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Sexual selection: the interface of theory and empiricism

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The aim of this paper is to point out some interesting directions for research that are inspired by recent developments in sexual selection theory. I touch here on only a few new results that seem important and do not attempt a survey comparable to the excellent reviews of Trivers (1972), Halliday (1978), Borgia (1979), and Thornhill (1979).

Much recent theoretical progress has come about by attaching concise mathematical definitions to familiar, but often ill-defined, concepts such as 'sexual selection', 'intensity of selection', and 'good genes'. In striving for conceptual clarity, the goal is not merely to make such terms mathematical, but to find their explicit relationship to expressions for evolutionary change (dynamic equations). A mathematical conception is important because sexual selection can often be so complex that intuition, unaided by equations, can be an untrustworthy guide.

In the following sections, I am concerned with techniques for measuring the impact of sexual selection and with models for evolution by sexual selection. Field workers are increasingly successful at measuring the key variables needed to characterise the impact of sexual selection (e.g. Downhower & Brown, 1980; Kluge, 1981; Lenington, 1980). Such data can be analysed so that they have a direct relationship to formal evolutionary theory (Wade & Arnold, 1980; Arnold & Wade, MS; Lande & Arnold, MS). This is an improvement over *ad hoc* analysis that lacks theoretical motivation, but it is not a panacea. The aim is merely to characterise sexual selection by its statistical effects on phenotypic characters within a generation. This, of course, tells us nothing about how selection actually worked in the past, nor does it enable us to extrapolate into the future. The goal is simply to understand the process of sexual selection by direct measurement of its contemporary impact.

This is a timely approach to the subject. Much confusion has recently been generated by anthropomorphic discussions that rely on charming, but misleading metaphors (e.g. females ‘shopping for good genes’) rather than on a direct analysis of evolutionary process. Although the approach adopted here is, at first, more difficult to handle than one based solely in metaphor, I believe that in the long run it will yield more penetrating insights.

With regard to evolutionary models of sexual selection, I focus primarily on a model by Lande (1981) that describes evolutionary change in continuous characters (like tail size or bill length) in which variation is produced both by genes at many different loci and by the environment. Most of the characters that interest students of sexual selection are of this kind. The significance of Lande’s sexual selection model is two-fold: (1) it probably gives a more realistic portrayal of evolution than one-and-two locus models, and (2) the terms used in equations for evolutionary change can be directly estimated, even in natural populations.

Sexual versus natural selection

It is unfortunate that many modern authors do not use the term ‘sexual selection’ as it was employed by its originator, Charles Darwin (1859, 1871). The most prevalent mishandlings are to treat sexual selection either as a subcategory of natural selection or as referring to any type of selection dealing with reproduction. Bateman (1948), Ghiselin (1974), O’Donald (1980), Wade & Arnold (1980) already have reviewed various misrepresentations of Darwinian sexual selection but their arguments seem to be unappreciated by most workers in this field. Rather than attempt another review of the sad history of abuse, I shortly present an annotated passage from Darwin (1871) that contains all the essential points.

A central problem for Darwin was to explain the origin of sexually dimorphic characters that probably hindered survival. His solution was a process of sexual selection that would promote characters that were deleterious under ordinary or natural selection. In the following passage, Darwin (1871: 256–7) defines sexual selection by contrasting it with natural selection.

We are, however, here concerned only with that kind of selection, which I have called sexual selection. This depends on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction.

In order to illustrate the distinction between sexual and natural selection, Darwin next gives four examples of traits elaborated by natural selection

rather than sexual selection. They were obviously carefully chosen to make important, but subtle points. The first example concerns sexually dimorphic traits, like the bills of a Hawaiian bird (*Neomorpha acutirostris*), that are perfected by natural selection.

When the two sexes differ in structure in relation to different habits of life, as in the cases above mentioned, they have no doubt been modified through natural selection, accompanied by inheritance limited to one and the same sex.

In the second example, Darwin points out that primary sexual characteristics (e.g. genitalia and reproductive tracts), as well as mammary glands and other organs for feeding offspring, evolve by natural selection. This key passage shows that natural selection is not simply selection for survivorship and that sexual selection does not act on all aspects of reproduction.

So again the primary sexual organs, and those for nourishing or protecting the young, come under this same head; for those individuals which generated or nourished their offspring best, would leave, *caeteris paribus*, the greatest number to inherit their superiority; whilst those which generated or nourished their offspring badly, would leave but few to inherit their weaker powers.

In the third example, he notes that some characters may be favoured by both natural and sexual selection.

As the male has to search for the female, he requires for this purpose organs of sense and locomotion, but if these organs are necessary for other purposes of life, as is generally the case, they will have been developed through natural selection.

Darwin notes in his fourth example that some secondary sexual characteristics will evolve by natural selection, as will primary sexual characters, even though they are used exclusively in mating.

When the male has found the female he sometimes absolutely requires prehensile organs to hold her; thus Dr. Wallace informs me that the males of certain moths cannot unite with the females if their tarsi or feet are broken. The males of many oceanic crustaceans have their legs and antennae modified in an extraordinary manner for the prehension of the female; hence we may suspect that owing to these animals being washed about by the waves of the open sea, they absolutely require these organs in order to propagate their kind, and if so their development will have been the result of ordinary or natural selection.

The juxtaposition of this example with the last one suggests that Darwin was swayed by the similarity between prehensile organs needed by males to resist wave action during copulation and primary organs, like testes; both are, as he says, absolutely required for reproduction and hence are perfected by natural selection.

The unifying theme of these four examples is that in each of them evolution is by natural selection, not by sexual selection, even though the characters are sexually dimorphic and reproductive in nature. These are the exceptions that help differentiate the two selection processes. In the next paragraph, Darwin opens by putting aside such troublesome exceptions and focuses on unambiguous instances of sexual selection.

When the two sexes follow exactly the same habits of life, and the male has more highly developed sense or locomotive organs than the female, it may be that these in their perfected state are indispensable to the male for finding the female; but in the vast majority of cases, they serve only to give one male an advantage over another, for the less well-endowed males, if time were allowed them, would succeed in pairing with the females; and they would in all other respects, judging from the structure of the female, be equally well adapted for their ordinary habits of life. In such cases sexual selection must have come into action, for the males have acquired their present structure, not from being better fitted to survive in the struggle for existence, but from having gained an advantage over other males, and from having transmitted this advantage to their male offspring alone. It was the importance of this distinction which led me to designate this form of selection as sexual selection.

In other words, the chief defining feature of sexual selection is that sexually mature males differ in ability to inseminate females. The main reason for calling this sexual selection, distinct from natural selection, is that structures that confer mating success may hinder the male in the struggle for survival: sexual selection and natural can be opposing processes. In the next passage Darwin indicates that female mate choice need not depend on any aesthetic sense and that rival males may constitute an immediate agent of sexual selection.

‘So again, if the chief service rendered to the male by his prehensile organs is to prevent the escape of the female before the arrival of males, or when assaulted by them, these organs will have been perfected through sexual selection, that is by the advantage acquired by certain males over their rivals.’

He ends with the disclaimer that, although the action of sexual selection may sometimes be clearly revealed, its effects will often be confounded with those of natural selection.

But in most cases it is scarcely possible to distinguish between the effects of natural and sexual selection.

It is clear from these paragraphs and other passages that Darwin did not view sexual selection as a subcategory of natural selection. Sexual selection was proposed to explain extraordinary sexually dimorphic characters troublesome to his concept of natural selection. It is also clear that Darwin did not design the concept of sexual selection to cover all aspects of reproduction; differences in offspring survivorship induced by differences in parental care, for example, constitute natural selection.

The key to seeing Darwin's distinction between sexual and natural selection is to focus not on the variety of sexually selected characters but instead to consider the effects of such characters on fitness. Characters that evolve by sexual selection are those that cause differences, or variance, in male mating success. An effect on this component of total fitness is the common denominator of the major categories of sexually selected characters listed by Darwin (1871: 257–8): weapons of offence and defence used in male combat; courage and pugnacity in fighting; male ornaments, sound-producing structures and odours that serve only to attract the female or elicit her sexual response. In this context, male mating success is taken as the number of mates that bear the male's progeny: it is not merely the male's copulatory success, but his success in actually siring progeny with a number of mates. Moreover, mating success is conditional on survival to sexual maturity. If we view sexual selection as arising from variance in mating success and natural selection as arising from variance in all other components of total fitness (e.g. survivorship, fertility per mate, offspring survivorship), we come very close to Darwin's concepts, perhaps as close as we can come in exact, statistical terms (Wade & Arnold, 1980; Arnold & Wade, in preparation). This statistical view has the further advantages that: (a) one need not actually identify the agent of sexual selection (e.g. rival males versus discriminating females) in order to measure its impact, and (b) that sexual selection can be measured with conventional statistics.

Dynamic models of evolution by sexual selection

It is important to approach theoretical models with the proper expectations. The goal of a model is to determine what *can* happen: only empirical work can determine what actually *does* happen in the real world. Models are always designed to solve a particular theoretical issue under

specified assumptions. In other words, the goal of a model is to explore the consequences of assumptions about the real world rather than to show how the world actually operates. Models should be viewed as guides for field and laboratory work: only empirical work can produce generalisations about the natural world.

Modelling strategies

Dynamic models have many advantages over other formal approaches to evolution by sexual selection. Such models specify how the composition of the population changes through time, from generation to generation. It is worth reviewing the virtues of dynamic models, since they often require more involved mathematics than short cut methods, such as optimisation and evolutionarily stable strategy (ESS) approaches, that merely describe the population at equilibrium. The two sets of approaches have been recently compared by Lewontin (1979), Maynard Smith (1978*b*, 1980) and Lande (1982*a*). The principal advantages of the dynamic approach are: (a) it permits genetic constraints to affect the evolutionary outcome; (b) it does not rely on an optimisation principle; and (c) it specifies the rate and direction of evolution as well as the location and stability of the outcome or equilibrium.

In contrast, short-cut methods suffer from severe limitation. For example, the principle that selection will maximise fitness or optimise behaviours that contribute to fitness (e.g. mate choice) does not apply in the case of sexual selection. Because the fitness of males varies according to the frequencies of female phenotypes exercising mate choice and rival male phenotypes, sexual selection is a form of frequency-dependent selection. In general, neither mean population fitness nor average inclusive fitness is maximised when selection is frequency-dependent (Wright, 1969: 121–2). Thus optimisation arguments about the fate of populations evolving by sexual selection can be very misleading.

ESS models of sexual selection suffer from a milder problem. Since such models implicitly assume asexual reproduction, genetic phenomena (e.g. meiosis and pleiotropy) can play no role in evolution. This too can be misleading since dynamic models of sexual selection indicate that inheritance as well as selection determines how fast the population evolves and where it goes (O'Donald, 1980; Lande, 1980, 1981, 1982*b*; Kirkpatrick, 1982).

Fisher's runaway sexual selection model

R. A. Fisher seems to have been the first person to examine the genetic consequences of sexual selection and to propose a specific, dynamic

process. Fisher (1915) sketched the outlines of a model in which mate choice by females led to a self-reinforcing process of evolution. Fisher (1930, 1958) later presented a more explicit version and reached the surprising conclusion that a male character and female preferences could evolve together at ever increasing speed. He reached this conclusion by noting that females choosing the most sexually favoured males would produce sexually favoured sons as well as daughters with strong preferences.

Fisher never presented a mathematical development of his runaway sexual selection model. O'Donald (1967, 1977, 1980) modelled the essential features of sexual selection with genetic models in which one or two loci specified the male character and another locus specified female mating preference. These models did reveal that the assortative mating aspect of sexual selection can create a genetic coupling between male attribute and female mate preference and demonstrated the possibility of polymorphism at equilibrium, but O'Donald was unable to confirm the runaway aspect of Fisher's model (O'Donald, 1980). The runaway feature has recently been confirmed in polygenic models for sexual selection developed by Lande (1981, 1982*b*). These models, as well as those by O'Donald (1980) and Kirkpatrick (1982), have also yielded results not predicted by Fisher. In particular, there may be a great variety of outcomes at genetic equilibrium.

Polygenic models for evolution by sexual selection

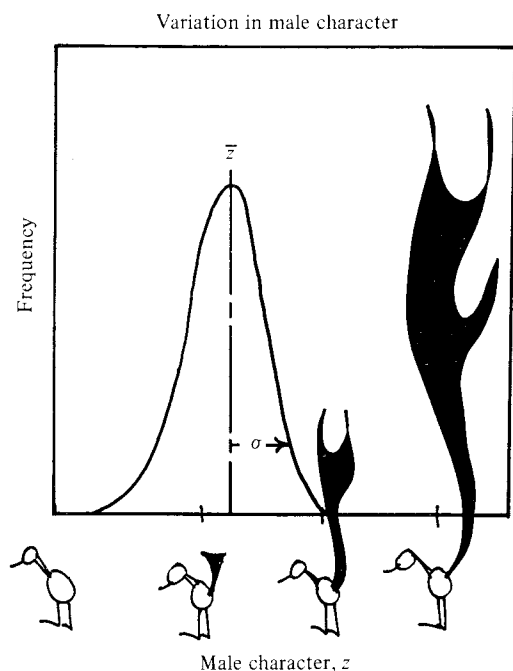
The following account of a model by Lande (1981) gives only the flavour of the main ingredients and results. The original article and related papers (Lande, 1980, 1982*b*) should be consulted for a full mathematical development and justification of assumptions.

Lande's (1981) model gives the expected evolution of a sex-limited* male character and the female mate preference based on that character. In the following discussion of this model, it is helpful to conceive of a specific male character, such as tail length in a bird population, that is expressed only in males and female mate choice based on that character. The basic assumptions of the model are as follows. Suppose that male tail length, z , is normally distributed with mean of \bar{z} and a standard deviation of σ . In an actual example, a size-related character, like tail length, first might be transformed by taking the logarithm of tail length (Fig. 4.1).

* Sex-limited characters are characters that are expressed only in one sex; they need not be sex-linked in inheritance. A contribution to sex-dimorphism is often made by autosomal genes with different expression in males and females.

Natural selection on male character. Tail length might be subject to selective forces other than mate choice. Suppose that these forces of natural selection are stabilising in nature. For example, an intermediate tail size might be optimal under natural selection because a very small tail produces poor flight performance while an extremely long tail makes the male very vulnerable to predators. This situation can be represented by a concave curve shaped like a normal distribution and known as a Gaussian selection function. The top of this curve denotes optimal tail size, θ , or the adaptive peak under natural selection (Fig. 4.2). The width of this natural selection function, ω , describes the intensity of natural selection on tail size. When the function is broad (large ω), male tail size experiences weak stabilising selection; strong stabilising selection is represented by a narrow width (small ω). This width variable is analogous to the standard deviation of a normal distribution, but here we are dealing with a function rather than with a frequency or probability distribution.

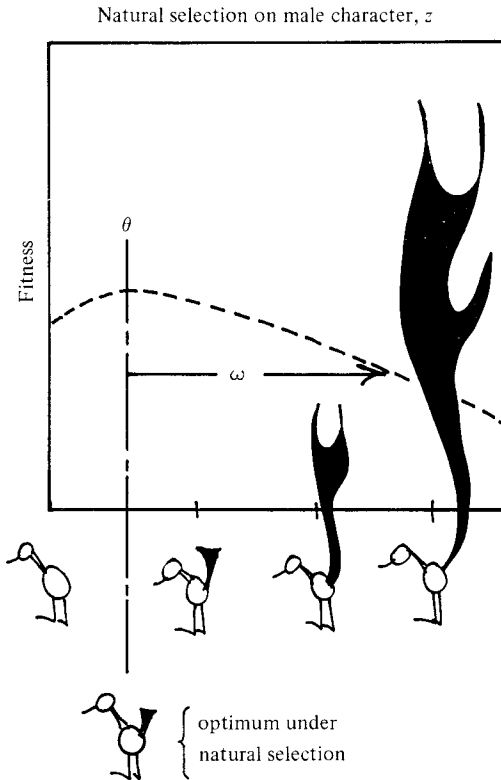
Fig. 4.1. In Lande's (1981) model for evolution by natural and sexual selection, a hypothetical sex-limited character, such as male tail size, is normally distributed with a mean of \bar{z} and a standard deviation of σ .



Female mate choice. Consider next the mating preferences of females based on the male character, z . Focusing on a particular female, we imagine that her tendency to mate with a particular encountered male is given by a Gaussian curve like the one shown in Fig. 4.3. Mate preference is assumed to be unaffected by the male composition of the population and in this sense the female's preferences are absolute. Lande (1981) also considers the case in which the characteristic mate preference of the female is relative to the mean of the male population, \bar{z} , and the case in which the female's mating preference is an open-ended, increasing (exponential) function of male character. Remarkably, the progress of evolution is qualitatively similar under these disparate models of female choice, so only the absolute preference case is illustrated here.

In order for the mate preferences of females to evolve, there must be

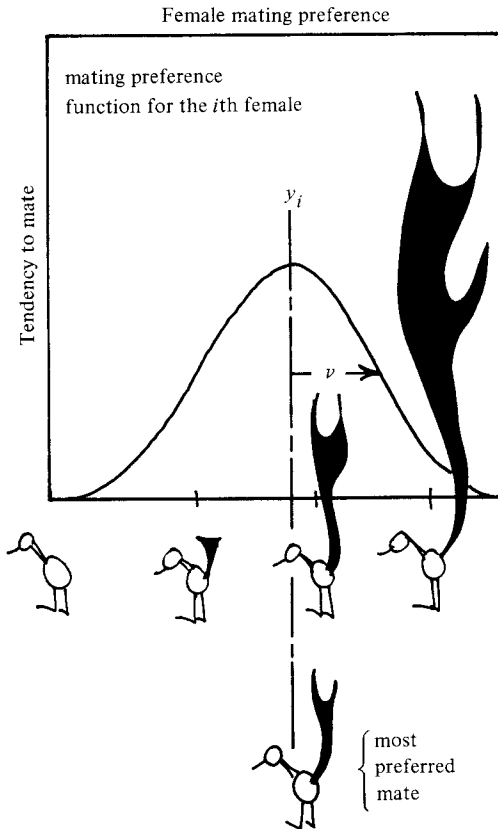
Fig. 4.2. The male's fitness under natural selection is a Gaussian function, shaped like a normal curve, with an optimum at the tail size specified by θ and a characteristic width of ω .



variation among females in mate preference: females must not all prefer the same mate. Let the most preferred mate of a female, y_i , be designated by the male character value corresponding to the maximum of her Gaussian preference function (Fig. 4.3). The females differ in most preferred mate and these are normally distributed with mean \bar{y} (Fig. 4.4).

No selection on female preferences. Assume that males do not protect or provision their mates or offspring, as in many lek-breeding species. Consequently, females have the same number of offspring irrespective of mate choice. There is no immediate benefit to mate choice and in this sense

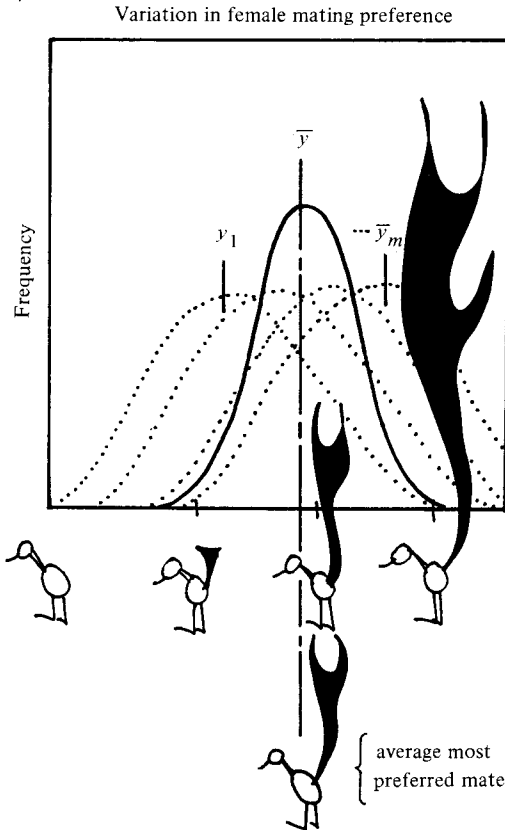
Fig. 4.3. Suppose that a particular female most prefers mating partners with a tail size of y_i . Her tendency of mating as a function of male tail size falls off on either side of this tail size so that her mating preference function is shaped like a Gaussian curve with characteristic width v .



there is no direct selection of female mating preference. Nevertheless, female mating preferences can evolve, as we shall see, as a correlated response to selection on males.

Polygenic inheritance of male character and female preference. Assume that each character is affected by many genes, each having a small effect, so that inheritance is polygenic. Fisher (1918) showed that the inheritance of such a character can be summarised by a genetic parameter of the population known as the *genic* or *additive genetic variance*. This parameter enables us to predict the phenotypes of offspring from the phenotypes of their parents. One way of estimating the additive genetic variance of the

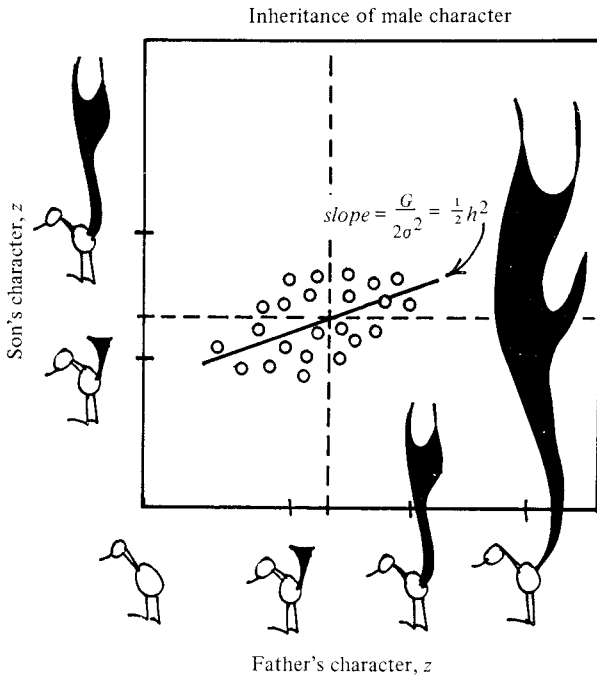
Fig. 4.4. Females differ in the tail size of their most preferred mate, y_i , but the preference functions of all female (dotted curves) have the same characteristic width, v . The most preferred mates of the females are normally distributed (solid curve) with a mean of \bar{y} .



male character z is to calculate the least squares regression of son's character on father's character (Fig. 4.5). This regression slope estimates one half the ratio of genic to phenotypic variance; this ratio of variances is commonly known as the *heritability* of the trait (Falconer, 1960). Likewise, the regression of daughter's most preferred mate on the most preferred mate of her mother would estimate one half the heritability of female mate preference.

We assume now that the genic variances of the male and female characters remain constant during evolution because loss of variance due to selection is balanced by input from polygenic mutation and recombination. The empirical and theoretical justification for this assumption is discussed by Lande (1976).

Fig. 4.5. Each point in the plot represents the average tail size of the sons of a particular male. The data are hypothetical. If there are no non-genetic causes of resemblance between father and sons, the slope of the least squares regression of son's tail size on father's tail size (solid line) will estimate one half the ratio of genic variance in tail size, G , to phenotypic variance in tail size, σ^2 , or one half the heritability of male tail size, h^2 . Means are indicated with dashed lines.



Genic covariance between the sexes. One of the most important consequences of the model is that a genetic coupling arises between male and female characters. This coupling, or *genic covariance*, is a consequence of assortative mating and heritable variation in the two characters. Genic covariance is not an assumption of Lande's (1981) model but rather one of its results or consequences.

Production of this coupling or genic covariance can be visualised in the following way. In each generation, females with the most extreme preference will tend to mate only with males displaying the most highly developed tails; this aspect of assortative mating yields the points in the upper right-hand corner of Fig. 4.6. Likewise, females preferring males with small tails will tend to mate primarily with such males; this aspect of assortative mating yields the points in the lower left-hand corner of Fig. 4.6. In both cases, mating produces sons that resemble their fathers and daughters that resemble their mothers. Thus the overall effect of assortative mating is to produce a correlation or covariance between sons and daughters. This correlation is known as an additive genetic or genic covariance. It arises from assortative mating and reflects linkage disequilibrium, which is the non-random association or linkage of alleles at different loci in gametes. Thus, in this example, alleles promoting large tails in males tend to become associated with alleles that promote female mating preference for large-tailed males. The regression of daughter's most preferred mate on son's character in Fig. 4.6 estimates the ratio of genic covariance between the sexes to genic variance in male character, B/G . Later this ratio will play a critical role in predicting the joint evolution of female preference and male character.

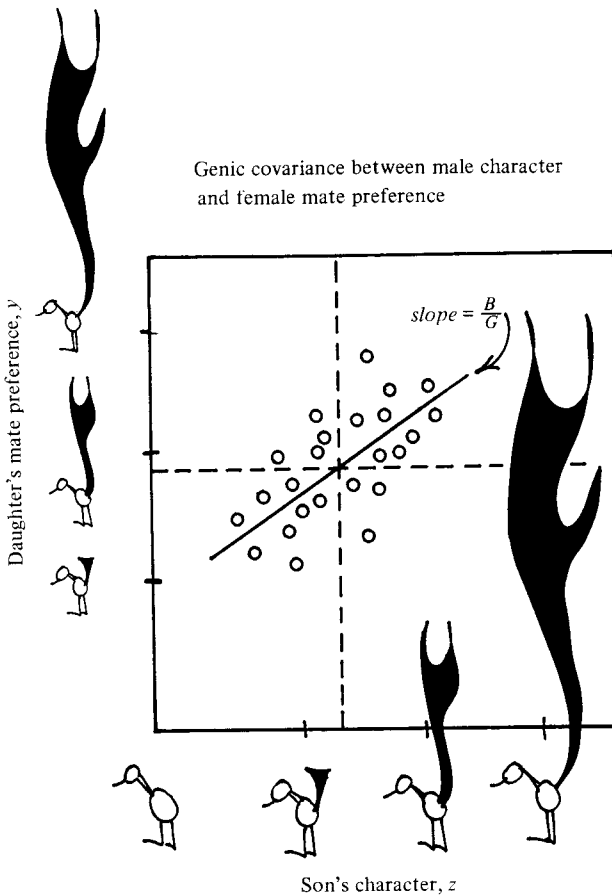
*Forces of natural and sexual selection.** Natural selection exerts one force, tending to drive the male population towards the optimal tail size, θ . Female mate preferences exert another force that, in general, tends to drive male tail size away from the natural selection optimum. This is the force of sexual selection. It is present whenever the average tail size of sexually successful males differs from the average tail size assessed for the entire

* Bradbury & Gibson (this volume) argue that the models of Lande (1981) and Wade and Arnold (1980) are misleading because they do not incorporate natural selection during or after the episode of sexual selection. This is not a troublesome issue. Lande's (1980, 1981) models incorporate natural selection on male attributes that acts prior to sexual selection. These models were extended to cover multiple episodes of selection, including natural selection that follows sexual selection, by Arnold & Wade (MS), but Lande's basic conclusions were unaffected.

population of adult males. The force of sexual selection is proportional to this deviation. Similarly, the force of natural selection is proportional to the deviation of average male tail size for the optimum, θ .

From these considerations we can see that, for any force of natural selection forcing male tails towards their optimum, there might be an

Fig. 4.6. Each point in this hypothetical plot represents the averages of female and male progeny from a particular male parent mated to a large sample of females. These progeny averages are proportional to the males' breeding values for female mate preference and male tail size, respectively. The covariance of breeding values for two such traits is known as the genic covariance, B . The variance in breeding values for the male tail size is the genic variance, G , so the least squares regression of daughters' male preference on sons' tail size is the genetic regression, B/G . Dashed lines show the means for the two characters.



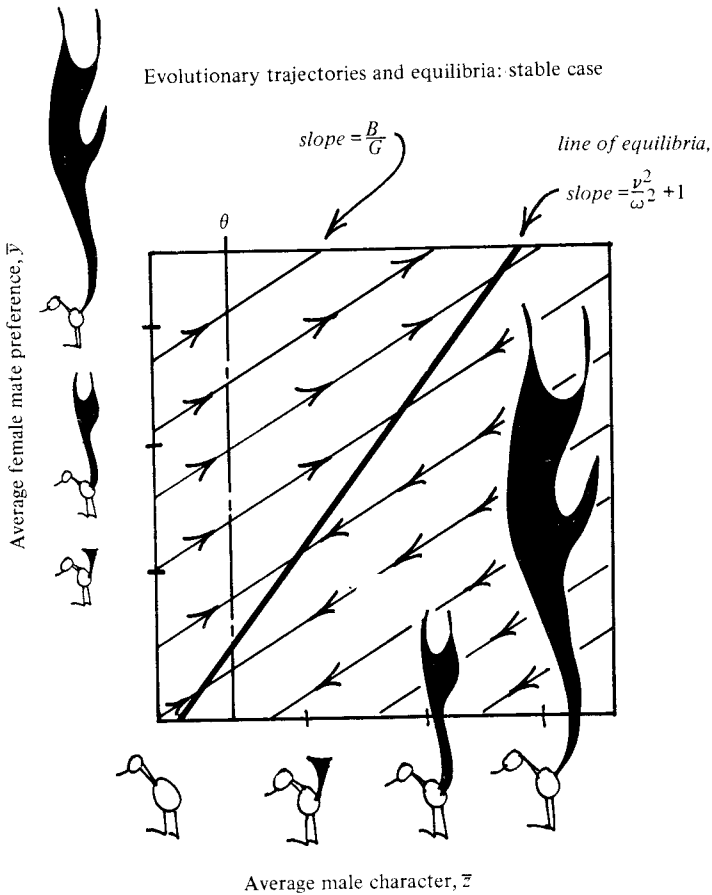
exactly equivalent force of sexual selection, forcing tail size in the opposite direction. When these two forces are equal, there is no net force of selection on male tail size; thus mean tail size ceases to evolve and the population is said to be in genetic equilibrium. When there is no immediate penalty associated with extreme mate preference, very strong preferences can evolve. Consequently, it is conceivable for there to be a tremendous force of sexual selection exerted by females, a force strong enough to balance the force of natural selection when the average tail is very large and far from the optimum. In this model, female mate choice is selectively neutral and there is no force to oppose directly the development of extreme preferences in the population. Thus, it is not surprising that Lande (1981) finds that there is no unique combination of average male and female traits at genetic equilibrium, rather there is a line of equilibria (Figs. 4.7 and 4.8). In other words, the evolutionary outcome is indeterminate because the balance between natural and sexual selection can be achieved in many different ways. As we shall see, the outcome of evolution depends largely on the starting point of the population.

The proposal that female mate preference might be selectively neutral is counter to intuition and to some popular views of sexual selection. It is commonly argued that females are favoured by selection if they mate with the fittest males. But if only male gametes are transferred to the female, as in lek-breeding birds, the argument is circular, since it is the females themselves that confer the purely sexual advantage on males. The theoretical justification for the view that female mate choice might be selectively neutral is taken up in a later section.

Evolutionary outcomes. Some of the following results will probably not be intuitively obvious unless one is fluent with basic concepts in quantitative genetics. Strained intuition commonly engenders mistrust, but in the present case it should encourage consultation of Falconer's (1960) excellent text and Lande's (1981) own account of his model.

The evolution of the population can be represented by the movement of a point in two-dimensional space in which one axis describes the average of the male character and the other describes average female mating preference. Because natural and sexual selection act directly *only* on the male character, the trajectory of evolving population turns out to be a straight line specified by the genetic regression slope, B/G (Fig. 4.7). A further consequence of selection not acting directly on female mate preference is, as just mentioned, that there is no unique evolutionary equilibrium. Instead, if the line of equilibria is stable, the population

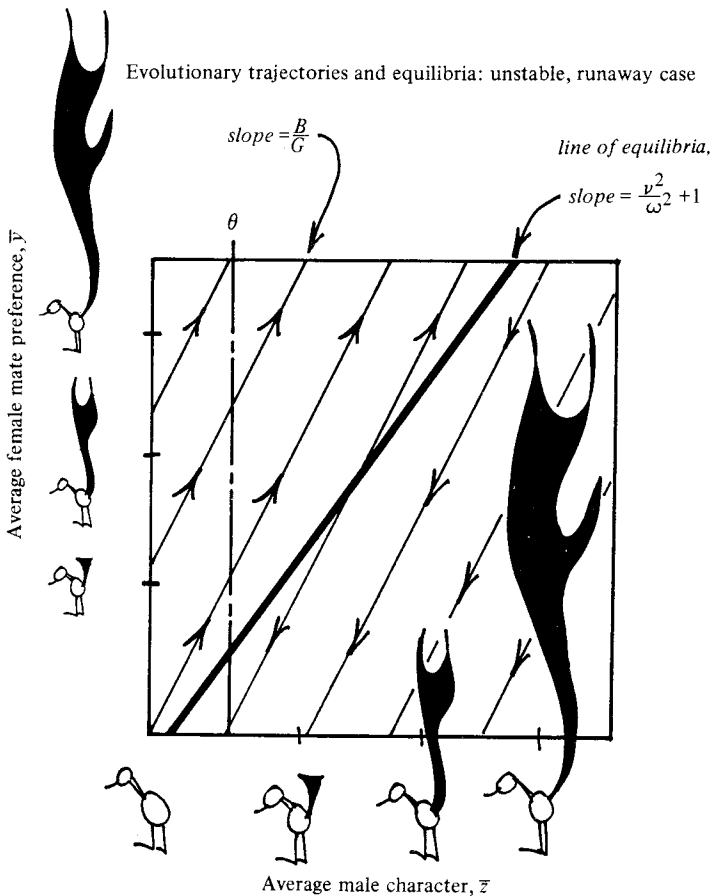
Fig. 4.7. The evolution of the population is described by its change in average female mate preference and average male tail size. The tail size of males most preferred as mates is shown on the vertical axis. In Lande's model the population will evolve along trajectories specified by the genetic regression, B/G . The male tail size that is optimal for survivorship and other non-sexual aspects of life is indicated with the dashed line, θ . Populations stop evolving when they reach the line of equilibria specified by the diagonal heavy line. Thus the composition of the population at equilibrium depends on its starting point. There are many possible combinations of mate preference and tail size at equilibrium.



gradually decelerates and finally stops evolving when it encounters any point along the line of equilibria (Fig. 4.7). The composition of the population at equilibrium is in large part a consequence of its starting position.

Furthermore, a population starting on the left side of the line of equilibria in Fig. 4.7 will experience a gradual elaboration of male tail size

Fig. 4.8. According to Lande's (1981) model, Fisher's runaway process of sexual selection is triggered when the genetic regression B/G (see Fig. 4.6) exceeds a critical value determined by the stereotypy of female mating preference, ν , and the strength of natural selection on male tail size, ω . When this condition is satisfied, populations will evolve away from the line of unstable equilibria, denoted by the heavy diagonal line, at ever increasing speed. Notice that male tail size might be exaggerated or diminished. Other conventions as in Fig. 4.7.



and female preference, but a population starting on the right side will actually evolve a smaller male tail size by sexual selection.

In general, the male tail size at equilibrium will not be the optimal size, θ , specified by natural selection. Notice in Fig. 4.7 that there is only one point of intersection between the line corresponding to the optimum, θ , and the line of equilibria. If we drew in contour lines on Fig. 4.7, connecting points with equal mean fitness, we would see a ridge along the vertical dashed line, θ , with mean fitness falling off on both the left and the right. Fig. 4.2 shows the ridge in cross-section but its width would be $\sqrt{(\omega^2 + \sigma^2)}$ rather than ω . (In general such adaptive topographies change with time when selection is frequency-dependent but, in the present case, since by assumption all females are inseminated, the effect of sexual selection is merely to distribute fitness among males without affecting mean fitness. Consequently only natural selection contributes to the adaptive topography and it does not change with time.) Whenever evolving populations pass over this ridge, as they generally will, they evolve towards lower average fitness, towards a state of maladaptation. It is even possible for sexual selection to contribute to the extinction of a population (Lande, 1980).

The sexual selection process can lead to stable or unstable equilibria. Fig. 4.7 illustrates the stable case. It is also possible for the line of equilibria to be unstable, so that evolution corresponds to Fisher's runaway process. This will happen when females have such strong, stereotyped mating preferences (small v^2) and when there is such weak natural selection on the male character (large ω^2) that the slope of the line of equilibria ($[v^2/\omega^2] + 1$) is less than the genetic regression, B/G . When this is the case, populations evolve away from the line of unstable equilibria at ever increasing speed (Fig. 4.8). In direct confirmation of Fisher's (1930, 1958) account, Lande (1981) finds that the rates of evolution of male and female traits increase geometrically with time. Notice that a population starting above the line of unstable equilibria will accelerate towards large male tails while a population starting below the line will run away towards smaller tails. Thus Fisher's process could elaborate or diminish male attributes.

Evolutionary predictions. Four promising lines of research are suggested by Lande's (1981) sexual selection models. The models are predicted on variation in female mate choice, yet we know surprisingly little about such variation in natural populations. Many workers seem to have a typological attitude, assuming that there might be preferences of females for particular males, but implicitly assuming that all females concur in this preference,

so that there is no variation. A full characterisation of female variation would require testing individual females so that their separate response curves can be specified. If the aim is to relate the results to sexual selection in nature, it is critical to offer females choices of natural, not artificial, variation in male phenotypes (e.g. natural variation in plumage, songs or pheromones). It may be practical to estimate response curves accurately by testing individual females with many simultaneous stimuli using, for example, multiple viewing chambers like those described by P. Bateson, in this volume. It is also important to relate behavioural responses of females in such a choice apparatus to actual mating inclination, since we want a behavioural indicator of actual mate choice. This could be accomplished in a separate experiment, in which females are given actual access to males, so that behavioural responses can be calibrated against mating responses.

The lack of actual data on the form of female mating response curves thwarts further development of sexual selection theory. We do not know whether female responses to particular attributes of males commonly are open-ended or unimodal. Statistical techniques for identifying the characters used by females in mate choice are described in a later section. Such statistical analysis of responses to a random sample of males from a particular natural population might be a useful precursor to detailed experimental work; assessments of this sort can quickly narrow the field of possible characters used in mate choice.

In addition to investigating the nature of variation in female mate choice a second line of research suggested by Lande's models concerns the prediction that a genetic correlation will arise between the sexes during sexual selection. This prediction can be directly tested in natural populations. Both polygenic and two-locus models indicate that the assortative aspect of mating in sexually selected populations should produce and maintain a genetic correlation between male character and female mate choice based on that character (O'Donald, 1980; Lande, 1981; Kirkpatrick, 1982). Thus genetic analysis emerges as an obvious step in studies of sexual selection. Such analysis requires the development of assays for female mate preference. One can then estimate the magnitude of genetic correlation between the two traits by calculating the regression of daughter's mate preference on father's character or from the regression of son's character on mother's mate choice. Alternatively, one can make character measurements in only a single generation; for example, by siring offspring from several females for each of a few dozen males and plotting the means of sons and daughters for each male as in Fig. 4.6. Falconer (1960) and

Bulmer (1980) discuss these and other estimation procedures. A design that permits the estimation of genic covariance between the traits will usually also yield estimates of genic variances (or heritabilities).

The third prediction based on Lande's models is that the forces of sexual and natural selection will balance at genetic equilibrium. This prediction can be tested by actually measuring the forces of selection on characters. Measurements of this kind are most feasible using organisms with short life spans and non-overlapping generations since the estimation of the forces of selection is more complicated in age-structured populations. Estimation procedures are discussed by Arnold & Wade (MS), Lande & Arnold (MS) and in a later section.

Fourth, Lande's models predict very different evolutionary scenarios depending on whether there is direct selection of female preferences. In the case discussed above, there is no direct selection on female mating preferences. Species of this type (e.g., lek-breeding species and those with no paternal care of mates and offspring) should show extraordinary geographic variation in male attributes for several reasons:

(a) The evolutionary outcome is indeterminate (Figs. 4.7 and 4.8), so that the composition of the population at equilibrium depends on its starting point. Small differences in starting point can be amplified by sexual selection into large differences at equilibrium (Fig. 4.7). Such small differences in starting point could be produced by random drift or by geographic differences in natural selection.

(b) Once populations reach equilibrium, further diversification may occur by an interaction of drift and selection (Lande, 1981). Suppose, for example, that two populations lie close together on the equilibrium line in Fig. 4.7. If one population should drift a short way above the line, while the second drifts a short distance below the line, the male character will be elaborated in the first population and diminished in the second as they are driven by selection back towards the line of equilibria in opposite directions. Furthermore, once a population reaches the line of stable equilibria, there is no force impeding movement along the line. Again, drift can promote diversification by causing movement along the line. Drift due to sampling is not unlikely in sexually selected populations. Intense sexual selection (one or a few males siring most progeny) creates a small effective population size which encourages drift (Wright, 1931; Crow & Kimura, 1970).

(c) When many male characters are subject to female mate choice, a tremendous variety of evolutionary outcomes is possible. In the stable case there can be a hyperplane of possible equilibria, rather than the simple line

of equilibria shown in Fig. 4.7 (Lande, 1981). A hyperplane of outcomes can arise either because females choose males using many criteria simultaneously or because one epoch of selection on one male character is later followed by an epoch of selection on other characters.

(d) Speciation as well as geographical variation, is promoted by sexual selection. Lande (1982*b*) has recently confirmed Fisher's (1930, 1958) suggestion that sexual selection arising from mate choice can cause parapatric speciation.

For all these reasons we can expect extraordinary diversity in courtship structures and behaviours in groups where only gametes are transferred to the female. The amazing radiations of birds of paradise and pheasants are probably products of sexual selection.

In contrast to this potential for diversification, Lande's models indicate that there will be much less variation in male attributes if males protect or provision their mates or offspring. In this case natural selection acts directly on female mating choices. The consequence is to change the equilibrium possibilities from a line, plane or hyperplane to a point, a single unique equilibrium (Lande, 1981). There still may be geographic variation in male attributes (e.g. the size of nuptial gift) but this would arise mainly from processes other than sexual selection and the variation would be less extreme. As in the case of pure sexual selection, there can be both stable and unstable cases. Thus, if female preferences are strong and if natural selection on the male character is weak, a Fisherian runaway process can occur even for characters, like size of nest revealed in prenuptial display, that affect the female's fitness directly. It is important to note that in species with male parental investment, Fisher's runaway process could operate (as described above) on male characters that do not influence male parental care.

The origin and cessation of Fisher's runaway process. Fisher (1958) discussed an origin for his runaway process in which a male trait was initially favoured by both natural and sexual selection. Subsequent work indicates that the process can be triggered under a broader class of conditions. Preferences can evolve and the runaway process may be initiated even when there is no directional force of natural selection on the male attribute (Kirkpatrick, 1982; Heisler, MS).

What is the fate of a population experiencing Fisher's runaway process? No limits to the process are specified in Lande's (1981) model. Fisher (1930, 1958) suggested that a stable limit might be achieved once natural selection against extravagant male characters balances the sexual selection that

favours them. Lande (1981) has pointed out that the fitness of males must fall off faster than a Gaussian curve, of the type shown in Fig. 4.2, in order to stop the runaway. Such Gaussian curves produce a restraining force of natural selection that is proportional to the deviation of the population mean from the optimum and such linear forces are insufficient to halt the runaway. Another possibility, also suggested by Fisher (1930, 1958), is that the survivorship of males may become so low that some females with extreme mating preferences fail to find a mate, and this selection directly on female mating preferences may stop the runaway process.

Panglossian females, 'Good genes' and genetic variance for fitness

In contrast to the Darwinian and Fisherian views of sexual selection, the Panglossian view imagines that females always employ adaptive criteria in mate choice. The essential features of this position can be seen most clearly in the case where females receive no direct or immediate benefit from mate choice, as in lek-breeding species. According to the Panglossian view, the 'good genes' of the female's mate might indirectly benefit the female by promoting the fitness of her progeny. The female is likened to a shopper in a supermarket, striving to bring home the best genes for her family. There is competition among shoppers for the best genes and eventually the best shopper prevails in the population. According to the metaphor of the Panglossian female, females using arbitrary, non-adaptive criteria for mate choice will be replaced in evolutionary time by females using the most direct, failsafe indicators of male fitness and hence of good genes. Rigorous formulations of the sexual selection process indicate that these conclusions often may be erroneous.

The Panglossian view of sexual selection leads to indefensible conclusions for two major reasons:

First, there is no guarantee that sexual selection will promote adaptation in the population. Because the mating success of male phenotypes varies both with the frequency of other male phenotypes and with the ensemble of females choosing mates, sexual selection is frequency-dependent. In general, fitness is not maximised when selection is frequency-dependent; nor is inclusive fitness maximised (Wright, 1969; Crow & Kimura, 1970; Lewontin, 1974). Consequently there is no theoretical justification for the optimism that females will arrive at the most adaptive criteria for mate choice. Moreover, there is an irony to supposing that females use only adaptive criteria: Darwin originally proposed the concept of sexual selection to explain structures that were maladaptive under natural selection. Especially in species with no male parental care, we expect

equilibrium populations to settle below adaptive peaks, rather than on top of them, so that the mate most preferred by females is actually suboptimal or maladaptive (Lande, 1981; Kirkpatrick, 1982).

The vulnerability of populations to maladaptive evolution by sexual selection has recently been illustrated by Kirkpatrick (1982). He shows with genetic models that even when males are maladaptive at equilibrium, due to sexual selection exerted by females, there is no inherent tendency for more adaptive female preferences to evolve. Indeed there seems to be no known mechanism operating within populations that can unfailingly rescue populations from maladaptation promoted by sexual selection (Lande, 1980; Kirkpatrick, 1982). However, if the maladaptation induced by sexual selection is so severe that it enhances the possibility of local extinction then selection among leks or demes may lessen regional maladaptation.

Second, it is misleading to imagine a selective force on female mating preference if the social system involves only transfer of gametes by males. Under these circumstances the most manageable theoretical formulation is to describe the evolution of female mating preferences as a correlated response to selection (Lande, 1981; Kirkpatrick, 1982). Since the number of progeny produced by the female is unaffected by her mate choice, there is no immediate cost or benefit, no direct force of selection on mating preferences. This formulation follows the tradition in population genetics of tallying fitness by simply counting the number of progeny produced by a particular zygote (Crow & Kimura, 1970). The value of this approach is that inheritance can be cleanly separated from fitness (or selection) in equations for evolutionary change. Thus the circumstance that the sons of females exerting mate choice might experience higher than average mating success is best treated as an issue of inheritance (the genic regression that enables us to predict son's phenotype from mother's phenotype). An alternative but less manageable approach (the so called 'sexy-son' approach) is to tally the fitness of females by counting grandchildren or great-grandchildren. This practice appears logical since females exerting mate choice might produce an above average number of grandchildren through their sexually superior sons. Unfortunately this mode of fitness accounting does not permit a precise dynamical formulation since it confounds selection and inheritance. A further logical difficulty with the tallying of distant descendants is that there is no obvious stopping point. Should we tally great-great-great grandchildren?

Thus recent theoretical results yield a new perspective on the question 'What does the female of lek-breeding species get out of mate choice?' Quite possibly she gets nothing. This is an excellent hypothesis for

empirical work not only because of its strong theoretical justification but because it can be unambiguously falsified. Bradbury & Gibson (this volume) report that there is currently no evidence for selection on female choice in any lek species. In order to test rigorously for selection on female choice one would need to determine the statistical relationship between the relative fitness of sexually-mature females (number of progeny divided by the population mean) and female mate choice. This would be no small undertaking. Although several investigators have successfully measured fitness in natural populations of birds, for example (e.g. McGregor, Krebs & Perrins, 1981; van Noordwijk, van Balen & Sharloo, 1981; Smith, 1981) female mate choice may be even more difficult to measure. The most informative approach would be to score the mating tendencies of individual females under standardised conditions, as well as in the field, to yield a multivariate characterisation of female mate preference (see later section). Once female mate choice has been characterised and measured the most appropriate measure of selection is the selection gradient or partial regression of female relative fitness on each mate choice variable (Lande & Arnold, MS; Lande, 1979; Arnold & Wade, MS). If female mate choice is selectively neutral then these partial regressions should approach zero within the limits of sampling error.

Partridge's (1980) elegant experiment with *Drosophila* should not be construed as a test for selection on female choice, and she does not attach this interpretation to her results. Partridge found that the progeny of females that had free access to mating partners were superior in larval competition to the progeny of females that were assigned mates at random. Thus Partridge performed artificial selection on female mate choice and detected a correlated response to this selection in larval competitive ability. This clever experiment suggests that there may be heritable variation for one component of fitness (larval competitive ability) and there may be a genetic correlation between this component and some sexually selected attribute (Partridge, 1980). The experiment does not indicate whether there was any natural variation in the mate choice behaviour of females nor does it demonstrate natural selection on female choice.

'Good genes'. The concept of 'good genes' has produced much confusion in discussion of sexual selection. The argument is often made that females are selected to prefer males with genes that produce a phenotype that is optimal for survival and male combat. By the use of such reasoning (e.g. Trivers, 1972) one is forced to maintain that all sexually dimorphic characters, no matter how extravagant, are optimal for survival and

combat. However, this argument is fallacious because it ignores the fact that mating preferences, once established, constitute a selective force in their own right. 'Good genes' must then be defined with respect to total fitness, which is composed of both survivorship *and* mating success. Female mating preferences also figure in the determination of 'good genes'. Thus suppose that the evolution of mating preferences has produced a population with an extreme male trait that is deleterious for survival but is strongly preferred by females. This condition can be a stable evolutionary equilibrium for the following reason: a rare female genotype that chooses to mate with a male phenotype that is optimal for survival will produce sons that resemble their father in having high survivorship, but they will go unmated (if there is no inbreeding) since most females prefer males with an exaggerated phenotype. Males with the optimal phenotype for survival may be ignored by females. Thus the metaphor of females 'shopping for good genes' must be used very carefully, if it is used at all. If the potentially conflicting forces of mate choice and survivorship are ignored, the metaphor can easily lead to erroneous conclusions.

Genetic variance for fitness. Williams (1975, 1978) and Maynard Smith (1978a) have argued that the tendency for genic variance in total fitness to vanish at genetic equilibrium presents a serious difficulty for the maintenance of female mate choice behaviour. The expectation of no heritable fitness variation at equilibrium is a corollary of Fisher's (1930, 1958) fundamental theorem: the rate of evolutionary change in mean fitness equals the genic variance in fitness. Thus when there is no change in mean fitness (fitness equilibrium), there must be no heritable fitness variance. If there is no male contribution to the female besides gametes, as in lek-breeding species, then 'a female who selects as a mate a male of high fitness does not increase the expected fitness of her own offspring' (Maynard Smith, 1978a), because there can be no heritability of fitness at equilibrium. This is, however, not a serious difficulty for several reasons: (1) The absence of selection of female preference at equilibrium cannot be construed as a problem because female mate choice can be maintained, and even evolve, in the absence of any direct selection on mate preference (Lande, 1981; Kirkpatrick, 1982). (2) Even equilibrium populations may be vulnerable to episodes of evolution driven by the sexual selection exerted by females (Heisler, MS). (3) Zero genic variance in fitness is a most precarious equilibrium. For example, mate choice can actually produce genic variance in male fitness. Imagine a population in evolutionary equilibrium with the mean of some heritable male attribute at an optimum specified by natural selection. Now

if the net preferences of females for males with extreme values of this attribute should shift, for any reason, so that a net force of sexual selection is exerted on the male character, this shift will *create* genic variance in total male fitness. This can happen because fitness itself is a function of mating success and other fitness components. Because fitness is a complex variable, even when there is no heritable variance in total fitness, there may be heritable variance in any or all of its components (Lande, 1982a). Consequently a change in the balance among the heritable components of fitness can change the genic variance in total fitness. Thus an increase in genic variance for mating success can create genic variance in total fitness where none existed. We might expect equilibrium populations to vacillate between production and erosion of heritable fitness variance but not to exist long without it. Finally, as Lande (1976) showed, there may be an appreciable input to genic variance in fitness each generation from polygenic mutation and recombination.

The analysis of selection: a special case of the analysis of variance

Many enigmatic aspects of selection can be understood by breaking selection into its component parts. Crow (1958) showed how this can be done. He noted that the expression for the change in mean fitness each generation is mathematically equivalent to the product of fitness heritability and the variance in relative fitness.* He called the variance in relative fitness the intensity of or opportunity for selection, since it limits the rate of evolution. When there are no differences in fitness, there is no selection; when there are great differences in fitness, there is great opportunity for selection. The fact that selection can be formally represented by a variance is important. Armed with Crow's insight that the opportunity for selection is proportional to variance in fitness, we can see that many conceptual problems involving selection can be treated as problems in analysis of variance. The sexual difference in variability of reproductive success is the first of several such problems that are considered in the next few sections.

* The variance in relative fitness can be calculated by dividing the absolute fitness of each individual (the number of progeny surviving to the age of the parents) by the average absolute fitness and taking the variance of these relative measures. A simpler method is to divide the variance in absolute fitness by the square of average absolute fitness.

The intensity of selection on males and females

Bateman (1948) showed that the fitness of *Drosophila* males was more variable than female fitness. He found that this sexual difference in fitness variance was largely due to the fact that mating success was more variable in males than in females. He suggested that this basis of sexual difference in fitness variances should hold in many plants and animals.

The explicit relationship between fitness variances of males and females can be readily derived for many social systems. A first step is to note that there always will be a simple relationship between the mean fitness of males and females. This is because in sexual species each offspring has exactly one mother and one father. Consequently the total number of progeny produced by females must equal the total produced by males. When the breeding sex ratio (number of adult males/number of adult females) is unity these totals are each divided by the same number of parents to give the mean number of progeny per sex: in this case, the means are the same. When the sex ratio is R , the progeny totals are still the same but the mean fitness of females will be R times the mean fitness of males (Fisher, 1930). This last relationship is general and holds irrespective of the breeding system. The fact that the frequency distributions of fitness for males and females are tied together by this simple relationship in means suggests that they might also be coupled by a relationship in variances. This turns out to be true, but the form of the relationship changes, often markedly, with the social system.

In many social systems the male variance in reproductive success will be greater than the female variance as a mathematical necessity (Wade & Arnold, 1980). In the present discussion the units for reproductive success (total fitness) are numbers of progeny and the units for mating success are numbers of mates bearing progeny. For example, consider social systems in which there is no correspondence between the mating success of males and the per capita fertility of their mates and in which all the progeny of a female have the same sire. Under these conditions the total variance in the relative reproductive success of males, I_m , is equal to the variance in the relative reproductive success of females, I_f , times the sex ratio, plus the male variance in relative mating success, I_s ,

$$I_m = RI_f + I_s$$

The three terms representing variances in relative fitness can also be viewed as opportunities for selection. Thus the opportunity for selection on males will often exceed the opportunity for selection on females because of sexual selection on males, I_s , just as Bateman (1948) argued.

There are two prevalent misunderstandings about the sexual relationship in fitness variances or selection opportunities discussed by Wade (1979) and Wade & Arnold (1980). The first error is to suppose that the results depend on an assumption of normality. This is not the case. The analysis of variance used in the derivation of the results does not depend on normality of distribution. (Analysis of variance is usually not applied to data that depart markedly from normality, but this is because the F ratio used in significance testing is predicated on normally distributed errors; the analysis itself is perfectly valid, irrespective of normality.) Even though fitness and its components commonly show non-normal distributions, variance is still the most useful measure of dispersion because of its key role in equations for evolutionary change.

A second misunderstanding concerns the goal of the analysis. The aim is not to claim that nature always fits the assumptions of a particular model, but rather to find mathematical guides to empirical work. For example, male mating success may be correlated with the average fertility of mates and when this is true we require a formulation more complicated than the one just given. Thus if the correlation is positive (say, because more fertile females are attracted to or monopolised by the most sexually successful males) then the male variance will generally exceed the female reproductive variance because there will be a positive covariance term added on to the right side of the expression above. But if the correlation is negative (say, because of a trade off between males resources expended on mating and on offspring) then male variance might be less than female variance (Wade, 1979). Results such as these can simplify field work by directing attention to crucial issues such as covariances between mating and parental success. As another example, consider polyandrous breeding systems.

It is commonly supposed that sexual selection is more intense among females in polyandrous breeding systems (e.g. seahorses and other syn-gnathid fish, some dendrobatid frogs, phalaropes). If we characterise selection using variance analysis, we can see how to test this proposition. The analysis is particularly straightforward if the breeding success of each and every adult male is monopolised by particular females. A first goal in field studies might be to see if this is so. If it is, and if the mating success of females is uncorrelated with their brood size per mate, then we can use the above formulation and simply reverse the sexual labels. The opportunity for sexual selection on females is then the variance in relative number of males that sire their broods, and one could reasonably argue that there is no sexual selection on males. If both males and females can have multiple mates then one must actually calculate the variances in relative mating success to see which sex experiences the most intense sexual selection.

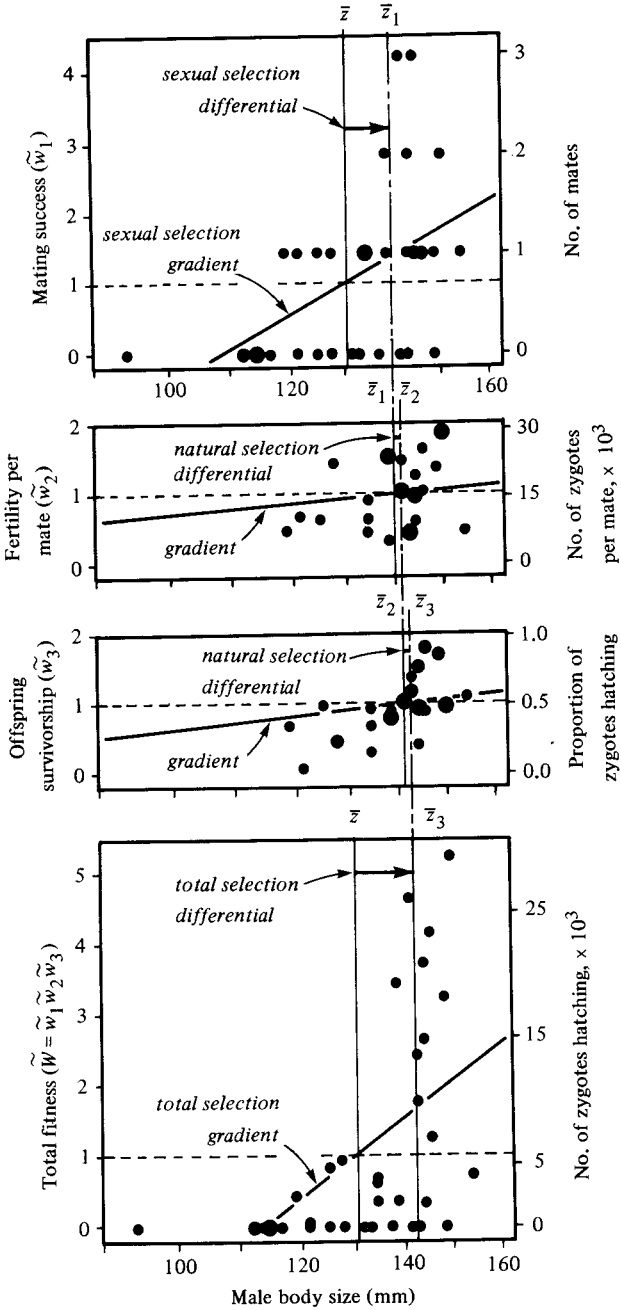
Comparing the intensities of natural and sexual selection

It is useful to measure the separate forces of natural and sexual selection so that they can be compared. For example, one might want to test the hypothesis that a particular sexually dimorphic character is at equilibrium due to a balance between the opposing forces of natural and sexual selection. Or one might suppose that a particular structure is favoured by both sexual and natural selection and the question is which force predominates. Howard's (1979) exemplary study of mating dynamics in a Bullfrog (*Rana catesbeiana*) population illustrates a problem of the latter kind.

Howard (1979) suggested that large male body size might be favoured for three reasons in a Bullfrog population: (a) larger males tended to mate with more females (sexual selection); (b) larger males sired larger clutches because they tended to mate with larger females which laid larger clutches (a kind of natural selection); and, finally, (c) larger males controlled territories with fewer predators and better temperatures for egg development, so their progeny's hatching success might be higher than average (another kind of natural selection).

The key in analysing this and similar problems is to realise that the total fitness of an individual can be represented as a product of fitness components (Arnold & Wade, MS). In the case of a male Bullfrog, total fitness (not total lifetime fitness, but the fitness that can be measured during a breeding season) is the total number of eggs that hatch (since tadpoles disperse shortly after hatching, it was not practical for Howard to tally later components of fitness). This total number of hatching eggs is the product of three observed fitness components: (a) the number of mates that spawn with the male (mating success); (b) the average number of eggs laid per mate (average mate fertility); and (c) the production of eggs that survive to hatching (offspring survivorship). Since Howard measured the size of each male Bullfrog, it is possible to calculate the force of selection on male size exerted by each of the three fitness components as well as the total force. The results are shown graphically in Fig. 4.9. In the Bullfrog data it turned out that sexual selection was responsible for most of the selection on male size; forces of natural selection acting through differences in mate fertility and offspring survivorship were not statistically significant. The predominant effect of sexual selection is revealed by the large shift in the size distribution of males that can be attributed to differences in mating success (Fig. 4.9, top).

Such shifts in mean are called *selection differentials*; they play a key role in equations that predict evolutionary change. In order to see the



relationship between the selection differential and evolution, it is necessary to review some recent developments in quantitative genetics.

We require information about inheritance in order to predict evolution (the response to selection that occurs across generations), but selection itself is a purely phenotypic event and no knowledge of genetics is required to measure its immediate effects, within generations. When selection acts only on a single character, one that shows neither phenotypic nor genetic correlations with other characters, we can readily predict how much evolution will occur just by knowing the heritability of the character and the selection differential: the expected change in mean from one generation to the next is simply the product of heritability and the selection differential (Falconer, 1960). The measure of selection that figures in the equation is purely phenotypic: the shift in average character value or the difference in means measured before and after selection.

Multivariate selection. Most evolutionists and behaviourists, however, are concerned with selection as it occurs in nature: selection acting simultaneously on many characters that may be intercorrelated. In order to predict evolutionary response to such multivariate selection, we must know more than heritabilities and selection differentials (Falconer, 1960; Robertson, 1968). We must also know the patterns of genetic and phenotypic correlation among characters (Lande, 1979). The complication introduced by phenotypic character correlations is the easiest to visualise. A selection differential, or shift in mean within a generation, may occur either because selection has acted directly on the character (*direct selection*) or because selection has acted on a correlated character and indirectly induced a shift in mean (*indirect selection*) (Pearson, 1903). Thus, in the

Fig. 4.9. An analysis of selection on male body size in a Bullfrog (*Rana catesbeiana*) population studied by Howard (1979) and reanalysed by Arnold & Wade (MS). Each data point represents the mating success (top panel), average mate fertility (second panel from top), offspring survivorship (third panel from top) and total fitness (bottom panel) of a particular male Bullfrog. In each panel relative fitness is shown on the left-hand scale and absolute fitness is shown on the right-hand scale. Mean fitnesses are shown with horizontal dashed lines. The total shift in the mean size of males ($\bar{z}_3 - \bar{z}$) within a breeding season, the total selection differential, can be partitioned into three parts corresponding to the effects of sexual selection (top panel) and natural selection (middle and bottom panels). Likewise, the total, univariate selection gradient (the regression of total relative fitness of male body size) can be partitioned into three additive parts corresponding to sexual selection and two kinds of natural selection.

case of Howard's Bullfrogs, the total selection differential on male body size (illustrated in Fig. 4.9) may represent indirect selection on characters correlated with body size as well as direct selection on body size. For example, female mate choice based on loudness of mating call could have caused the observed shift in average male body size if larger males called louder (indirect selection on size); however, some of the selection differential may have been due to actual size advantages (direct selection on size).

When only a single phenotypic character is measured, it is impossible to tell whether selection has acted on that character or on a phenotypically correlated character. It is only possible to separate the direct and indirect effects of selection by measuring the selection differentials of a set of characters and correctly accounting for their phenotypic intercorrelations. The measure of selection that accomplishes this task is the *selection gradient*, which is equal to the partial regression of relative fitness on the character, holding all other characters constant (Lande, 1979; Lande & Arnold MS). The selection gradient measures only the direct force of selection on the character, whereas the selection differential measures both the direct and indirect forces of selection. The selection gradient on each character can be readily calculated from the table or matrix of phenotypic correlations (or from covariances) and selection differentials. This is because Robertson (1966) showed that selection differentials are mathematically equivalent to covariances between relative fitness and the character, irrespective of the form of selection.

Selection is not evolution. In order to predict how a character will evolve we must know the magnitude of genetic coupling with other characters as well as the selection gradients on each character. Genetic coupling, properly known as *additive genetic or genic covariance*, can arise from pleiotropy (particular genetic loci affect two or more characters) or from linkage. The genic covariance between two characters can be estimated by regressing the values of one character in the offspring on the values of another character in their parents (e.g. Fig. 4.5; Falconer, 1960). The consequence is that, when selection acts on one character, it can cause evolution in other characters that are genetically correlated with it. Thus the expected evolution of a character will be due both to direct selection on that character (acting on its additive genetic variance) and to direct selection on other characters (acting through additive genetic covariances). This can be expressed mathematically by defining three terms: (1) let β_{wz_i} represent the selection gradient, or direct force of selection, on character z_i ; (2) let G_{11} represent the genic or additive genetic variance for character

z_1 , and (3) let G_{1i} represent the genic covariance between x_1 and character z_i . Lande (1979) shows that the expected change (across one generation) in the mean value of the character, z_1 , is

$$\Delta \bar{z}_1 = G_{11}\beta_{wz_1} + G_{12}\beta_{wz_2} + G_{13}\beta_{wz_3} + \dots + G_{1k}\beta_{wz_k}.$$

The term $G_{11}\beta_{wz_1}$ represents the contribution of selection on the character to its own evolution, while the other terms represent the contributions through genetically correlated characters. These latter contributions are known as *correlated responses to selection* on other characters (Falconer, 1960). Notice that the genic covariances could be negative and that the selection gradients on the characters may differ in sign. Because of this, it is possible for a character to evolve in the opposite direction from the direct force of selection acting on it. This can happen if the correlated responses to selection swamp the direct response to selection.

These points can be made more tangible with the Bullfrog example. We wish to predict the evolution of male body size from the observed selection differential on size (a differential which summarises the observation that large males leave more progeny during a breeding season). The first problem, already discussed, is that we need to account for the phenotypic correlations among characters. Let us suppose that we have solved this problem by measuring a variety of characters on each male, as well as reproductive success, so that we can calculate the selection gradients, β_{wz_i} . Let β_{wz_1} represent the selection gradient on male body size* and let G_{11} be the additive genetic variance of body size. We cannot predict the amount of evolution in body size merely by taking the product of genic variance for body size and the selection gradient, $G_{11}\beta_{wz_1}$. Suppose, for example, that call loudness, z_2 , also has a direct positive effect on mating success, so that β_{wz_2} is positive. If there is a positive genic covariance between male body size and call loudness (e.g. because some loci affect variation in both male characters), then male body size will also evolve because of a correlated response to direct selection on call loudness, $G_{12}\beta_{wz_2}$. Now, suppose that pulse rate of the male's call, z_3 , also has a direct effect on mating success (thus accounting for the selection gradient, β_{wz_3}), but

* If the axes in Fig. 4.9 actually were the residual values of relative fitness and body size holding all other characters besides male body size constant, then the illustrated regressions would actually be the desired, multivariate selection gradients. Although the linear regressions of relative mating success and of total fitness on male body size in Fig. 4.9 appear to give poor fits to these data, the slopes of these lines are nevertheless the desired selection gradients. Curvilinear regressions would give better fits to these data but the linear terms in such equations would be identical to the ones graphed in Fig. 4.9 (Lande & Arnold, MS).

that this character has negative genic covariance, G_{13} , with body size: the sons of larger males tend to have slower pulse rates, for example because loci with positive effects on body size tend to have negative effects on pulse rate. It is even possible that the correlated response to selection on pulse rate, $G_{13}\beta_{wz_3}$, is so large that it swamps out both the direct response to selection on size and the correlated response to selection on call loudness and other characters. Thus the population might evolve towards a smaller male body size even though selection actually favours larger males each generation!

This example, of course, was contrived to illustrate the worst evolutionary prediction that can be made with purely phenotypic data. The basic point is that 'natural selection is not evolution' (Fisher, 1958: vii): evolution cannot be predicted from measures of selection only. Nevertheless, there are many valid questions that can be answered with data on selection. Is male body size under sexual selection? Is large size also favoured by natural selection? Another series of questions deals with the analysis of variance in fitness itself. Here again we encounter the issue of correlation in the form of *co-intensities or covariances between fitness components*.

The analysis of fitness variance. The total opportunity for selection, or the total variance in relative fitness, can be broken down into segments corresponding to different episodes of selection. This analysis breaks down the total opportunity for selection but does not address the issue of how much selection acts on any particular character. However, one advantage of the analysis is that it does not depend on character measurements. Unlike the estimates of selection gradients, it is insensitive to the particular sample of phenotypic characters that were measured. The essential points are easier to grasp with an example, such as Howard's (1979) study of selection in Bullfrogs, reanalysed by Arnold & Wade (MS).

We can partition the total selection opportunity, or fitness variance, in Howard's Bullfrog population into three parts corresponding to sexual selection (mating success) and two types of natural selection (variances in fertility of mates and in offspring survivorship). In general these three selection opportunities will not add up to the total because of covariances between them. For example, in Howard's (1979) data there was a positive covariance between the total number of eggs laid in a male's territory ($w_1 w_2$) and the average fertility of his mates (w_2). This positive association may have been caused by a tendency for larger, more fecund females to be attracted to territories where eggs had already been laid. But whatever the causes of this covariance, $COI_{12, 2}$, it accounted for 13% of the total opportunity for selection on males (Table 4.1) and was more important

than either natural selection exerted through mate fertility, I_2 , or through offspring survivorship, I_3 . The three other co-intensities in Table 4.1 were of minor importance but they each have biological interpretations. For example, $COI_{1,2}$ measures the tendency of sexually successful males to mate with the most fecund females. If this covariance were negative, it would have indicated a trade off between mating success and mate fertility. The other two co-intensities, $COI_{12,3}$ and $COI_{123,3}$, measure respectively the statistical trends between the male's total count of eggs or tadpoles and his offspring survivorship rate. There is certainly no indication that hatching rate is depressed in large egg masses, say due to crowding; it may have been slightly enhanced.

Triver's (1972) concept of parental investment is an important example of a selection co-intensity. In Trivers' argument there is a trade off between current parental effort per offspring and future fertility. This often may

Table 4.1. *Partitioning of the total opportunity for selection on a reproductive population of male Bullfrogs (Rana catesbeiana) studied by Howard (1979), and reanalysed by Arnold & Wade (MS)*

| Source of variance in fitness | Contribution to total opportunity for selection | | |
|--|---|-------|------------|
| | Symbol | Value | Percentage |
| Sexual selection (number of mates, w_1) | I_1 | 1.382 | 59 |
| Natural selection (number of eggs per mate, w_2) | I_2 | 0.212 | 9 |
| Natural selection (offspring survivorship, w_3) | I_3 | 0.160 | 7 |
| Covariance between number of mates (w_1) and number of eggs per mate (w_2) | $COI_{1,2}$ | 0.081 | 3 |
| Covariance between total number of eggs ($w_1 w_2$) and number of eggs per mate (w_2) | $COI_{12,2}$ | 0.312 | 13 |
| Covariance between total number of eggs ($w_1 w_2$) and offspring survivorship (w_3) | $COI_{12,3}$ | 0.032 | 1 |
| Covariance between total number of eggs that hatch (= number of tadpoles, $w_1 w_2 w_3$) and offspring survivorship (w_3) | $COI_{123,2}$ | 0.150 | 6 |
| Total selection (number of tadpoles, $w_1 w_2 w_3$) | I_T | 2.238 | 100 |

be present since most parents have limited resources to expend on reproduction and survival. In the analysis of fitness variance, parental investment (along with other covariances between fitness components), is represented by a co-intensity (Arnold & Wade, MS). This is certainly not a cause of sexual selection and Trivers' (1972) definition of parental investment as the 'single variable controlling sexual selection' is misleading. Parental investment is but one of many co-intensities that contribute to overall selection. Furthermore, the intensity of sexual selection can vary independently of parental investment (Wade, 1979), and the evolutionary effect of parental investment will be exerted through the additive genetic version of the covariance and not by the more readily observed phenotypic covariance (Lande, 1982a).

Partitioning sexual selection

Many puzzling aspects of sexual selection can be resolved by focusing on its separate aspects (Arnold & Wade, MS; Arnold & Houck, 1982). We can, for example, break down mating success (number of mates bearing progeny) into parts due to separate phases: winning combat with other males, encounter with females, insemination success and paternity. Mating success, w_m , can be represented as a product of fitness components corresponding to these four phases (e.g. $w_m = w_e w_e w_s w_p$). A trait may affect one or more of these components of mating success. For example, Waage (1979) has described a genital device in male Damsselflies that is used to extract the spermatophores of rival males from the female's tract as a prelude to mating. Presumably the elaboration of this device affected the conditional probability of paternity, but probably no other aspect of mating success.

Sexual selection through male combat and female mate choice. Darwin (1859, 1871) and Fisher (1930, 1958) emphasised the common features of sexual selection exerted by male combat and female choice. Most modern authors stress the distinction between them and complain about the difficulty in separating their effects. In general, it will be difficult to ascribe a particular structure of behaviour to evolution by sexual selection exerted through mates or rivals. The separation may be possible, however, in some experimental situations and sometimes in the field.

We can distinguish the effects of female choice from those of male combat if we carefully arrange a sequence of encounters and measurements. Whether this distorts the social biology of the population will depend on the peculiarities of the species and the inventiveness of the investigator.

It is possible to separate statistically the effects of the two kinds of selection if they are separated in time. This is accomplished in two experimental phases: a combat phase followed by a mate choice phase. Before the first phase, a series of behavioural and morphological characters are measured in each sex. These characters are chosen so as to include the most likely candidates for effects on combat or mating success. During the combat phase, the aim is to assign to each male a value, achieved from combat with as many males as possible, that predicts as accurately as possible his relative success in winning combat, w_c . Success in male combat (or, more properly, male-male encounter since bluffing may be the form of interaction) could be tallied from a design that rotates males among opponents in a random order, perhaps with replication of the opponent list or sequence. The difficult problem of ranking or scaling males by combat outcome is discussed by Boyd & Silk (MS). With this accomplished we begin the mate choice phase.

We desire a randomised sequence of encounters between mates that gives good estimates of male and female mating successes as well as interaction terms describing the complementarity of mating partners. If the females can mate with many males (as in some fish and salamanders) then both sexes can be assigned a sequence of mates using Latin Square or other designs. Our principal concern is with the relative insemination success of the males, w_s , holding constant by design the probability of mate encounter. From this, and from the combat success, we can calculate the forces of selection exerted by combat and mate choice. The contribution of each feature in males (e.g. antler size, running speed, body size) to combat success is measured as the partial regression of relative combat success on the character, holding all other characters constant: this is the *combat selection gradient* that measures the direct force of selection, accounting for character intercorrelation, $\beta_{w_c z_i}$. Likewise we can calculate the partial regression of relative insemination success on the character: this is the *mate selection gradient*, measuring the independent contribution of each character, z_i , to success in mate choice, $\beta_{w_s z_i}$. These can be calculated so that they sum to the total force of sexual selection on the character (Arnold & Wade, MS).

A standard multiple regression equation sets expected relative insemination success equal to a sum of contributions from separate characters,

$$\bar{w}_s = \beta_{w_s z_1} \bar{z}_1 + \beta_{w_s z_2} \bar{z}_2 + \dots + \beta_{w_s z_k} \bar{z}_k$$

where \bar{z}_i is the population mean of a particular character and $\beta_{w_s z_i}$ is the corresponding mate selection gradient or partial regression. Each mate selection gradient represents the amount that insemination success is

enhanced by a unit increase in a particular character. If mating success given encounter with the female is wholly controlled by the female, rather than by physical overpowering by the male, then the mate selection gradients can be construed as the weights attached to each male character by the average female during the mate choice process (the terms, $\beta_{w_s z_i} \bar{z}_i$, give the average contributions of the characters to insemination success). Thus, in a hypothetical lek-breeding bird, $\beta_{w_s z_1} = 0$ indicates that the first character, say eyebrow size, has no effect on mating success, whereas a positive value of $\beta_{w_s z_2}$ indicates that a second hypothetical character, z_2 , or tail size has a positive effect on mate choice. These effects, $\beta_{w_s z_i}$, can be added to the combat selection gradients to give the total force of sexual selection on each character (Arnold & Wade, MS).

The interaction between the combat and mate choice phases of sexual selection could be evaluated with an analysis of fitness variance. We can calculate the separate intensities of combat and mate selection. The total opportunity for selection includes also two co-intensities representing the correlation between combat and mating success (Arnold & Wade, MS). When these co-intensities are zero, or nearly zero, either there is no overlap in the sets of characters effective in combat or mate choice, or their effects cancel. When the co-intensities are positive and large, some characters are effective in both combat and mate choice. Negative co-intensities would describe the enigmatic result that losers in male combat are the most successful in mate choice. Thus the co-intensities provide a convenient way to test for correspondence between combat and mate choice phases of sexual selection.

Summary

- 1 Darwin's distinction between natural and sexual selection can be formulated in statistical terms that permit measurement of the two processes. Sexual selection arises from variance in mating success whereas natural selection arises from variance in other components of fitness (e.g. survivorship, fertility of mates).
- 2 Dynamic models of sexual selection with polygenic inheritance confirm the possibility of Fisher's runaway process: male characters and female mating preferences based on those characters can advance together at ever increasing speed. Alternatively, there may be many possible evolutionary outcomes, but no runaway process. The nature of the process depends on genetic parameters, the form of and variation in female mating preferences and the restraining force of natural selection.

- 3 Because sexual selection is frequency-dependent, there is no theoretical justification for the opinion that females will always employ adaptive criteria in mate choice.
- 4 The mathematical relationship between male and female variances in reproductive success can be specified for particular breeding systems. Such analyses confirm Bateman's supposition that sexual selection will often be the cause of greater reproductive variance in males.
- 5 It is possible to break down the total force of selection on particular characters into parts due to natural and to sexual selection.
- 6 In some situations it may be possible to identify the male attributes used by females in mate choice and to distinguish advantage conferred in mate choice and in male combat.

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