continuously distributed traits of potential importance in reproductive and sexual behavior include size, weight, color, duration or intensity of signaling, and number of gametes produced. Heritability is a measure important in the context of continuous traits, but it is often misunderstood with respect to measurement or interpretation. Analysis of variance techniques allow environmental and additive genetic variation underlying a trait to be identified. Heritability in the "broad sense" is the proportion of phenotypic variance due to genetic variation. That proportion of variation due to additive genes is termed "heritability in the narrow sense," and may be determined by crosses of inbred strains (diallel crosses), and analysis of variance on measurements between different types of relatives. The upper limit of heritability can be estimated by repeated measurements of the same trait in the same individuals (repeatability). "Realized heritability" is the proportion of phenotypic variance due to additive loci as determined by response to artificial selection to change phenotypic means. Heritability may range from 0 to the theoretical maximum of 1, although estimated values sometimes exceed 1. All heritability measurements incorporate statistical tests of significance, and rely on assumptions which limit interpretive value (Falconer, 1960). These aspects of heritability are considered more fully later.

*Sexual vigor, courtship, and mating propensity*

Vigor is the strength, intensity, and rate of performance of a behavioral pattern. In a sexual context vigor may be characterized as frequency of courtship, mating, and associated activities. Vigor is often involved

in successful competition, and is sometimes proposed to have negligible heritable variation (West-Eberhard, 1979; Thornhill, 1980a). Karyotype data, single allele substitutions, and studies of quantitative traits, however, indicate genetic variation is often correlated with variation in sexual vigor.

Substitution of alleles at a single locus may cause *Drosophila* males to depart from the normal mating sequence in various ways. The "cacophony" mutation, for example, causes males to change the normally species-specific rate of wing vibration during courtship (Schilcher, 1977). Other mutations result in increased courtship of males, inability to mount or dismount females, and reduced duration of copulation (reviewed by Hall, 1981). Single allele changes also affect female receptivity in mosquitos, *Aedes atropalpus*, where affected individuals mate at an early age (Gwadz, 1970).

Mating speed is probably the most important factor affecting male fitness in *Drosophila* (reviewed by Parsons, 1974). Rapidly mating males mate more frequently and leave more offspring than slowly mating males (Prakash, 1967). Male mating speed is correlated with inversions of the third chromosome in *D. pseudoobscura* (Speiss and Langer, 1964), and Dobzhansky (1943, 1958) demonstrated that inversion frequencies varied seasonally for over 20 yr, suggesting selection was taking place. Anderson *et al.* (1979) compared the frequency of male third chromosome inversions in *D. pseudoobscura* with that of offspring from females inseminated in the field. There were significant differences between male and offspring karyotypic frequencies, indicating differential male mating success. Karyotypes varied between localities and months, with a change of 20–30% in some combinations annually. The rarest karyotypes persisted in sample populations, suggesting genetic variation was maintained under selection.

Heritability studies show that additive genetic variation is associated with *Drosophila* mating speed. Diallel crosses demonstrated a heritability of 0.3–0.6 for mating speed (Parsons, 1964), and Manning (1961) showed a realized heritability of 0.3

in selection experiments lasting 25 generations in *D. melanogaster*. Flies from the fast line mated in 3 min on average, whereas 80 min was the mean mating time for the slow line. Females from the fast line were more receptive to male courtship than females from the slow line. Males from the fast line courted females more often than slowly mating males. Reduced mating speed may also be produced by artificial selection on only one sex or the other in *D. melanogaster* and *D. simulans* (Manning, 1963, 1968).

Selection on duration of male courtship behavior in *Drosophila* (rather than mating speed) has resulted in lines with males which vibrate and scissor their wings differing amounts (McDonald, 1979; Wood and Ringo, 1982). Artificial selection has also changed *Drosophila* female receptivity to particular male phenotypes (Dow, 1976), and the latent period of female receptivity (Pyle and Gromko, 1981). *Drosophila* mating speed is affected by artificial selection on non-reproductive traits such as geotaxis (Pyle, 1978), and genetic strains differ in their sensitivity to the same environmental factor (Ikeda, 1976). Speiss (1970) reviewed the genetic basis of mating propensity in *Drosophila*.

Field cricket males, *Gryllus integer* (this species is under taxonomic revision), call and attract mates or silently intercept females near calling males. Duration of individual calling is continuously distributed, and population density, male-male aggression, and time of night affect individual calling time (Cade, 1979). Laboratory experiments demonstrated realized heritability of approximately 50% for the duration of nightly calling (Cade, 1981). Also, laboratory lines of males differed significantly in nightly calling duration in the selected directions under field conditions (Cade, unpublished data).

Male mating speed has a significant heritability in chickens and quail (Siegel, 1972; Cunningham and Siegel, 1978). Diallel crosses show heritabilities of 0.1–0.2 for the time from one mating until the next in lab mice, and for the time from intromission to ejaculation (McGill, 1970). General activity, aggressive behavior, and other

aspects of vigor have heritable variation in mice (Scott, 1966; DeFries and Hegmann, 1970; Southwick, 1970), and some of these traits may be involved in sexual selection.

#### *Morphological variation*

Body size is often involved in mating competition. Large male bees, *Centris pallida*, patrol female emergence sites, while small males hover nearby. Patrolling males mate more often than hoverers (Alcock, 1979). Large male spiders, *Nephila clavipes*, mate near the hub of a female's web, whereas small males occur on the periphery and seldom mate (Christenson and Goist, 1979). Male size or weight correlates with mating success in other bees and wasps (Alcock, 1981; Severinghaus *et al.*, 1981), flies (Thornhill, 1980*b*; Borgia, 1981, 1982), and beetles (McLain, 1981; Johnson, 1982). Heritability of size is not known in these species. It is sometimes asserted that body size does not show heritable variation (West-Eberhard, 1979; Thornhill, 1980*a*), but studies on various animals demonstrate additive genetic variation is often associated with body size.

Large male *Drosophila* outcompete and mate more often than smaller males (Ewing, 1961). Realized heritabilities for wing length, thorax length, and the ratio of wing to thorax length in *D. melanogaster* are 0.4–0.5 (Reeve and Robertson, 1953; Latter and Robertson, 1962; Robertson, 1962). Body size has a realized heritability of 0.3–0.4 (Robertson 1957, 1960). Developmental rate, a parameter related to body size, has a realized heritability of 0.1–0.2 in *Drosophila* (Sang and Clayton, 1957; Sang, 1962; Prout, 1962).

Heritability of body size or weight has not been studied in other species where this trait is of known importance in sexual competition. Parent-offspring comparisons of body size in field populations of some species do exist, however. Boag and Grant (1978) found heritabilities in Darwin's finches, *Geospiza fortis*, of 0.5–1.0 for adult body weight, and wing, tarsal and bill measurements. Beak and tarsal lengths in song sparrows, *Melospiza melodia*, have heritabilities of 0.3–0.6 (Smith and Zach,

1979), and body weight at 75 days of age in Red Grouse, *Lagopus lagopus*, has a heritability of 0.6 (Moss and Watson, 1982).

Laboratory experiments also show additive genetic variation underlying animal body size. Flour beetles, *Tribolium castaneum*, have realized heritabilities of 0.2–0.7 for pupal weight, and 0.4–1.0 for larval and adult weight (Enfield, 1977; Bell and Burris, 1973; Kaufman *et al.*, 1977). Developmental rates have a realized heritability of 0.2–0.4 in *Tribolium* (Bell and Burris, 1973). True bugs, *Dysdercus bimaculatus*, have a heritability of 0.5 for body size in parent-offspring comparisons (Deer, 1980). Size also has a realized heritability of 0.1–0.2 in mice (MacArthur, 1949; Rahnefeld *et al.*, 1963).

Intraspecific variation important in male mating success sometimes involves coloration. In some Canadian populations of three-spined sticklebacks, *Gasterosteus aculeatus*, male throats range in color from dull to bright red. Females prefer brightly colored males (Semler, 1971), but red males are more susceptible to trout predation (Moodie, 1972). Intermediate coloration was produced in crosses between phenotypes, thus suggesting underlying additive genetic variation for male coloration involved in sexual selection (McPhail, 1969).

Substitution of single alleles results in morphological differences in *Drosophila*. Variations in color, texture, and eye shape result from allelic substitution. Ehrman (1978) reviewed the effects of morphological variation on male courtship behavior and mating success in *Drosophila*.

#### *Egg production, nesting, and oviposition*

Egg size affects survival to fledging in some birds (Schifferli, 1973; Davis, 1975; Lundberg and Vaisanen, 1979). Survival of Red Grouse chicks, *Lagopus lagopus*, correlates with egg size, but is largely independent of known environmental variation (Moss *et al.*, 1981). Repeatability measurements and regressions on measurements between relatives demonstrate a heritability of 0.6–1.2 for egg size in field popula-

tions of Red Grouse (Moss and Watson, 1982). Significant heritability of egg size has also been shown in Great Tits, *Parus major* (van Noordwijk *et al.*, 1981b).

Clutch size results from a complex interaction of environmental and ontogenetic factors (Klomp, 1970), and models of clutch size evolution assume heritable variation (Lack, 1968). A 20 yr study of Great Tits, *P. major*, shows that the number of fledglings generally increases with clutch size, suggesting selection on egg number. Heritability estimates from repeatability measurements and regressions on mother-daughter-grandmother clutch sizes are approximately 0.4 (van Noordwijk, 1981a). Heritability for clutch size in other Great Tit populations is 0.4–0.5 (Perrins and Jones, 1975). Additive genetic variation is also associated with the rate of egg production in domestic fowl (King and Henderson, 1954; Nordskog *et al.*, 1967).

Hatching synchrony relative to other birds in a colony affects individual fitness, and is a function of egg laying date. Lesser Snow Goose chicks, *Anser caerulescens*, have maximum survival rates if they hatch at the mean date for the population. Chicks hatching a few days before or after the mean date have significantly lower survivorship. Female geese breed at natal sites, and repeated measurements of 3,000 individuals over 6 years gave estimates of 0.4–0.5 for relative hatch date heritability (Cooke and Findlay, 1982; Findlay and Cooke, 1982a, b).

Types of nests or oviposition sites might often affect fitness. Nest size, for example, is important in thermoregulation in house mice, *Mus musculus* (Lynch and Possidente, 1978). Diallel crosses and selection experiments demonstrated heritabilities from non-significant levels to 0.3 for the amount of material incorporated into nests by *M. musculus* females (Lynch and Hegmann, 1972; Lee, 1973; Lynch, 1980). Differences in the type of surface preferred by ovipositing *D. melanogaster* (Takamura and Fuyama, 1980), and in the tendency for *D. pseudoobscura* to oviposit gregariously have underlying additive genetic variation (Del Solar, 1968).

#### *Sex ratio and parthenogenesis*

Models of sex ratio evolution assume some genetic influence (Bulmer and Bull, 1982). Sex ratio in *Drosophila* is affected by X chromosome inversions. Male *D. pseudoobscura* with the sex ratio trait produce mostly female offspring. The sex ratio trait shows latitudinal and seasonal fluctuations, and has persisted in field populations for over 20 yr (Dobzhansky, 1943, 1958; Bryant *et al.*, 1982). Falconer (1954) reviewed evidence for additive variation in the sex ratio of mice and *Drosophila*, including cases where heritabilities were non-significant.

Parthenogenetic individuals frequently occur in otherwise sexual populations of *Drosophila* and other insects, a condition known as tachoparthenogenesis. Parthenogenetic individuals are more common in field populations than in the lab, undergo meiosis and fusion of ootids to form diploid eggs, and are probably important in the evolution of parthenogenesis (Templeton, 1982). Experiments have increased the number of parthenogenetic females in selected lines of *D. mercatorum*, suggesting there is additive genetic variation underlying parthenogenetic reproduction (Carson, 1967).

There is also additive genetic variation for the sex ratio in fish (Kosswig, 1964), and in species with environmental sex determination. In Map turtles, *Graptemys ouachitensis*, males hatch from eggs kept at low temperatures, females at high temperatures, and both sexes are produced at intermediate temperatures. Parent-offspring comparisons of the primary sex ratio of eggs incubated at intermediate temperatures showed a heritability of 0.8 in the laboratory (Bull *et al.*, 1982).

#### *Estimates of heritability and meaning*

Heritability estimates do not provide information on the fate of genetic variation, but they do test the null hypothesis that genetic variation underlying a trait is negligible. Studies reviewed here reject this hypothesis for traits involved in sexual behavior and reproduction which may be

important in fitness. Field studies and laboratory studies on animals taken from the field demonstrate the presence of genetic variation. Genetic variation is even present in highly inbred laboratory strains, although these conditions reduce genetic differences (Shire, 1979). Traits important in sexual and reproductive behavior respond to artificial selection and may also respond to sexual selection or other forms of natural selection.

Interpretation of data on genetic variation for selection in field populations is difficult. Single allele substitutions have major effects on male and female reproductive behavior in laboratory populations of *Drosophila*, but the frequency of such alleles in natural populations is unclear. Chromosome data from *Drosophila* and other species do not have this limitation. Karyotypes fluctuate in frequency, affect male mating speed, and provide evidence of differential male mating success in the field. Karyotype data demonstrate persistence of genetic variation under sexual selection. Chromosomal analysis provides only gross estimates of genetic variation, however, and may not be a suitable technique for many species.

Interpretation of narrow sense and realized heritability estimates is complicated by assumptions of quantitative genetic models and the commonly observed variation in replicated experiments (Yoo, 1980). Phenotypic variation includes genetic and environmental components. Heritability measurements often assume that the environment interacts with all genotypes in the same way. Selection experiments are performed under controlled conditions, but it is unlikely that environment and genotype interactions are constant. Also, estimates of heritability under controlled conditions in the laboratory may be greater than heritabilities determined in a fluctuating, natural environment. Effects of the environment on different genotypes can be measured by heritability estimates under different environmental conditions (Thoday, 1979; Giesel *et al.*, 1982).

Heritability calculations generally assume that each locus has a small additive effect, and that the non-additive components of dominance and epistasis are minimal.

Although additive effects are the main source of phenotype-genotype correlation, dominance and epistasis are also important. Non-additive sources of variation may change the mean effects of additive loci, and therefore result in variable responses to artificial selection in different lines or replicates and lead to incorrect estimates of heritability (Jinks, 1979; Johnson, 1979). Other factors which may lead to variation in estimates of heritability are genetic drift, mutation, and natural selection within experimental populations which oppose artificial selection (Hill, 1971, 1977; Jinks, 1979; Mukai, 1979). Statistical techniques are available to partition total phenotypic variance into additive, non-additive, and environmental components (Mather, 1949; Lerner, 1958; Falconer, 1960; Mather and Jinks, 1971).

Pleiotropy, or the multiple phenotypic effects of alleles, is important in the context of heritability. Little is known about gene action in polygenic systems. Correlated responses to selection are due to linkage, but also to the multiple effects that loci have on biochemical processes and protein synthesis (Johnson, 1979). Polygenes are not specific for any character being measured, but affect underlying developmental processes shared by other characters. There is, for example, extensive pleiotropy between egg laying at different ages, rate of egg laying, and longevity in *Drosophila melanogaster* (Rose and Charlesworth, 1980). Although it is convenient to describe selection for a particular character, selection on all phenotypic characters associated with alleles is important in altering genetic variation (Lande, 1979; Thompson, 1979).

Estimates of additive variation are generally valid for the particular population and generation under study. Replicated tests and the use of different experimental techniques are advisable (Falconer, 1977). Although heritability is affected by experimental and genetic conditions, properly designed experiments provide the only estimate of additive genetic variation which may be available for selection (Richardson *et al.*, 1968; Thompson and Thoday, 1979). Such experiments demonstrate that additive genetic variation underlying sexual

behavior and reproduction is the rule, rather than the exception.

#### *Maintenance of variation*

The question of how genetic variation is maintained in natural populations has received extensive empirical and theoretical attention. Genetic mechanisms and fluctuations in the intensity and direction of selection are involved in the maintenance of additive variation. Depleted variation is usually predicted from single or few locus models, but the rate of depletion is inversely proportional to the number of loci (Crow and Kimura, 1970). Allelic substitutions and independent segregation of multiple loci result in many possible genotypes. Additive genetic variance will be reduced slowly in polygenic systems, and is likely to be retained at some level unless the population size is small and selection intense (Crow and Kimura, 1970; Bulmer, 1971). Mutations also contribute to genetic variance. Lande (1976*a*, 1977) showed that mutation rates could account for much additive genetic variation in multiloci regardless of the mating system, and Maynard Smith (1978) considered mutations to be a likely source of male genetic variation available for female choice (but see Taylor and Williams, 1982).

Linkage disequilibrium is the association of alleles in gametes at different frequencies than expected from random segregation. Selection may increase one allele's frequency, but act against other alleles in disequilibrium (Bulmer, 1971; Futuyma, 1979). Taylor and Williams (1982) considered linkage disequilibrium to be the most likely source of genetic variation in natural populations, and that heritabilities in the range of 33% could be maintained by disequilibrium.

Predictions on the reduction of additive genetic variation assume that selection operates at some constant level. Selection is not often constant, however, and genotypes do not have constant fitness values (Kojima, 1971). Intensity and direction of selection on the total phenotype may vary because of population density, frequency of competing phenotypes, and temporal or spatial variations in the environment (Clarke, 1979). Different selective pres-

ures in variable environments are probably responsible for much genetic variation (Beardmore, 1970; Selander and Kaufman, 1973; McDonald and Ayala, 1974). Selection for particular phenotypes may also be countered by predator or parasite pressure on those phenotypes (Cade, 1975; Lande, 1976*b*).

Parasites might conserve genetic variation in hosts in other ways. Hamilton and Zuk (1982) reasoned that females choose males whose vigorous displays correlate with absence of parasites. Resistance to parasites shows heritable variation, and parasite-host cycles may maintain additive variation. Hamilton and Zuk assumed negligible heritability of male sexual traits. Female choice based on parasite resistance is an interesting and important possibility, but this hypothesis is not essential to account for additive genetic variation associated with traits affecting male fitness.

Variation in intensity and direction is well documented for natural selection. Some argue, however, that sexual selection is fundamentally different from natural selection since male reproductive success varies more than survivorship. For example, very few males in a population may reproduce due to female choice for particular traits. Male survivorship may be high, however, if other resources are not limiting. West-Eberhard (1979) proposed that natural selection would be relaxed under intense sexual selection. Relaxation of natural selection would thus provide the genetic variation essential for evolution of non-reproductive traits such as foraging ability. This type of strict separation of sexual and natural selection is without merit, however, and ignores extensive pleiotrophic relationships in the genome. Also, various selective agents interact in producing the phenotype (Otte, 1979).

#### MAGNITUDE OF VARIATION

Both the existence and relative magnitude of additive genetic variation are important considerations. There is a general trend for traits important in fitness to have relatively lower heritabilities than traits without high fitness value (Falconer, 1960). Important exceptions exist to any correlation between heritability and fitness

value of a trait, however, and many comparisons rely on data from inbred strains. Comparisons of heritabilities are also complicated by experimental and genetic factors discussed previously.

If heritability is negligible, then male-male competition and female mate choice will not change gene frequency over time. But additive genetic variation as judged by the best techniques available is almost always non-zero. Even in traits with low but statistically significant heritabilities, artificial selection usually alters phenotypic means. Additive genetic variation underlying reproductive traits is probably generally available for selection through male-male competition, a well documented mode of sexual selection.

Female ability to mate with males who pass on beneficial additive loci to offspring is more difficult to assess. Since females appear to choose mates in various species, Maynard Smith (1978) proposed that even very low levels of additive genetic variation would make female choice adaptive. Taylor and Williams (1982), however, suggested that heritabilities in the range of 0.3 were not sufficient for evolution by female choice. Quantitative models are not available on the degree of heritability necessary to allow female detection, and there are few experimental data available. In a rare exception, *D. melanogaster* females which were allowed to choose mates produced more offspring than females who were randomly assigned males. Productivity values were repeatable and highly significant. The two female groups differed by only about 2% (Partridge, 1980), suggesting that small genetic gains were made by the choosing group. Also, heritability of larval developmental rates in *Drosophila* is not high, and this trait may have been involved in Partridge's experiments. Female *Drosophila* appear to be able to detect and benefit from mate choice based on relatively low heritabilities.

#### CONCLUSION

Heritable variation is often associated with traits involved in sexual behavior and reproduction, and many of these traits may be important in determining fitness. Re-

liable predictions about reduction of additive genetic variation in natural populations cannot be based on simple quantitative models with unrealistic assumptions. Dynamic genetic models are now becoming available, however, which incorporate age-structured populations, polygenic inheritance, and variations in selective pressures (Lande, 1980, 1981, 1982a, b). Data are available on heritable variation to test genetic models, but most studies of genetic variation are conducted independently of field studies on behavioral and morphological variation. Long range studies of heritable variation and selection in field populations are needed. Claims of negligible heritability underlying traits important in fitness, however, ignore much empirical evidence, as well as quantitative treatments on the maintenance of additive genetic variation.

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