Repeatability: its role in evolutionary studies of mating behavior

CHRISTINE R. B. BOAKE

Hawaiian Evolutionary Biology Program, The University of Hawaii, 1993 East-West Rd, Honolulu, HI 96822, USA

Summary

Repeatability, a concept derived from quantitative genetics theory, is a statistic that describes the degree to which variation within individuals contributes to total variation in a population. Its usual application has been to set an upper limit on heritability but it may also be useful for studies of stereotypy of behavior. The repeatability of the production of male mating signals gives information both about whether males differ sufficiently for selection to act and whether the differences could be appreciably heritable. Measures of the repeatability of female mating preferences will provide data that can describe the preference functions used in mathematical models of the evolution of sexually selected traits, as well as putting an upper bound on the heritability of preferences. A survey of the few measures in the literature shows that the repeatability of male signal production varies substantially (range 0.21 – 0.85) and does not necessarily reflect heritability. The repeatabilities of female preferences have not been published previously: for the response to conspecific pheromones by female flour beetles (*Tribolium castaneum*), my best estimate is zero. Measuring the repeatability of other traits such as parental care and foraging behavior may also lead to insights about selection on and the evolution of these traits.

Keywords: Repeatability; sexual selection; mating behavior; evolution; communication; female preferences.

Introduction

The evolution of behavior, like the evolution of any trait, is a result of both selection on phenotypic variation and inheritance of the variants (Fisher, 1958). Although published studies of the evolution of behavior have emphasized analyses of the factors that impose selection on behavior, the role of inheritance is receiving increasing attention. A serious obstacle to examining genetic factors in the evolution of behavior has been the difficulty of making measures of heritability that could be relevant to natural populations. Estimates of heritabilities can rarely be made in field studies (but see Boag, 1983; Findlay and Cooke, 1983), but many field workers can make repeated observations of the behavior of marked individuals. Therefore they have the opportunity to measure a parameter which puts an upper limit on heritability, the repeatability of behavior (Falconer, 1981, defined below).

Accurate statements about the selective value of a behavior pattern and about its inheritance can only be made if one understands how variable that behavior is both within and between individuals. Yet these measurements have rarely been published for evolutionarily important behavior. One reason for this lack may be the desire to be sure that all measures are independent, which leads to an emphasis on avoiding repeated measures of individuals. Repeatability may be a particularly useful measure of variation for behavioral ecologists because of its relationship to

heritability. Although the relationship is not sufficiently close to allow substitution of repeatability for heritability in equations for evolutionary change (Falconer, 1981), repeatability allows an evaluation of the feasibility of measuring heritability. It also provides a readily understood measure of stereotypy, which is central to analyses of selection, as will be discussed.

Mating behavior is a topic which has received substantial recent attention as a consequence of quantitative genetic models of its evolution (reviewed in Bradbury and Andersson, 1987). The models make numerous assumptions about the nature of inheritance of male signals and of female preferences. Although the genetical assumptions may be difficult to evaluate directly, phenotypic analyses of repeatability can allow estimates of the validity of some of the assumptions, as is described below. This paper begins with definitions of repeatability and heritability, followed by a discussion of the repeatability of mating behavior. I shall consider both the inheritance of behavior and selection for certain patterns. I intend to demonstrate that by using a perspective which allows considering the repeatability of the behavior under analysis, new evolutionary insights may be gained.

Repeatability and heritability

Repeatability indicates the proportion of total variation in a trait that is due to differences between individuals (Falconer, 1981). It is based on repeated measures of the same individuals followed by an analysis of variance. Its computation is thoroughly discussed, with examples, by Lessells and Boag (1987). The necessary analysis of variance, sometimes referred to as model II (Sokal and Rohlf, 1981), is designed for the estimation of components of variance rather than strictly for hypothesis testing. Repeatability is defined as:

$$r = \frac{V_g + V_e}{V_t}$$

where V_g is the genotypic variance, V_e is the general environmental variance, and V_t is the total phenotypic variance. Genotypic plus general environmental variance are the between-individual component of variance, and total variance includes the within-individual component as well. Heritability (in the narrow sense) is:

$$h^2 = \frac{V_a}{V_t}$$

where V_a is the additive genetic variance (Falconer, 1981). The total genotypic variance, V_g, may be larger than V_a if non-additive effects such as dominance influence the character. Thus, the numerator for heritability can never be larger than that for repeatability (unless sampling errors result in inaccurate estimates of repeatability), and repeatability may often overestimate heritability. In computations of repeatability, relationships between individuals need not be known, so the two components of the numerator are not distinguished. Because heritability measures are made on individuals of known relationship, the additive genetic component of variance can be estimated to form the numerator. Lessells and Boag (1987) point out a major pitfall in the computation of repeatability: if mean squares are used rather than components of variance, repeatability will be overestimated.

The role of heritability in equations for evolutionary change has been developed in detail (Falconer, 1981, ch. 11; Lande, 1976, 1981). The change in phenotype between generations can be predicted by multiplying the heritability of a trait by the selection differential on that trait. Low heritability will result in slow evolution (little change in a phenotype from generation to

generation), even if a trait is subject to strong selection. Repeatability can be used to indicate whether efforts to measure heritability are likely to be worthwhile. The algebraic definitions of repeatability and heritability show that low repeatability cannot accompany high heritability, unless small sample sizes have resulted in erroneous estimates. Low repeatability puts a low ceiling on heritability. A knowledge of repeatability allows one to estimate the sample size that will be necessary for making proper measures of heritability, and it will help in developing the breeding design that minimizes the standard error for the work involved (Falconer, 1981; Shaw, 1987). It may not be possible to bound estimates of substantial heritability away from zero if the sample size is too small or if random noise is too high. If the heritability of some behavior is likely to be low, the effort necessary to estimate it accurately may be extremely time-consuming and expensive. Thus, preliminary measures of repeatability are useful to identify traits which could be amenable to genetic analysis.

High repeatability indicates that repeated measures of the same individual have substantially less variation than measures of different individuals. High repeatability may accompany high heritability, in which case environmental variation is low and most of the genetic variation is additive in nature. The cause of repeatability being substantially higher than heritability could be that environmental variation is high, or that non-additive variance (such as dominance effects) makes a major contribution to genetic variance. A combination of high repeatability and low heritability could indicate that a trait has been under strong selection in the past and is still closely associated with fitness. The strong past selection would reduce additive genetic variance and increase the role of dominance variance (Mather and Jinks, 1971). The continued need to perform the behavior in a very specific way could select for high repeatability within each generation even if the trait could no longer improve between generations.

Repeatability can be low for two reasons because it is computed as a ratio. First, the numerator can be relatively small, which will occur if all individuals are very similar. The similarity might be attributable to either genetic or environmental effects, but further experimentation would be necessary to understand the relative influence of each effect.

A second cause of low repeatability is a relatively large denominator, which is a consequence of environmental influences. These influences may arise when behavior is measured in conditions that are insufficiently controlled. Factors such as temperature, diurnal rhythms, or hormonal state could affect an animal's performance. If the organism's behavior is highly sensitive to random environmental fluctuations, the behavior would only susceptible to appreciable evolutionary change if the natural environment lacked such randomness. On the other hand, if low repeatability can be traced to some cause such as a hormonal cycle, the effect can be controlled, and repeatability might increase with more careful measurement. Repeatability could also be low if learning occurred between successive measurements of the behavior: activities such as nesting success or foraging appear to improve with experience, so they might show low repeatability.

In the case of learning or in cases where context strongly influences behavior, repeatability may not be a useful measure, because it is only defined if the trait that is being re-measured is indeed the same as before. For example, successive measures of body size in adult birds (e.g. Boag, 1983) are likely to be measurements of the same trait, but measurements of wing length in nestlings and fledglings may be of different traits. The issue of whether successive measurements represent different traits or the same trait is still being debated. Cattle breeders do not agree whether milk yield in successive lactations should be considered as repeated measures of the same trait or not (White *et al.*, 1981).

It is often possible to increase repeatability by experimental manipulation. In some cases in which repeatability is low, for example when undetected hormonal cycles influence behavior,

control of environmental variation during measurement might allow a more accurate assessment of repeatability. However, environmental variation may often be high in natural populations. If the goal of the measurement of repeatability is to make inferences about selection or evolution in natural populations, then experimental control may be inappropriate. In some cases, experimental control aimed at increasing repeatability might create a character that could not exist in nature.

Repeatability, consistency and selection

Repeatability is directly useful as a measure of the within-individual consistency of displays and other aspects of behavior. Only traits that are manifested consistently within individuals as well as differing between individuals can respond to selection. Sexual signals are often assumed to be

Table 1. Repeatabilities and heritabilities of traits that are used during mate attraction or courtship. Standard errors are provided where published.

Organism	Trait	Repeatability	Heritability	Reference
Chorthippus brunneus (grasshopper)	chirp length	0.56	0.28	Butlin and Hewitt, 1986
	syllables per chirp	0.56	0.10	Butlin and Hewitt, 1986
	peak amplitude	0.21	−0.09	Butlin and Hewitt, 1986
	chirp interval	0.40	0.06	Butlin and Hewitt, 1986
	syllable length	0.25	−0.21	Butlin and Hewitt, 1986
Gryllus integer (field cricket)	proportion of calls with long bouts	0.85	0.75±0.25	Hedrick, 1988; pers. comm.
Yponomeuta padellus (ermine moth)	quantities of components of pheromone blend	0.59–0.77[a]		Du *et al.*, 1987[b]
Harpobittacus nigriceps (scorpionfly)	prey size	0.47		Thornhill, 1983[b]
Gasterosteus aculeatus (stickleback)	territorial aggression	0.62	0.23±0.05	Bakker, 1986[c]
	courtship aggression	0.54	0.52	Bakker, 1986[c]

[a] Range of values for five components of the blend.
[b] Re-computed from published data, using the method of Lessels and Boag (1987).
[c] An estimation of narrow-sense heritability based on analyses of full sibs; realized heritabilities after selection for lowered aggression were the same as those computed from the sib analyses, and zero after selection for increased aggression.

stereotyped, but their repeatabilities (Table 1) are often much lower than those for morphological traits (Falconer, 1981, Table 8.3; Boag, 1983, Table 1). Finding significant differences between individuals does not indicate that repeatability will be high: for salamander feeding behavior, which had been assumed to be stereotyped, repeatability of components of the gape ranged between 4% and 63%, although all components showed significant differences between individuals (Shaffer and Lauder, 1985). The proportion of courtship devoted to wing fanning differs significantly between male *Drosophila silvestris*, but repeatability of this act is only about 22% (my unpublished data). Such disparities are possible because the components of variance from which repeatability is computed are often smaller than the corresponding mean squares which are used in significance tests.

Very few of the published data on behavior are described in a way that allows the reader to distinguish variance due to differences between individuals from that due to changes in one animal's behavior. This problem of confounding the two sources of variation has been discussed from a statistical point of view by Machlis *et al.* (1985). It is a serious error if used in discussion of the evolution of behavior because random within-individual variation diminishes the maximum detectable heritability, whereas between-individual variation is available for the action of natural or sexual selection.

Repeatability of male displays

The rate of evolution of a display depends on both the heritability of the display and the strength of selection on it. When a male's mating display has low repeatability, not only will it have low heritability, but also it may not confer mating success on the male. This is because the more likely a male's signal is to deviate from the mean of the females' preferences (discussed later), the less likely he is to mate. Both the mean value of the signal that a male produces and the variance around that mean will influence his mating success. The question of repeatability of mating signals is similar to the issue of comparing short-term studies of reproductive success with lifetime studies: if a male's signal allows high mating success one season, does it have the same structure in other seasons, and (all other things being equal) does it continue to be associated with success? Repeatability could be used to describe the consistency of a male's signal across days, seasons, years, or any other circumstance that may be relevant.

In some cases repeatabilities have been published for behavior patterns which are associated with male mating success (Table 1). Gibson and Bradbury (1985) and Hedrick (1986) identified acoustic signals which are correlated with male mating success and demonstrated that males are consistent in the nature of the signal produced, but in neither case were the results expressed in terms of repeatabilities. When the estimation of heritabilities is possible (Zeh, 1987; Hedrick, 1988), they are obviously preferred over repeatabilities, but for many species, the reporting of repeatabilities would provide a standard measurement of individual consistency.

It will be difficult to measure the repeatabilities of signals which are dependent on context for their form. The call rates of anuran amphibians and crickets are temperature-dependent (Walker, 1975), so the repeatability of male calls will be low if temperature is not taken into account. But in these species, female sensory systems appear to be similarly temperature-dependent (Gerhardt, 1982). Consequently, the male variation may well be biologically meaningful. In such cases, repeatability could be measured for a given temperature (e.g. Hedrick, 1988). A more ambitious approach might be to determine the slope of the regression of signal rate on temperature for each male, and compute the repeatability of that measure. If repeatabilities were measured separately for several temperatures, it would be possible to learn whether the signals were least variable at the temperatures in which the species normally called.

The repeatability of context-dependent signals has been measured for the mating behavior of male sailfin mollies (Travis and Woodward, 1989). Large males tend to court females, whereas small males are more likely to attempt to force insemination. Large and small males are consistent in their behavior, regardless of the presence or absence of other males. The rates of these two kinds of behavior were intermediate for intermediate-sized males, when such males were tested alone. However, when intermediate-sized males were in the presence of other males, they behaved like small males, regardless of whether the other males were large of small. Within size classes, the repeatability of each kind of precopulatory behavior was zero for a behavior typical of the class, and 0.6 or greater for the less common behavior shown by that size class.

Repeatabilities and heritabilities of mating displays can be very similar and also very different (Table 1). When repeatability and heritability are similar (e.g. Bakker, 1986; Hedrick, 1988), the environmental contribution to differences between individuals must be low. Substantial differences, as in Butlin and Hewitt's (1986) data on grasshopper songs, could be the result of strong environmental influences. Possibly this could be due to effects on the development of the nervous system.

A common objection to various models of the evolution of sexual behavior is that such behavior is under strong selection and will have low heritability (reviewed by Maynard Smith, 1978; Charlesworth, 1987). The data in Table 1 indicate that efforts to compute repeatabilities and heritabilities are not doomed from the start.

Repeatability of female preferences

It is often quite straightforward to demonstrate that females prefer the signals of conspecifics to those of heterospecifics (e.g. Lloyd, 1966; Gerhardt, 1982; Hoy *et al.*, 1982). In most female-choice experiments, within-species variation is considered to be trivial compared with the signal differences between species, and a single signal is chosen as 'typical' of the species. Even in these circumstances, all females do not choose the conspecific signal (e.g. Gerhardt, 1982). However, females are rarely tested more than once, so the repeatability of preferences cannot be measured.

I have been unable to find published measures of repeatabilities of female preferences. One reason may be the great difficulty of measuring these preferences. The lack of data concerning the repeatability of female preferences can also be explained because most studies of sexual signals have concentrated on fitness consequences to the signalling male rather than to the choosing female. If male mating success is the focus of a study, a knowledge of the repeatability of female preferences may not affect the conclusions. However, when the evolution of female preferences themselves is being considered, a knowledge of their repeatability is critical. The recent debates about 'good genes' and female preferences (reviewed in Boake, 1986; Bradbury and Andersson, 1987) can in part be resolved by examining repeatability of female preferences: if females are inconsistent in their preferences for male signals, they cannot accurately respond to superior male genotypes.

Some supposedly stereotyped behavior patterns, such as the response to pheromones, may be extremely variable, as I found in a study of flour beetles (*Tribolium castaneum*). I examined the tendency of females to approach a filter paper disc which had been impregnated with a known quantity of synthetic male pheromone. I predicted that because females had a choice between pheromone and a blank, they would show consistently high responses to the pheromone stimulus; if these responses were high for all females, repeatability might be low because there was little between-female variation. The choice was between a disc impregnated with the pheromone dissolved in hexane, and one with pure hexane (the hexane had been allowed to evaporate from each disc). Twenty-four females were tested individually, three times each, with at least a day

separating successive tests. I attempted to keep the environmental conditions as constant as possible, using only virgin females, testing them at the same time in their light cycle each day, and in a room that was held at an equivalent humidity and temperature to the incubator where they lived.

The response to pheromone was expressed as the proportion of observations in which the female was within 1 cm of the disc holding pheromone, and on each day the average response to pheromone over all females was about 67% ($p < 0.01$ that the overall response was random). Despite my precautions with environmental variation, the repeatability of response to the pheromone was zero. Different females were highly responsive on different days, with no consistent patterns. These results could be explained in a variety of ways, but all the explanations can be summarized by stating that either the test conditions varied in a fashion that I did not detect or that the females' preferences varied between days. If it is valid to conclude that this behavior has zero or near-zero repeatability, then the opportunity for further evolution of the

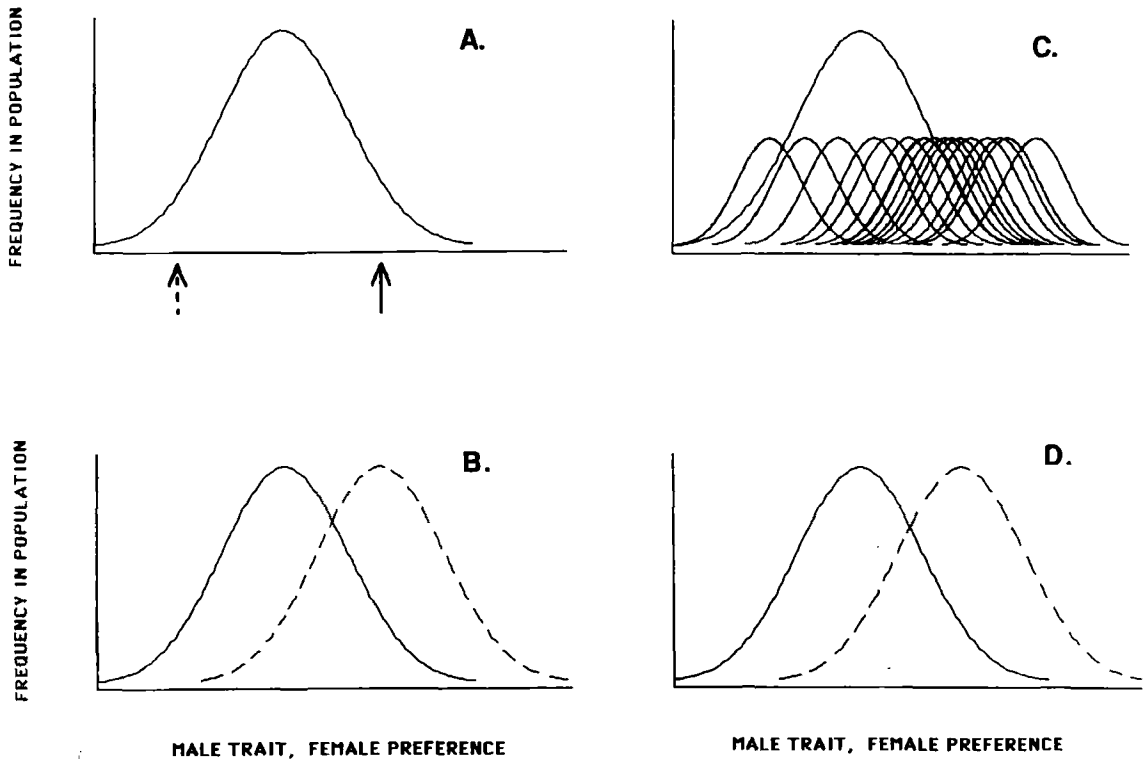**MALE TRAIT, FEMALE PREFERENCE**   **MALE TRAIT, FEMALE PREFERENCE**

Figure 1. Representations of female preferences with respect to male traits. In all cases the solid curve represents the distribution of a male sexual signal in the population. (A) In most behavioral tests, females are tested with two extremes of the male trait, represented by the solid and dotted arrows. The solid arrow is the stimulus to which most females respond. The assumption underlying this test is that all females have a similar preference for an extreme male trait. (B) In this case, female behavior (dashed line) is represented by a probability distribution, with all females having an equal probability of choosing a particular male phenotype. (C) Each female has her own probability distribution with a different mean (the curves along the base of the graph). The majority of females concur on the general expression of the trait they prefer. These are the preference functions used in quantitative genetic models of mate choice. (D) The dotted line illustrates the net effect of (C), which looks like (B), but which arises from differences between females, rather than from all females being alike.

response to male pheromones is virtually non-existent, because additive genetic variation must be extremely small.

The process of measuring repeatability of female preferences will provide data that begin to address a component of several of the recent models for the evolution of sexually selected traits: the 'preference functions' that are used to model processes of mate choice (Lande, 1981; Kirkpatrick, 1985, 1986; Heisler, 1984, 1985). These preference functions assume that each female's preference for male phenotypes can be described by a (genetically determined) function, rather than by a single point (Fig. 1). The functions provide each female with a probability of mating with any male she encounters, rather than a certainty of mating with only one type of male. Conceivably, the behavior of each female could be described with a function that is the same as the population's, but on the other hand, each female could have her own preference function (Fig. 1C), and it is this between-female variation (and within-female repeatability) that is assumed in the models (Heisler, 1985). This critical assumption can be evaluated by inquiring whether all females prefer the same trait and whether a female's preference is invariant. Genetic differences between females can only be detected if phenotypic differences exist, which would be tested by a thorough analysis of female choice behavior.

Repeatability in studies of other kinds of behavior

Students of other categories of behavior might also find that considerations of repeatability are useful. I shall discuss parental care and foraging behavior briefly, raising questions that could have evolutionary implications.

The repeatability of parental care is much more difficult to consider than the repeatability of mating displays and female responses because parental care may involve considerable changes due to experience. A perspective of repeatability and analysis of variance allows several intriguing questions to be addressed. For example, the variance in parental effort could be partitioned into components due to differences between individuals and to differences between sexes. A measurement of repeatability of effort for individuals which change mates would reveal whether parental effort stayed the same. A high degree of repeatability of the level of effort across breeding attempts or seasons would indicate that individual variation is more important than these other factors. Studying the repeatability of the major components of parental care in related species might lead to evolutionary insights. Repeatability could be used in longitudinal studies of helping at the nest to evaluate whether the work done by individual helpers is similar to the work they do as parents.

Foraging behavior can contain such a major component of learned behavior that attempts at genetic analyses have been deemed unlikely to be rewarding (Schoener, 1987). The ability to learn differs between species, and has been demonstrated to have a genetic basis within species (Plomin *et al.*, 1980). The repeatability of learning could be evaluated with several types of tests. It might be particularly interesting to study the context-dependence of learning by examining foraging in different types of habitats and asking whether the process of learning is repeatable across habitat types. Another study might be to examine the repeatability of the rate of learning for different types of food (or for food that is preferred to different degrees).

Genetic analyses of foraging behavior have been shown to be feasible for at least three species. Larval foraging tactics, whether to be a 'sitter' or a 'rover' are under genetic control in larvae of *Drosophila melanogaster* (Sokolowski, 1986). Choice of high-protein or high-energy content diets by larval *Drosophila melanogaster* is also under genetic control (Wallin, 1988). Diet choice is constrained by heredity in California garter snakes (Arnold, 1981). Populational differences in the latency to attack prey in the spider *Agelenopsis aperta* have a genetic basis (Hedrick and Riechert, in prep.).

A knowledge of the degree of stereotypy of various kinds of behavior would allow a better understanding of the phenomena of learning and phenotypic plasticity. Traits with high repeatability will show significant differences between individuals, and these individual differences could be compared for learned and non-learned behavior. An approach which uses the analysis of variance allows the assignment of variation to effects due to individuals and due to differing environments. Different aspects of behavior might be more or less stereotyped in different species, which could allow a search for ecological correlates of behavioral stereotypy and stimulate measurements of selection on different components of a species' repertoire.

Thinking about male signals and female preferences in terms of repeatability requires a view of organisms as variable within some larger pattern that is characteristic of the population or species. From this perspective, mating behavior is assumed to be in the process of evolving rather than having reached the endpoint of evolution. The view requires repeated measurements of known individuals, an activity that is often feasible even in the field. Ultimately the results of studies using repeated measures will allow a discussion of possible rates of evolution, because both the rate of selection and the magnitude of heritability are constrained by repeatability.

Acknowledgments

References

Arnold, S. J. (1981) Behavioral variation in natural populations. II. The inheritance of a feeding response in crosses between geographic races of the garter snake, *Thamnophis elegans. Evolution* 35, 510–15.

Bakker, T. C. M. (1986) Aggressiveness in sticklebacks (*Gasteroesteus aculeatus* L.): a behaviour–genetic study. *Behaviour* 98, 1–144.

Boag, P. T. (1983) The heritability of external morphology in Darwin's ground finches (*Geospiza*) on Isla Daphne Major, Galapagos. *Evolution* 37, 877–94.

Boake, C. R. B. (1986) A method for testing adaptive hypotheses of mate choice. *Amer. Natur.* 127, 654–66.

Bradbury, J. W. and Andersson, M. B. (eds) (1987) *Sexual Selection: Testing the Alternatives.* Dahlem Konferenzen. John Wiley, Chichester, UK.

Butlin, R. K. and Hewitt, G. M. (1986) Heritability estimates for characters under sexual selection in the grasshopper, *Chorthippus brunneus. Anim. Behav.* 34, 1256–61.

Charlesworth, B. (1987) The heritability of fitness. *Sexual Selection: Testing the Alternatives.* J. W. Bradbury and M. B. Andersson (eds), pp. 21–40. Dahlem Konferenzen. John Wiley, Chichester, UK.

Du, J. -W., Lofstedt, C. and Lofqvist, J. (1987) Repeatability of pheromone emissions from individual female ermine moths *Yponomeuta padellus* and *Yponomeuta rorellus. J. Chem. Ecol.* 13, 1431–41.

Falconer, D. S. (1981) *Introduction to Quantitative Genetics*, 2nd edn. Longman, NY, USA.

Findlay, C. S. and Cooke, F. (1983) Genetic and environmental components of clutch size variance in a wild population of lesser snow geese (*Anser caerulescens caerulescens*). *Evolution* 37, 724–34.

Fisher, R. A. (1958) *The Genetical Theory of Natural Selection*, 2nd edn. Dover, NY, USA.

Gerhardt, H. C. (1982) Sound pattern recognition in some North American treefrogs (Anura: Hylidae): Implications for mate choice. *Amer. Zool.* 22, 581–95.

Gibson, R. M. and Bradbury, J. W. (1985) Sexual selection in lekking sage grouse: phenotypic correlates of mating success. *Behav. Ecol. Sociobiol.* **18**, 117–23.

Hedrick, A. V. (1986) Female preferences for male calling bout duration in a field cricket. *Behav. Ecol. Sociobiol.* **19**, 73–7.

Hedrick, A. V. (1988) Female choice and the heritability of attractive male traits: an empirical study. *Amer. Natur.* **132**, 267–76

Heisler, I. L. (1984) A quantitative genetic model for the origin of mating preferences. *Evolution* **38**, 1283–95.

Heisler, I. L. (1985) Quantitative genetic models of female choice based on 'arbitrary' male characters. *Heredity* **55**, 187–98.

Hoy, R. R., Pollack, G. S. and Moiseff, A. (1982) Species-recognition in the field cricket, *Teleogryllus oceanicus*: behavioral and neural mechanisms, *Amer. Zool.* **22**, 597–607.

Kirkpatrick, M. (1985) Evolution of female choice and male parental investment in polygynous species: the demise of the 'sexy son'. *Amer. Natur.* **125**, 788–810.

Kirkpatrick, M. (1986) The handicap mechanism of sexual selection does not work. *Amer. Natur.* **127**, 222–40.

Lande, R. (1976) Natural selection and random genetic drift in phenotypic evolution. *Evolution* **30**, 314–34.

Lande, R. (1981) Models of speciation by sexual selection on polygenic traits. *Pr. Nat. Acad. Sci., US* **78**, 3721–5.

Lessells, C. M. and Boag, P. T. (1987) Unrepeatable repeatabilities: a common mistake. *Auk* **104**, 116–21.

Lloyd, J. E. (1966) Studies on the flash communication system in *Photinus* fireflies. *Misc. Publs. Mus. Zool. Univ. Mich.* **130**, 1–95.

Machlis, L., Dodd, P. W. D. and Fentress, J. C. (1985) The pooling fallacy: problems arising when individuals contribute more than one observation to the data set. *Z. Tierpsychol.* **68**, 201–14.

Mather, K. and Jinks, J. L. (1971) *Biometrical Genetics*. Chapman and Hall, London, UK.

Maynard Smith, J. (1978) *The Evolution of Sex*. Cambridge University Press, Cambridge, UK.

Plomin, R., DeFries, J. C. and McClearn, G. E. (1980) *Behavioral Genetics: A Primer*. W. H. Freeman, San Francisco, USA.

Schoener, T. W. (1987) A brief history of optimal foraging ecology. *Foraging Behavior*. A. C. Kamil, J. R. Krebs and H. R. Pulliam (eds), pp. 5–67. Plenum Press, New York, USA.

Shaffer, H. B. and Lauder, G. V. (1985) Patterns of variation in aquatic ambystomatid salamanders: kinematics of the feeding mechanism. *Evolution* **39**, 83–92.

Shaw, R. G. (1987) Maximum-likelihood approaches applied to quantitative genetics of natural populations. *Evolution* **41**, 812–26.

Sokal, R. R. and Rohlf, F. J. (1981) *Biometry*, 2nd edn. W. H. Freeman, San Francisco, USA.

Sokolowski, M. B. (1986) *Drosophila* larval foraging behavior and correlated behaviors. *Evolutionary Genetics of Invertebrate Behavior: Progress and Prospects*. M. D. Huettel (ed.), pp. 197–213. Plenum Press, New York, USA.

Thornhill, R. (1983) Cryptic female choice and its implications in the scorpionfly *Harpobittacus nigriceps*. *Amer. Natur.* **122**, 765–88.

Travis, J. and Woodward, B. D. (1989) Social context and courtship flexibility in male sailfin mollies, *Poecilia Labipinna* (Pisces: Poeciliidae). In Press *Anim. Behav.*

Walker, T. J. (1975) Effects of temperature on rates in poikilotherm nervous systems: evidence from the calling songs of meadow katydids (Orthoptera: Tettigoniidae: *Orchelimum*) and reanalysis of published data. *J. Comp. Physiol.* **101**, 57–69.

Wallin, A. (1988) The genetics of foraging behaviour: artificial selection for food choice in larvae of the fruitfly, *Drosophila melanogaster. Anim. Behav.* **36**, 106–14.

White, J. M., Vinson, W. E. and Pearson, R. E. (1981) Dairy cattle improvement and genetics. *J. Dairy Sci.* **64**, 1305–17.

Zeh, D. W. (1987) Life history consequences of sexual dimorphism in a chernetid pseudoscorpion. *Ecology* **68**, 1495–1501.