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## Quantitative genetic models of sexual selection

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**Summary.** Quantitative genetic models of sexual selection have disproven some of the central tenets of both the handicap mechanism and the 'sexy son' hypothesis. These results suggest that the 'good genes' approach to sexual selection may generally lead to erroneous results.

Runaway sexual selection seems possible under a wide variety of circumstances. Quantitative genetic models have revealed runaway processes for sexually selected attributes expressed in both sexes and for attributes of parental care. Furthermore, the runaway could occur simultaneously in a series of populations that straddle an environmental gradient. While the models support the feasibility of runaway processes, empirical studies are needed to evaluate whether runaways actually happen. Estimates of critical genetic parameters are particularly needed, as well as measures of natural and sexual selection acting on the same population.

The models also show that sexual selection has tremendous potential to produce population differentiation, particularly in epigamic traits. Differentiation is promoted by indeterminacy of evolutionary outcome, transient differences among populations during the final slow approach to equilibrium, sampling drift among equilibrium populations, and the tendency of sexual selection to amplify geographic variation arising from spatial differences in natural selection. Recent work with two- and three-locus models of sexual selection has produced results that parallel the results of the polygenic models<sup>36-38, 58</sup>. Thus the feature of indeterminate equilibria (outcome dependent on initial conditions) is common to both types of model.

**Key words.** Sexual selection; quantitative genetics; handicap principal; sexy son; runaway models; 'good genes'.

### 1. Introduction

The aim of this paper is to survey recent quantitative genetic models for evolution by sexual selection. These models treat the evolution of continuously distributed traits such as tail length in the males of a lek-breeding bird and female mating preference based on such an attribute. The quantitative genetic models have some advantages over two- and three-locus models of sexual selection, recently discussed by O'Donald<sup>54</sup>, Kirkpatrick<sup>36</sup> and Seger<sup>58</sup>. Most traits of interest to students of sexual selection are continuously distributed with polygenic inheritance rather than composed of two or three discrete classes with single factor inheritance. Secondly, the parameters of inheritance and selection used in the quantitative genetic models can be measured in natural populations, whereas the crucial gene frequencies and selection coefficients in the oligolocus models are virtually always inaccessible to measurement. The polygenic models also permit sustained evolution, but the oligogenic models may quickly reach limits imposed by gene fixation, which may obscure some evolutionary phenomena. In defense of the two- and three-locus models, we may note that their logic is sometimes found to be more tractable. In

any case, the principal conclusions are the same using both types of models.

A review of the quantitative genetic models is timely for two reasons. Models of this type have recently proliferated and it is easy to become overwhelmed by new results. Secondly, the model family is now large enough to provide some generalizations about equilibria and stability conditions that instruct our intuition about evolutionary phenomena in general, as well as our understanding of sexual selection. For both these reasons I will focus on the common denominators in the models and on a comparative analysis of their conclusions.

Several terms are used here in a formal sense that sometimes differs from popular usage. *Sexual selection* refers to selection acting via effects on the mating success of surviving males (or females) whereas *natural selection* refers to effects on other components of fitness (e.g. viability). This usage is common to all the theoretical models discussed here. The use of mutually exclusive terms ranks some, despite the fact that Darwin<sup>14, 15</sup> used 'natural' and 'sexual selection' in just this way<sup>3, 28, 65</sup>. Some prefer to see sexual selection as a subset of natural selection. The important point is that viability, or other forms of, selection may act in a different direction than sexual selection,

as when the peacock's tail makes him vulnerable to predators but attractive to peahens. Separate terms are useful to describe such opposition of selective forces but it may be a sterile semantic issue to quibble about the precise labels.

In the models discussed here *fitness* is measured as a zygotic progeny count<sup>13</sup>. The number of zygotes produced by an individual is taken as that individual's fitness, *not* the quality of offspring or the number surviving to sexual maturity. The point in so defining fitness is that inheritance and selection can be explicitly separated in the models. A count of surviving offspring is a bad fitness measure because it confounds the reproductive success of parents (zygotic progeny count) with the viability of offspring. A better tack is to treat parental care as a parental attribute, viability as an offspring attribute, and fitness as a zygotic progeny count in both generations. The effects of parental care on offspring viability can then be treated as separate inherited and direct parental effects<sup>5, 12</sup>.

### 2. Common denominators

Certain features are common to all the models. These common denominators include: assumptions about the frequency distributions and mode of inheritance of the characters, the form of viability selection and the modes of female choice that produce sexual selection. The principal differences among the models lie in the number of evolving characters and the modes of selection on the characters (table).

All of the models deal with the evolution of a male secondary sexual trait, sometimes referred to as a handicap and sometimes simply as the male trait. The extraordinary development of such characters in some species (e.g. the peacock's tail, the newt's crest, the cricket's mating call) led Darwin<sup>14, 15</sup> to propose the concept of sexual selection. The models deal with only one type of Darwinian sexual selection, mate choice, and do not treat the evolution of characters used in male-male contest or combat.

The characters are assumed to show normal (Gaussian) frequency distributions. This is an assumption that

greatly facilitates getting mathematical results, because, for example, a Gaussian character distribution acted on by a Gaussian selection function yields a Gaussian character distribution after selection. It is also an assumption with solid empirical foundation. Many characters are normally distributed or can be transformed to normality, often with simple logarithmic transformations<sup>68</sup>. Evolution is then modeled on the transformed scale.

Character inheritance is assumed to be polygenic with numerous loci contributing to genetic variation in each character. Continuously distributed characters of the kind used in the models often show polygenic or multifactorial inheritance<sup>23, 69</sup>.

In all the models the male trait is acted on by both natural (viability) and sexual selection. In other words, the trait influences both the male's survivorship and his mating success. Viability selection is assumed to be of a Gaussian form, with selection acting against extremes and favoring intermediate development of the male trait (fig. 1). A Gaussian form is a noncontroversial assumption because any strength or peakedness of the function is allowed (the width of the selection function is a parameter in the model). Furthermore when the population mean lies far from the intermediate optimum, the population mainly experiences directional selection favoring, say, smaller tails or softer calls. Very weak or no viability selection can be accommodated by making the function nearly or actually flat.

All of the models specify one of three types of female mate preference and many of them treat all three types (fig. 2). Hardly any empirical work has focused on individual differences in mate preference within populations (a critical issue in evolutionary models) and so the modes are meant to represent three diverse possibilities. Surprisingly, the different modes of preferences have relatively little effect on the qualitative results of the models. *Absolute preferences* describe a situation in which each female is most prone to mate with a certain male phenotype (fig. 2a). Females vary in most preferred mate, with a Gaussian frequency distribution. *Relative preferences* differ from absolute preferences in that each female's most preferred mate is some characteristic distance from the average male phenotype instead of being an absolute

A summary of quantitative genetic models of evolution by sexual selection and their equilibrium properties

Name of model	Reference	Characters in addition to the male trait ('handicap')	Selection in addition to selection on male trait	Dimensionality of equilibrium
Sexual dimorphism	Lande <sup>43</sup>	Homologous female trait	On female trait	Point
Mate choice	Lande <sup>45</sup>	Female mate choice	None	Line
Sexual dimorphism and mate choice	Lande and Arnold <sup>48</sup>	Homologous female trait, female mate choice	On female trait	Line
Sexy son	Kirkpatrick <sup>37</sup>	Female mate choice	On female mate choice	Point
Handicap	Kirkpatrick <sup>38</sup>	Male viability trait, female mate choice	On male viability trait	Line
Sexual selection in a cline	Lande <sup>46</sup>	Female mate choice	None	Line
Coevolution of plants and pollinators	Kiester, Lande and Schemske <sup>55</sup>	Plant trait, female mate choice	On plant	Line

(fig. 2b). As in absolute preferences, the tendency of the female to mate falls off as a Gaussian function in both directions away from her most preferred mate and the most preferred mates of all females in the population forms a Gaussian distribution. *Psychophysical* or *open-ended* preferences describe the common psychological phenomenon that perception increases exponentially with stimulus intensity. The tendency of a particular female to mate is an exponentially increasing function of male phenotype (fig. 2c). The exponent of the mating function varies among females with a Gaussian distribution.

Mate choice, as modeled for example by the three functional forms just discussed, is unfortunately often visualized as a cognitive process in which the male phenotypes are under conscious scrutiny and evaluation. Such a cognitive process is only one, narrow interpretation of the actual possibilities and is probably an uncommon vehicle for sexual selection via mate preferences. Broadly construed, 'mate preferences' capable of generating sexual selection include any morphological, behavioral or physiological differences that produce differences in mating success of the opposite sex: differential reaction to male aphrodisiacs, variation in genitalia, differences in auditory reception or processing, sensitivity to tactile stimuli, etc. The models discussed here could represent the joint evolution of any such female attribute with corresponding male stimuli or structures.

### 3. Anatomy of the models

The models share a basic structure, because they all employ the same evolutionary equation. The basic equation is derived by Lande<sup>42</sup> and is the multivariate version of

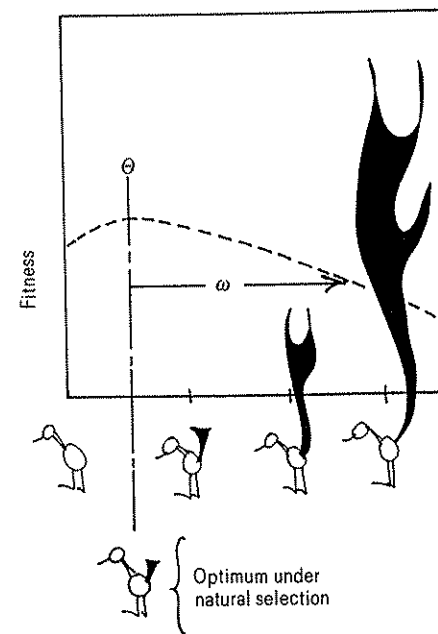


Figure 1. Viability of the male is affected by a hypothetical character, tail size. The curve specifying the relationship is a Gaussian function, shaped like a normal curve, with an optimum at the tail size specified by  $\theta$  and a characteristic width of  $\omega$ . Reproduced with permission from Arnold<sup>3</sup>.

the quantitative genetic equation that has been used for several decades by plant and animal breeders<sup>49</sup>. The equation gives the predicted change per generation in averages of an arbitrarily long list of phenotypic characters. The prediction is based on only three ingredients: 1) inheritance, 2) trait variation and covariation and 3) selection. The patterns of selection and trait variation transform the set of potential parents into the set of actual parents. The pattern of inheritance transforms the set of actual parents into a set of descendants in the next generation. The transformations are then iterated to extrapolate the

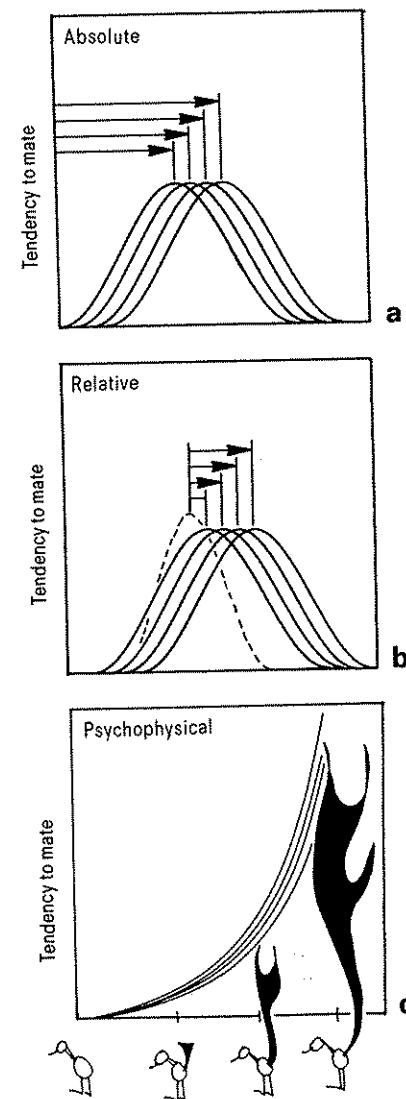


Figure 2. Three modes of female mate preference each based on the hypothetical male attribute of tail size. Individual variation is illustrated for each mode. The frequency of male tail sizes in the population is shown by the dashed curve in the middle figure. *a* Females with absolute preferences are most inclined to mate with male with a tail of the size indicated by the vertical lines at the ends of the arrows. For each female, mating tendency falls off as a Gaussian curve in both directions from that most preferred mate. *b* Females with relative preferences most prefer to mate with a male whose tail is some characteristic size larger than the male average. *c* The mating tendency of females with psychophysical preferences increases exponentially with male tail size (shown on a logarithmic scale). Females differ in rate of increase of mating tendency as a function of male tail size.

population into the future, generation by generation, and to predict its phenotypic composition at equilibrium.

The hereditary transformation consists of a matrix of genetic parameters. These parameters describe resemblance among relatives in the phenotypic traits. The parameters are called additive genetic variances and covariances and measure, respectively, the resemblance between offspring and parents in a particular character or the association between one character in offspring and some other character in parents<sup>23</sup>. Arnold<sup>3</sup> gives a graphical account of the main genetic parameters used in the models.

The matrix of additive genetic variances and covariances is treated as a constant in the models. Empirical work and some theoretical studies provide support for the supposition of constancy. Studies of polygenic characters have shown substantial influx of variation each generation from mutation. Theoretical models indicate that a stable equilibration of genetic variance and covariance can be achieved at which the production of variation and covariation by mutation and recombination is balanced by losses due to selection<sup>11, 40, 63</sup>. The present models assume that this equilibration of genetic variation has been achieved, so that the same hereditary matrix can be used generation after generation to predict evolutionary response to selection.

O'Donald<sup>55</sup> has objected to one of Lande's models on the grounds that it merely posits the existence of a critical genetic parameter, a genetic covariance that describes genetic coupling between a male trait and female mating preferences based on that trait. O'Donald apparently overlooked a critical section of Lande's<sup>45</sup> paper which models the maintenance of genetic variances and covariances. Constancy of genetic parameters is not a bald assumption, as O'Donald claims, but the result of a model within the main model.

In contrast to the constancy of the equilibrated genetic variation parameters, selection is perpetually changing in the evolving population. Selection is described in the models by the selection differential which gives the shift in the phenotypic mean of each character that is induced by selection. Usually two forms of selection act on the male secondary sexual trait: viability selection (a form of natural selection) and sexual selection induced by female mate choice. The total selection differential on the male trait is specified by writing the expression for the shift in mean due to viability selection and adding to it the shift in mean due to sexual selection. The relative strengths of those two selective forces change according to the value of the average male phenotype before selection each generation, which affects the strength of viability selection, and the average value of mate preference in the female population, which affects the strength of sexual selection.

In many of the models the mate choice of the females is assumed to not affect her fitness (measured as a zygotic progeny count). In such models there is no direct selection on mating preferences, so they evolve as a correlated response to direct selection on the male trait. In the models the selection gradient on mate preference, which measures the direct force of selection, is set to zero. Lande<sup>42</sup>, Lande and Arnold<sup>47</sup> and Wade and Arnold<sup>65</sup> discuss the concepts of selection differentials and gradients.

A major goal in using the models is to solve for the equilibrium composition of the population. What is the average value of the male and female traits when the population has stopped evolving? Equilibrium is not specified by exhaustion of genetic variation since that variation equilibrates at nonzero values, as described above. Instead the equilibrium is specified by the vanishing point for directional selection. Thus for the male trait described above, total directional selection will disappear when natural (viability) and sexual selection exactly balance. One solves for this equilibrium by setting the expressions for the total directional selection differential equal to zero. The resulting expressions give the composition of the equilibrium population in terms of the phenotypic averages of the male and female traits.

A second major goal is to analyze the stability properties of the equilibrium. Is the equilibrium stable and what is the rate of approach to or departure from the equilibrium? These questions can be answered by setting up a new system of dynamic equations which give the change in average character values measured as distance from the equilibrium. In order to determine whether the system is stable, one asks for the conditions under which the distance from the equilibrium will shrink each generation and assumes that selection is weak. The analysis consists of solving for the eigenvalues of the matrix of coefficients corresponding to the new set of linearized dynamic equations: the signs of the real parts of the eigenvalues indicate stability, their magnitudes indicate rate of approach to or departure from equilibrium. The corresponding eigenvectors give the direction of evolution in the vicinity of the equilibrium. Roughgarden<sup>56</sup> gives a readable, elementary account of stability analysis.

### 4. The evolution of sexual dimorphism

Lande's<sup>43</sup> model is in some ways the most general of the quantitative genetic models of sexual selection. The model is multivariate and features an arbitrary number of male and female characters. The focus of the model is on the joint evolution of homologous male and female characters. In contrast to later models, however, the sexual selection process is specified only in general terms. Mate choice and its impact on sexual success are not specified. Consequently the model does not illustrate evolutionary feedback or modification of behavior. It does provide a general perspective on the evolution of sexual dimorphisms.

The variables in the model are an arbitrary number of characters that are sexually homologous in the sense that they may be expressed to varying degrees in both sexes. An arbitrary pattern of genetic correlation is allowed both within the sexes and between the sexes. Natural selection is allowed to act on any or all of the characters. In addition the model specifies sexual selection on a subset of the male characters. A form of sexual selection is assumed such that the advantage of a phenotype in mate choice (or in combat) is a function of its deviation from the phenotypic mean. Such relative sexual selection yields a constant force of sexual selection from one generation to the next.

Several maladaptive features of sexual selection are revealed by the model. At evolutionary equilibrium the

opposing forces of natural and sexual selection on male secondary sexual characters perfectly balance. Lande shows that this balance point corresponds to a site downhill from an adaptive peak (see also Lande<sup>41,42</sup>). Thus mean fitness in the population is lowered by sexual selection (fig. 3). The magnitude of maladaptation at equilibrium can be measured as the vertical distance to the peak of the adaptive landscape from the equilibrium point. The distance corresponds to a loss in population mean fitness, a *sexual selection load*. In principle, strong sexual selection could impose such a large load that local populations could be vulnerable to extinction. Whether sexual selection actually promotes extinction in natural populations is an outstanding empirical issue. Sexual selection can also cause maladaptation in ordinary male characters that are not sexually selected. Sexually selected characters will generally deviate from

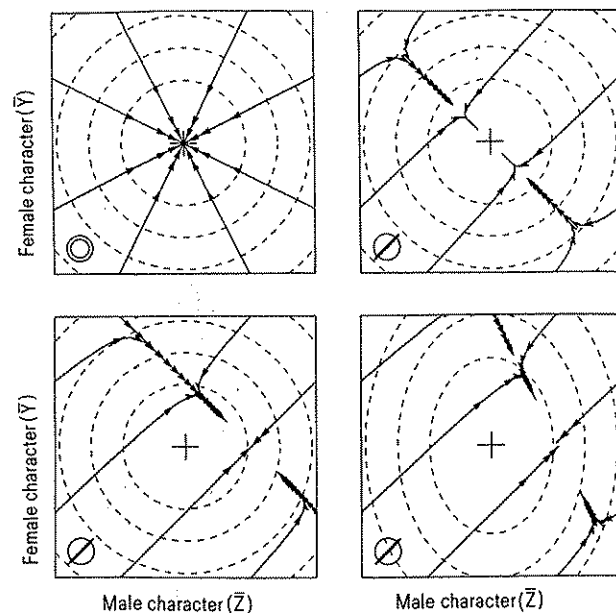


Figure 3. Lande's<sup>43</sup> model for the joint evolution of sexually homologous characters. Solid lines with arrowheads show the evolution of the population averages of the male and female characters. Dashed lines indicate fitness contours of an adaptive topography determined by viability. The adaptive peak (cross) is situated at the center of each figure. The solid circle in the lower left-hand corner of each figure has a radius of one phenotypic standard deviation. The inner ellipse indicates the pattern of additive genetic variation for the characters: a circle indicates no genetic correlation between the sexes, a narrow ellipse indicates a high genetic correlation between the sexes. The evolutionary trajectories were computed assuming a heritability of 0.5 for each of the two characters. Arrowheads are shown at intervals of 200 generations, except near the equilibria and the total elapsed time for each trajectory is 2000 generations. *a* Upper left. With no sexual selection and no genetic correlation between the sexes, populations evolve directly towards the adaptive peak. *b* Upper right. With no sexual selection and high genetic correlation between the sexes, populations make a very slow final approach to the adaptive peak. Sexual dimorphism evolves during this slow phase. *c* Lower left. With sexual selection and high genetic correlation between the sexes, the population equilibrates off the adaptive peak, in the direction favored by sexual selection. A constant force of sexual selection was assumed in computing the trajectories (a sexual selection gradient of one phenotypic standard deviation per generation). *d* Lower right. Same conventions as in the previous figure but with natural (viability) selection on females half as strong as on males. Reproduced with permission from Lande<sup>43</sup>.

their adaptive optimum at equilibrium. That maladaptation in the sexually selected characters can be translated into a maladaptation of the ordinary characters if the two sets of characters interact in their effects on fitness. As a hypothetical example, let the peacock's tail represent the sexually selected characters and let wing length represent the ordinary character. (Actually the peacock's wing may be sexually selected, since it is vibrated to produce sound during the sexual tail display, but let us suppose that the wing is only exposed to natural selection.) We imagine that the tail is maintained at its extraordinary size by a balance between sexual selection favoring even longer tails and natural selection favoring smaller tails. Because the wing and tail work together during such aerodynamic activities as takeoff, flight and landing, the wing and tail sizes probably interact in determining nonsexual aspects of fitness. Differently put, there may be an aerodynamic premium on a particular ratio of wing and tail sizes, a premium that could be measured by computing measures of correlational selection (selection that acts on character combinations and changes character covariances) for the wing and tail<sup>5</sup>. Lande<sup>43</sup> (eq. 14) shows that maladaptation in the peacock's tail will induce maladaptation in any interacting body part, such as the wing. The induced maladaptation in the wing may be permanent. Temporary maladaptation in other characters may arise due to genetic correlation with sexually selected characters, even in the absence of correlational selection. Temporary but long lasting effects may be exerted on genetically correlated male characters. Consider next the nonobvious consequences on female traits.

Sexual selection on the male will also cause temporary maladaptation in the female. The effect arises because pleiotropic gene effects tend to be similar in the two sexes, causing high genetic correlations between homologous traits in males and females<sup>33,48</sup>. Thus because of a large genetic correlation between male and female body size in *Drosophila*, we will increase female body size even if we only select larger males each generation, while choosing female parents at random<sup>27</sup>.

Genetic correlations induce correlated responses to selection in unselected characters<sup>23</sup>. In Lande's<sup>43</sup> model, with natural selection on both male and female characters, but sexual selection in only the male character, the genetic correlation between the sexes causes a correlated evolutionary response in the female to sexual selection on the male. The net consequence of this correlated response to sexual selection, together with the direct response to natural selection on the female, is a curved evolutionary trajectory (fig. 3). The evolving female population can actually evolve away from its optimal phenotype as it follows a curved trajectory (e.g. fig. 3c). Departure from the optimum or adaptive peak is only temporary, but the final approach to the optimum may require millions of generations. The reason for this slow approach is the necessary antagonism between genetic correlation between the sexes and genetic variance for sex dimorphism: when the genetic correlation between the sexes is high (as is usually the case) and genetic variances are comparable in the two sexes, then genetic variance for sex dimorphism is vanishingly small. Because of this antagonism, the evolution of the average of male and female traits (toward upper right and lower left in fig. 3c) is much

faster than the evolution of sex dimorphism (toward upper left and lower right in fig. 3c). Thus Lande's results confirm Fisher's<sup>26</sup> argument that the evolution of sexual differences will be prolonged compared with the evolution of the sexual average and will depend on the slow build-up of genes with sex limitation to their expression. Slatkin<sup>60</sup> presents quantitative genetic models for sexual dimorphism evolving in response to ecological pressures rather than in response to sexual selection. Slatkin makes the important point that a genetic correlation between the sexes in a homologous trait can affect the evolutionary outcome, as well as the trajectory, if there are two or more stable equilibria.

##### 5. Fisher's runaway process

Lande's<sup>45</sup> paper is formal model of Fisher's<sup>24-26</sup> account of a positive feedback process of sexual selection, although Lande discovered features apparently unappreciated by Fisher. The model describes the joint evolution of two traits, a male secondary sexual trait and female mating preference based on that male trait. The male trait is subject to both natural and sexual selection and is not expressed in females. Thus the male trait affects both male survivorship (viability) and mating success. In contrast, the fitness of the female is not affected by her mate choice: even females with the most extreme mating preferences are eventually mated and there is no penalty for

any incurred delays. In this sense mating preferences are selectively neutral. Maynard Smith<sup>51</sup> and Arnold<sup>3</sup> give explications of the model.

The main results of the model are that a variety of evolutionary outcomes are possible and the equilibrium may be stable or unstable. Remarkably, the qualitative results are unaffected by mode of female mating preference. The unstable case corresponds to the runaway process anticipated by Fisher<sup>25,26</sup>. In this case, the population evolves away from a line of unstable equilibria at ever increasing speed. The population may evolve towards elaborated or diminished male character depending on its initial condition (fig. 4a). Instability or the triggering of such a runaway process is promoted by a large genetic covariance between the sexes, weak natural selection on the male character and strong mating preference (narrow curves in fig. 2a and 2b). Relative preferences are more prone to trigger the runaway than absolute mating preferences. The stable case (fig. 4b) was not described by Fisher and is promoted by the converse of the conditions just listed: small genetic correlation between the sexes, strong natural selection, weak mating preferences and absolute rather than relative mate choice. In the stable case the population evolves towards any of a large number of possible stable combinations of average male character and female mate preference. The set of stable combinations forms a line, a so-called line of neutrally stable equilibria. The existence of a line of equilibria can be

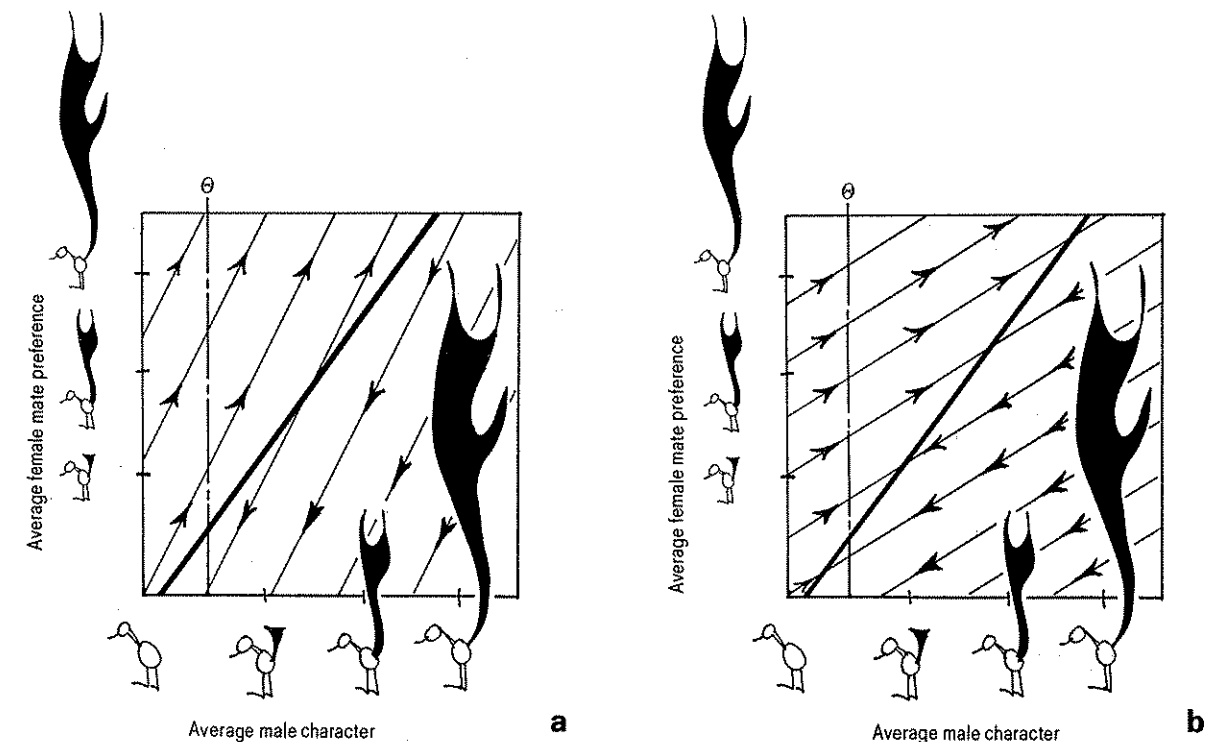


Figure 4. Lande's<sup>45</sup> model for the joint evolution of female mating preference and a sexually selected male character that is not expressed in females. The tail size of males most preferred as mates is shown on the vertical axis. Thus each male caricature on that axis corresponds to the average most preferred mate of a female population with absolute mating preferences. Evolutionary trajectories are shown with solid lines with arrowheads at arbitrary intervals. The heavy solid lines indicate lines of equilibria. The average tail size in a male population that is at the viability

optimum is specified by the vertical dashed line. *a* Runaway sexual selection occurs when the slope of the evolutionary trajectories exceeds the slope of the line of equilibria. In this case populations evolve away from the line of equilibria at ever increasing speed. *b* Stable outcome to sexual selection occurs when the slope of the evolutionary trajectories is less than the slope of the equilibrium line. Populations decelerate as they approach the line. Reproduced with permission from Harvey and Arnold<sup>29</sup>.

appreciated from the fact that sexual selection must balance natural selection on the male trait at equilibrium and for every strength of natural selection there is a conceivably strong force of mate preference that will exactly counterbalance it. Thus the force of natural selection increases as the population moves away from the optimum (dashed vertical line), say, to the right in figure 4b. A stronger force of sexual selection is required to balance an increasingly strong force of natural selection and so the line of equilibria slopes upward, towards more extreme female preference.

Populations that should drift off of equilibrium will be driven back towards it in the stable case. In contrast, populations are free to drift along the line, unopposed by selection (hence the line is neutrally stable). Lande<sup>45</sup> (eq. 20) has worked out the conditions that will promote diversification by sampling drift of populations in the vicinity of the line of equilibria. Diversification in male traits by drift per se will be promoted by small effective population size, strong female mating preferences, high heritability of the preferences and weak natural selection on the male trait. Genetic variance for mating preferences and small effective population size will promote differentiation in female mating preferences. In addition, drift can promote population diversity by interacting with selection. Thus sister populations that drift to opposite sides of the stable line of equilibrium (fig. 4b) will be moved back towards the equilibrium line in opposite directions.

#### Joint evolution of mate choice and sexual dimorphism

Lande and Arnold<sup>48</sup> treat the simultaneous evolution of three characters: a male secondary sexual trait, the homologous female trait and female mate choice based on the male character. The model thus combines features of Lande<sup>43</sup>, which treated the evolution of homologous traits in males and females, and Lande<sup>45</sup>, which modeled the joint evolution of a sex-limited male trait and female choice based on that trait. Primary motivations for the three-character model were to see whether expression in females of the male sexually selected trait might collapse the line of equilibria<sup>15</sup> to a point and to see whether bisexual expression might impede or eliminate the runaway process. Surprisingly, female expression of the male trait had relatively little effect on evolutionary dynamics and the feature of indeterminate equilibrium was retained.

Both the male and female (homologous) traits are under stabilizing natural selection, but a sexual difference in optima is allowed. Thus natural selection could be more stringent on females than on males, for example.

At equilibrium the female trait is found to have evolved to its optimum specified by natural selection. The possible combinations of average male trait and female preference form a line at equilibrium that is identical to the equilibrium line in Lande's<sup>45</sup> model for sexual selection on a sex-limited male trait (fig. 5). Thus expression of the sexually selected trait in the female sex does not affect the outcome of evolution.

Both stable and unstable equilibria are possible, just as in the simpler two-character case. Furthermore, the conditions for stability are identical in the two- and three-char-

acter models, if there is no pleiotropy between female mating preference and either of the homologous characters. Thus natural selection on the homologous female character does not make the conditions for instability more stringent or affect those conditions in any way. In the unstable case, the homologous female trait as well as the sexually selected male trait evolve at ever increasing speed.

The feature of a rapid phase of average character evolution followed by a gradual evolution of sexual dimorphism is present in the three-character case just as it was in the model of sexually homologous traits<sup>43</sup>. Thus figures 3c and 4 can be taken as two-dimensional projections of evolutionary trajectories occurring in three dimensions.

#### 7. Onset and cessation of the runaway

The onset of the runaway process and its cessation are not explicitly modeled in Lande<sup>45,46</sup>, Lande and Arnold<sup>48</sup>, Kiester et al.<sup>35</sup>, or Kirkpatrick<sup>37</sup>. Heisler<sup>30</sup> made a start at modeling the origination of mating preferences, starting with a randomly mating population. She shows that a gene causing a mating preference for an extreme male phenotype could increase in frequency when the male phenotype is under directional viability selection. Thus Heisler's results support Fisher's<sup>25,26</sup> argument that the early elaboration of preferences can occur when natural selection is promoting the evolution of male phenotypes. Another possibility is that alleles causing selectively neutral mating preferences (those that do not affect the female's progeny count) might drift upward from mutation frequency and then trigger the runaway process<sup>36,45</sup>. Pleiotropy provides yet another possible scenario for origination of preferences. Genes affecting mating preference for one character are likely to have pleiotropic effects so that

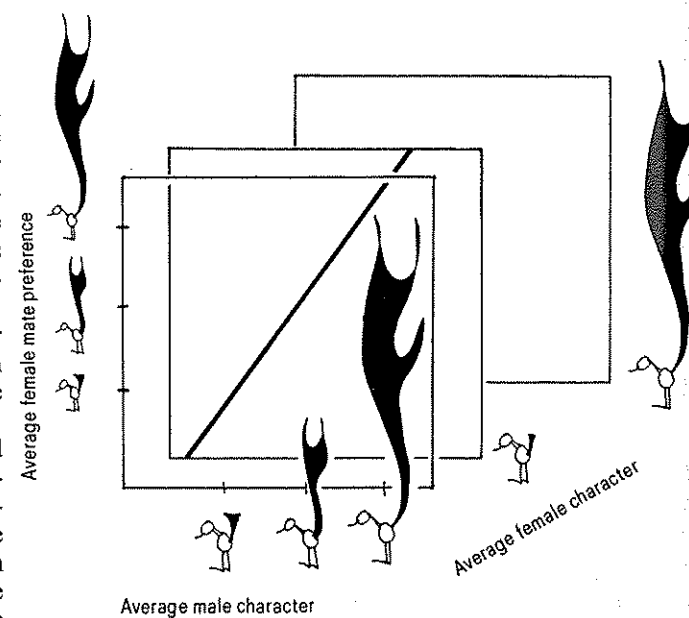


Figure 5. The equilibrium set for female mating preferences, a sexually selected male character and the homologous female character. Absolute female mating preferences and other conventions are the same as in figure 4. The line of equilibria (heavy diagonal line) lies in a plane at which female tail size is at a viability optimum.

mating is biased with respect to other male characters as well. Once genes affecting preference for one trait have increased in frequency, pleiotropic effects may become the vehicle for a new epoch of sexual selection on another character. Thus pleiotropy could lead to a perpetuating series of sexual selection episodes.

Fisher<sup>25,26</sup> argued that the runaway process might stop either because the mating preferences of females are so extreme that they fail to find mates or because of the intervention of strong counterselection against extreme males. In the latter regard Lande<sup>45</sup> has pointed out that in order to stop the runaway, viability must fall off faster than a Gaussian curve as males depart from the viability optimum. In addition, genetic parameters might change during the runaway so that the population reverts to a region of genetic stability<sup>37,38</sup>.

#### 8. Demise of the 'sexy son'

Kirkpatrick's<sup>37</sup> model is designed to test the logic of Weatherhead and Robertson's<sup>66</sup> 'sexy son' hypothesis. The hypothesis applies to species in which mate choice is based upon care which is given to mates or offspring. Weatherhead and Robertson supposed that females might evolve preferences for attractive males even though such males provide inferior care of offspring. The losses in the current generation would be offset in the next generation because the sexy sons of the attractive males would have many offspring. Kirkpatrick showed that such 'deficit financing' of fitness does not work.

Kirkpatrick adapted Lande's<sup>45</sup> model to the problem by letting the male character, which is the focus of female choice, affect the fecundity of the male's mates as well as his viability and mating success. While this additional component of fitness may seem a minor addition to the assumption of the original model, it considerably complicated the mathematics. In Kirkpatrick's model selection acts directly on female mating preferences, because female fecundity is affected by choice of mate.

Kirkpatrick also explored two possible relationships between the mating success and fecundity components of male fitness. In the first possibility, termed unlimited male reproductive potential, the average fecundity of mates is unaffected by the male's mating success. Thus in scorpionflies or other species in which males offer their mates nuptial feeding gifts<sup>61</sup>, a male's past sexual successes are unlikely to affect the size of future nuptial gifts and hence the fecundity of his mates. (In the case of unlimited male reproductive potential, Kirkpatrick assumed an intermediate fecundity optimum for male care, with Gaussian stabilizing selection.) In contrast, in polygynous species in which mates reside on the male's territory, it is conceivable that average fecundity is smaller in larger harems. Kirkpatrick termed this possibility *limited male reproductive potential* and modeled it by letting average mate fecundity fall off as a negative exponential function of male mating success.

The mode of interaction between mating success and mate fecundity had a major impact on the type of evolutionary equilibrium. In contrast, different modes of female choice produced qualitatively similar evolutionary results. Kirkpatrick used the three types of mate choice

devised by Lande<sup>45</sup>: relative, absolute and psychophysical.

Selection on mating preferences had a dramatic effect on the evolutionary equilibrium. Instead of a line of equilibria, as in Lande's<sup>45</sup> model, the equilibrium is a point, a unique combination of average male trait and average female preference (fig. 6). As in Lande, however, the equilibrium may be stable or unstable, with strong genetic coupling between the male trait and female preference promoting instability. Thus a runaway process is possible even when preference is based on an attribute that directly affects female fecundity.

The location of the equilibrium is affected by the existence of a tradeoff between male mating success and mate fecundity. When there is no tradeoff (unlimited male reproductive potential), the male trait equilibrates at a

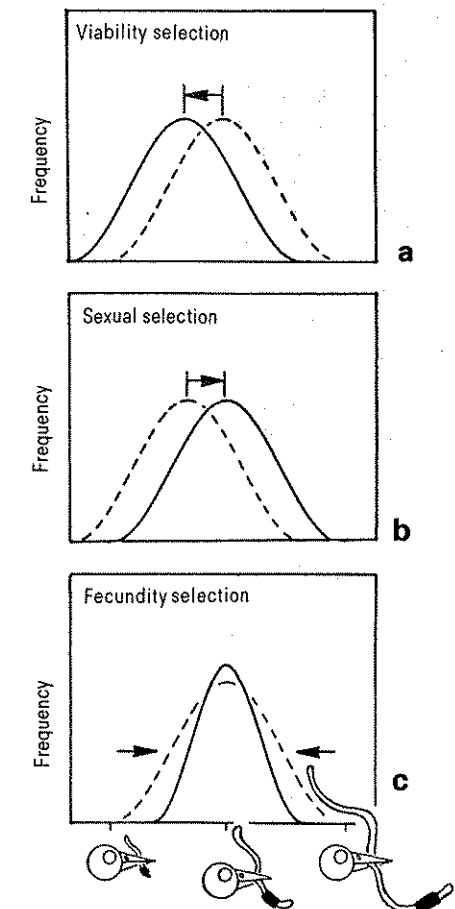


Figure 6. The equilibrium in Kirkpatrick's<sup>37</sup> 'sexy son' model when male reproductive potential is unlimited. Three episodes of selection act on a hypothetical male character, size of nuptial gift. The figures show the selection patterns when the population has evolved to an equilibrium. *a* Large nuptial gifts lower the male's survivorship (e.g. the larger the worms the male tends to pursue, the more vulnerable he is to predation during prey capture). The effect of viability selection is to shift the distribution of nuptial gift sizes towards lower values. *b* Females preferentially mate with males inclined to offer large nuptial gifts. At equilibrium this directional force exactly balances the opposing force of viability selection. *c* Males that offer intermediate sized gifts have the most beneficial effect on the fecundity of their mates (e.g. small worms yield lower fecundity but so do unwieldy, large worms which tend to escape). In equilibrium populations, the average size of nuptial gifts lies at an intermediate fecundity optimum.

level that maximizes mate fecundity. In the case of an evolving nuptial gift, the gift in the equilibrium population would maximize female fecundity, even if such a gift were deleterious to male survivorship. Females in the equilibrium population would prefer males with extreme gifts, but because this force of sexual selection exactly balances the opposing force of viability selection, which favors less extreme gifts (fig. 6), the equilibrium gift giving level is maladaptive for males, in the sense that it decreases their survival.

In contrast, when there is a tradeoff between male mating success and mate fecundity, the population equilibrates at the male trait level that maximizes male survivorship. Female preference for this male trait value also maximizes female fecundity. In the equilibrium population the average male will offer the least risky territory size or level of care and the average female will most prefer to mate with such an average male, and so will maximize her fecundity. Thus a tradeoff between mating success and mate fecundity dramatically changes the nature of equilibrium populations. Remarkably, it is the fact of tradeoff and not the magnitude of tradeoff that matters. No matter how small or large the tradeoff, the population will equilibrate at the same trait values.

Populations do not equilibrate at a level of male care or protection that is deleterious to females. Thus the particular maladaptive outcome predicted by Weatherhead and Robertson<sup>66</sup> is contradicted by Kirkpatrick's<sup>37</sup> results. Sexy sons in the next generation will not compensate for low fecundity arising from poor mate choice in the present generation. Thus the 'sexy son' fails because it violates an important principle in evolutionary biology: at equilibrium the opposing selective forces acting on genes or phenotypes must balance within each generation.

Weatherhead and Robertson<sup>67</sup> and Heisler<sup>30</sup> attempted to bolster the 'sexy son' argument by a 'good genes' argument in which fitness is tabulated by counting grandchildren. Neither paper, however, modeled the inheritance of mating preference and sexually selected traits and their joint evolution. Thus the contradiction of the 'sexy son' proposal by Kirkpatrick's explicit genetic model is a severe blow to the legitimacy of 'good genes' logic.

#### 9. Failure of the handicap mechanism

Zahavi<sup>70</sup> proposed a novel explanation of sexual selection processes. Zahavi embraced Darwin's<sup>15</sup> and Fisher's<sup>25</sup> view that male secondary sexual characters must often be deleterious for male survival and termed these characters *handicaps*. The central problem addressed by Zahavi is the adaptive significance of female mate preference. Rather than accept the view that mating preferences simply evolve as a corollary of the sexual evolution they cause, Zahavi sought an adaptive explanation for mate preference. He proposed that mating preferences based on elaborate characters, handicaps, evolve because such characters are indicators that males have passed a viability test. 'Females which select males with the most developed characters can be sure that they have selected from among the best genotypes of the male population'<sup>70</sup>. Maynard Smith<sup>30</sup> argued that Zahavi's mechanism was unlikely to work because the sons of discriminating fe-

males inherit the handicap as well as the genes that promote viability. Maynard Smith built a three-locus model to test Zahavi's proposition and concluded that the handicap as an indicator of male quality cannot cause mating preferences to evolve, even when the handicap is expressed only in males. Nevertheless, adaptive explanations for the evolution of mating preferences have much intuitive appeal and a series of authors have continued to press Zahavi's original case or modifications of it<sup>1, 6, 17, 22, 39, 53, 62, 71</sup>. In light of this advocacy, it is perhaps surprising that Kirkpatrick's<sup>38</sup> explorations using both three-locus and quantitative genetic models show that the handicap mechanism does not work.

What exactly is meant by the 'handicap mechanism'? The unique feature is *not* the notion of a handicap, since hardly anyone doubts that some sexually selected traits, such as the peacock's tail, actually expose the male to predatory risk. The key feature in Zahavi's proposal is that the handicap is an indicator of male genetic quality. Thus 'indicator mechanism' is a more revealing label, but 'handicap mechanism' is now firmly entrenched in the literature. The indicator aspect of the handicap is supposed to play an important role in the evolution of mating preferences. Making the query more exact we can ask, does the presence of a quality trait, for which the handicap is a marker or indicator, affect the equilibrium, its stability properties or the approach to equilibrium?

Kirkpatrick<sup>38</sup> addressed these issues by modeling the joint evolution of three quantitative traits: 1) a male secondary sexual trait (the handicap), 2) a viability trait (overall quality) expressed in both sexes and 3) a female mating preference based on the handicap. To allow the handicap to be a marker of genetic quality, the model assumes a correlation between the handicap and the viability trait. Normally in thinking about the handicap mechanism, the correlation between the handicap and the viability trait would be positive and genetic, but the model is more general, allowing a correlation of arbitrary sign or magnitude that might be partly or wholly nongenetic.

The model assumes stabilizing viability selection on the handicap towards an intermediate optimum. Sexual selection then acts via female mate choice among the survivors using the handicap as a criterion. The model is developed using absolute mate preferences, as described by Lande<sup>45</sup>, but relative and psychophysical choice functions gave qualitatively the same conclusions. Direct selection does not act on female mating preferences.

The model allows two forms of selection on the viability trait. In the first case, there is stabilizing selection towards an intermediate optimum. The viability trait in this instance might be general running or flying ability. In this case, the model allows the possibility of correlational selection on the handicap and viability trait. Thus there may be a premium on particular trait combinations, such that the subset of surviving males shows an increased correlation between handicap and viability trait. In the second case, there is no intermediate optimum for the viability trait and fitness increases monotonically with trait value. This case corresponds to equating the viability trait with the viability component of total fitness or to some feature, such as parasite resistance, for which selection is always directional. The mode of selection on the viability trait has a major impact on the nature on the

equilibrium. We will first consider the equilibrium when an intermediate optimum exists for the viability trait.

A major conclusion from Kirkpatrick's<sup>37</sup> model is that when mate choice is based on an indicator of male quality (viability), the mating preferences do not evolve to a unique equilibrium. Thus preference based on an indicator trait does not constrain the evolution to a single adaptive outcome of the sort found when mate choice directly affects female fecundity<sup>37</sup>. Instead Kirkpatrick<sup>38</sup> finds a line of equilibrium: many different combinations of the handicap, preference and viability traits can occur at equilibrium. In this sense the equilibrium is the same as in other models with no selection on female preferences<sup>45, 48</sup>. Furthermore, as in those models, the equilibrium may be stable or unstable, with strong genetic coupling between the handicap and mating preferences promoting a runaway process.

Contrary to the expectations of some proponents of the 'good genes' school of sexual selection, mate choice based on a quality indicator does not lead to the evolution of maximally adapted males. Instead Kirkpatrick<sup>38</sup> finds that males in equilibrium populations are pulled off of their adaptive, viability peak for the handicap by the force of sexual selection produced by female choice. Likewise, the viability trait (assumed to be identically expressed in both sexes) evolves to a compromise between the best values for the two sexes. It does not evolve to its optimum.

In the preceding discussion, the viability trait was assumed to be under stabilizing selection and the model specifies an equilibrium. Alternatively, when fitness is a continually increasing function of the viability trait, no equilibrium exists. Instead, the population continues to evolve so long as there is genetic variance for the viability trait, which is now equivalent to a fitness component. Kodrick-Brown and Brown<sup>39</sup> implicitly invoked such a nonequilibrium model when they proposed that mate choice might be based on the ideal indicator of male quality. As in Kirkpatrick's model, their figure 1, which graphs genetic quality of the male (or, more precisely, his breeding value for the viability component of fitness) as a linear function of the handicap trait, specifies a perpetually evolving, nonequilibrium system.

Kirkpatrick<sup>38</sup> explores the nature of equilibrium when such a system exhausts genetic variance for the viability trait. As before, the equilibrium is a line with innumerable possible combinations of handicap, viability and preference trait.

Kirkpatrick<sup>38</sup> also uses his model to test some variations of the original handicap proposal and to evaluate its effects. Thus one can ask whether the handicap mechanism would work in the absence of sexual selection<sup>6</sup>. The answer is no: with mate choice but no sexual selection the equilibrium is the same as with natural selection alone. Dominey<sup>17</sup> proposed that the handicap process would work if variation in the handicap were purely environmental, but again Kirkpatrick finds that the viability trait equilibrates as it would under natural selection alone. Finally, Zahavi<sup>74</sup> proposed that his process might work if the handicap was expressed in both sexes. Expression in both sexes seems the worst case for the process, because both sexes incur a liability<sup>30</sup>. Indeed, Kirkpatrick found

that a handicap expressed in both sexes yields a line of equilibria as before.

The discovery of lines of equilibria when mate choice is based on a quality indicator led Kirkpatrick<sup>38</sup> to re-examine the haploid three-locus models that had been proposed to support the handicap mechanism by Bell<sup>6</sup> and Andersson<sup>1</sup>. He found that those genetic models gave the same results as the quantitative genetic models: evolution of the viability trait to an ecological optimum, the evolution of preference and handicap dependent on initial conditions and towards a line of equilibrium. Thus at present there is no formal theoretical support for the handicap mechanism despite a decade of effort to give it life.

#### 10. Sexual selection in a cline

Lande<sup>46</sup> made the important contribution of building a sexual selection model for the process of clinal speciation. Fisher<sup>26</sup> proposed that a gradient in environmental conditions would cause tension in a species continuously distributed along the gradient, triggering the evolution of divergent mating preferences and eventually speciation. Mayr<sup>52</sup> objected to Fisher's model of 'semigeographic speciation' on the ground that migration and genetic cohesion would disrupt the process and argued that there was no possibility that the mechanism would work. Lande's<sup>46</sup> formalization of Fisher's suggestion refutes Mayr's contention and shows that clinal or semigeographic speciation is a real possibility. Furthermore, the model builds a bridge between discussions of sexual selection and speciation, closely related topics that have often been artificially separated.

The issue of whether clinal speciation actually happens in nature cannot, of course, be resolved by a theoretical model. Lande's model does give the earmarks for clinal speciation and these could be useful in designing field observations that might detect the process in nature.

Lande's<sup>46</sup> model describes the joint evolution of geographic variation in a male secondary sexual trait and female mating preferences based on that trait. The model is a more general version of Lande<sup>45</sup>, incorporating the same assumptions but adding a spatial dimension. In the earlier model, female preferences evolved as a correlated genetic response to sexual selection on the male trait; here geographic variation in preferences evolves as a genetic corollary of evolving geographic variation in the male trait.

Lande's model describes the outcome of the following scenario. Suppose that a continuously distributed species is suddenly exposed to a new spatial pattern in selection imposed by changing environmental conditions. Suppose too that the changed conditions affect natural (viability) selection on a male secondary sexual trait. If heritable female mating preferences for that trait exist, how will the male trait evolve and what new kind of equilibrium clinal variation in the male trait will be established? In particular could very sharp clines develop that could represent the initial stage of speciation?

Alternatively, the model gives the equilibrium clines that would evolve after a species suddenly invades a region with some new spatial pattern in viability selection. In the model the male trait is under spatially varying stabilizing

selection: the optimum varies in space, the width of the selection function is constant in space. Whether the environment changes suddenly or the species invades a new region rapidly, the initial condition for the species is no geographic variation in the male trait or in mating preference, with uniform population density and with migration. These conditions are the least favorable for the evolution of sharp clines and speciation, because there are no initial differences between populations (e.g. no premating or postmating isolation) and no barriers to gene flow. Clinal speciation demonstrated under these conditions might prevail under much more general circumstances in nature.

Thus the idea of the model is to impose a particular new spatial pattern of selection on the male trait and investigate the subsequent evolution of geographic variation in the trait. The model permits exploration of a large number of spatial patterns in selection, but all of them are one-dimensional. Ecologists or naturalists familiar with the ubiquity of multi-dimensional gradients in environmental variables should not be discouraged by the one-dimensional feature of the model. One-dimensional gradients are mathematically the most tractable. The results can be mapped directly onto species inhabiting linear habitats (e.g. stream courses), but they also instruct our expectations for more complex environmental gradients. A major result of the model is that sexual selection exaggerates geographic differences in the male trait. Thus sexual selection amplifies the steepness of equilibrium clines (fig. 7). Both genetic variance in mating preferences and the strength (stereotypy) of those preferences tend to amplify clines. Migration and strong stabilizing natural selection at each location along the cline oppose amplification and act to diminish the steepness of the equilibrium cline.

The amplification result extends the general conclusion that sexual selection has a tremendous potential to create population diversity. Earlier models stressed diversification arising from indeterminate equilibria and initial conditions, sampling drift interacting with selection in populations at or near equilibrium, slow approach to equilibrium caused by genetic coupling and, alternatively, runaway processes. To this catalog of diversifying mechanisms we can now add exaggeration of clinal variation, which can occur even without any initial, phenotypic differences between populations.

In contrast to their tendency to exaggerate the height of clines, strong and genetically variable preferences tend to lengthen the geographic width of the cline. In Slatkin's<sup>61</sup> terminology, they increase the characteristic length of the cline. At distances much shorter than the characteristic length (a distance considerably greater than individual dispersal distances) the population fails to track spatial differences in selection and no clines evolve. Ironically, strong, variable preferences promote tracking failure over short geographic distances. A second nonobvious finding is that the genetic variance and strength of mating preferences act to retard the approach to equilibrium. Again the effect is exerted through the relationship with characteristic length.

Another major result is that runaway sexual selection can occur simultaneously over a broad geographic area. As in previous models, equilibria may be stable or unstable. In

the unstable case the cline evolves exponentially so that the height of the cline becomes increasingly exaggerated (fig. 7c). The condition for stability is identical to the case without geographic variation<sup>45</sup>: genetic variance in preferences (acting through the genetic coupling between preference and sexually selected trait) must exceed a critical value that increases with the strength of natural selection and decreases with stereotypy of preference. The amplification result suggests that premating isolation could evolve rapidly along a cline that straddles an environmental discontinuity, just as Fisher<sup>25</sup> argued. Although Lande's models treat only the stages of speciation before coexistence, they do not confirm the popular notion of character displacement. Lande found that equilibrium clines were always monotonic and did not show

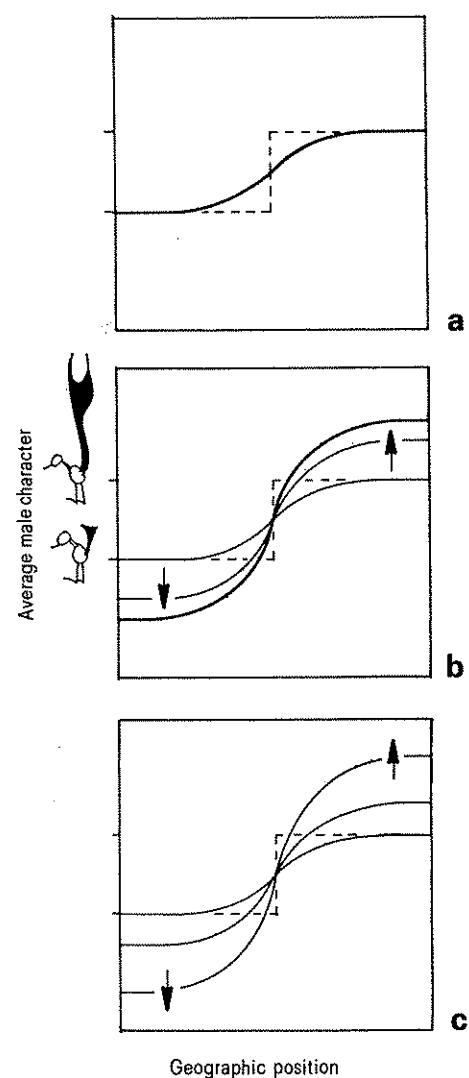


Figure 7. Lande's<sup>46</sup> model for stable and unstable clines in a male character. A sudden change in the environment favors a small tail size in one geographic region and a larger tail size in an adjoining region. The geographic change in optimum tails size favored by viability selection is shown by the dashed line. a In the absence of sexual selection, a stable cline forms (heavy line). b Sexual selection amplifies the character cline and may yield a new stable cline (heavy line). c Alternatively, a runaway sexual selection process may occur simultaneously across to the two geographic regions, with an ever increasing exaggeration of the original cline.

the feature of reversed clines, i.e. greater character divergence in parapatry than in allopatry, which might be the supposed precursor of sympatric character divergence between reproductively isolated populations.

### 11. Coevolution of plants and their pollinators

Kiester et al.<sup>35</sup> present a sexual selection model for the coevolution of plants and pollinators. In many species of euglossine bees, for example, males collect fragrances from orchid flowers and apparently use the fragrances to attract mates<sup>16, 19-21, 27</sup>. The intent of the model, as applied to such a system, is to trace the evolution of three traits: 1) amount (or mixture) of some chemical fragrance produced by the orchid, 2) preference of male bees for the orchid fragrance and 3) mating preferences of female bees based on the fragrances collected and carried by male bees. The model is interesting from a number of viewpoints, but for the present discussion perhaps the most relevant focus is on how mate preferences based on attributes derived from a second coevolving species affect evolution by sexual selection.

Aside from the plant character, the only major departure from Lande's<sup>45</sup> model is that the viability of the male is determined by the relative number of plants that he visits rather than by a Gaussian natural selection function. Two kinds of pollinator preference are modeled. Pollinators with *absolute* preferences most prefer a certain value of the plant character and preference falls off as a Gaussian curve in either direction from that most preferred value. 'Preference' is meant to cover a whole spectrum of plant-pollinator interactions. Thus, tongue length of the pollinator can formally be modeled as absolute pollinator preference because the pollinator will have most success with flowers whose corolla length matches his tongue length. In contrast, pollinators with *relative* preferences most prefer a value of the plant character that lies some characteristic distance from the plant population mean. This preference mode implies that the pollinator surveys the plant population and perhaps forms a search image for plants with, say, greater than average concentrations of fragrance.

The second force acting on male pollinators is sexual selection. Females are assumed to base their mate choice on the average of phenotype of plants visited by the male. In the orchid bee example, mate choice would be based on the average fragrance of the orchids successfully visited by an individual male bee. Kiester et al.<sup>35</sup> employ an open-ended or psychophysical model of mating preference in which the tendency of a particular female to mate with a male is an exponentially increasing function of her characteristic ability to discriminate among males and the average of plant phenotypes (e.g. fragrances) visited by the male.

Female mating preference is assumed to be selectively neutral, as in some previous models<sup>45</sup>. The assumption seems plausible for euglossine bees in which males neither protect nor provision their mates or offspring.

The model predicts both stable and unstable evolutionary outcomes. As in previous models, stability depends on the amount of heritable variation in female mating preference. That variation exerts its destabilizing influence through the genetic coupling between mate prefer-

ence and sexually selected character. Strong effects of plants on the viability of male pollinators increase stability; large phenotypic variance in the plant character (e.g. fragrance) promote instability. In the unstable case, the plant character, pollinator preferences and mating preferences evolve at ever increasing speed, at least initially. In the stable case, the female pollinator population tends to lose net mating preference so that at equilibrium there is no average mate preference exerted in the population. This unique female outcome contrasts with the variety of female outcomes that occur in the absence of a plant-derived male trait<sup>45</sup>.

The equilibrium combination of plant and male pollinator attributes, however, is not unique. Instead an infinite number of outcomes is possible, the set forming a line of equilibria. With either absolute or relative pollinator preferences, at equilibrium the pollinators most prefer the average plant phenotype.

### 12. Discussion

A major conclusion from the present survey is that quantitative genetic models often reveal critical features hidden or falsely evaluated in verbal accounts of sexual selection processes. Weatherhead and Robertson<sup>69</sup> argued, for example, that females might evolve mating preferences for mates that provide inferior parental care, this liability being offset by the production of 'sexy sons'. The argument sounds plausible, at least to some ears. Nevertheless, a formal genetic model of the process contradicts their conclusions and shows that females will evolve preferences for mates with the best parenting abilities<sup>37</sup>. 'Good genes' arguments can lead to other erroneous conclusions. Following Zahavi's<sup>70</sup> logic, one might expect the evolution of unique, optimal female mating preferences when mate choice is based on a trait that is an indicator of male genetic quality. Instead Kirkpatrick<sup>38</sup> finds that mating preferences do not evolve to a unique endpoint: there is no optimal mate choice. Why do these two apparently plausible accounts of sexual selection lead to indefensible conclusions?

The key to understanding the failure of the handicap and 'sexy son' arguments is gotten by focusing on whether mate choice yields immediate fitness effects. When the female's mate choice does not affect her progeny count, as in Zahavi's<sup>70</sup> original proposal, there is no tendency for the evolution of unique, adaptive mate choice. When mate choice does affect the female's progeny count, as in the 'sexy son' model, females evolve unique, adaptive mate preferences.

In contrast, a sure route to erroneous conclusions is to treat the attributes of offspring as fitness currency and follow the logic of optimization used in good genes arguments. If we argue that evolution will maximize the sexual success of sons or the quality of offspring, we are bound to go astray for two reasons. Offspring attributes are not a simple fitness currency. Unlike an individual's zygotic progeny count, the viability or mating success of progeny depends on inheritance from the individual and its mates. Verbal arguments that gloss over this inheritance issue or fail to account for genetic effects on evolution can easily lead to false conclusions. Secondly, sexual selection is by nature a frequency-dependent process and

in general such processes do not result in fitness maximization<sup>42,49</sup>. Maynard Smith<sup>51</sup> has discussed both points in stressing the need to use evolutionarily stable strategies or other approaches that do not depend on fitness maximization, to model evolution under frequency-dependent selection. He also points out that explicit genetic models are needed to treat sexual selection processes because the evolutionary dynamics depend on genetic phenomena, such as the genetic coupling between male trait and mate preference induced by assortative mating. Thus, while verbal accounts of sexual selection processes may often be provocative, they are unlikely to be the last word. Formal genetic modeling will usually be necessary to test expectations and mitigate disputes.

Indeterminacy of equilibrium is a feature common to many of the models (table). Thus whenever selection does not act directly on female mate choice, there is a line of equilibria, with many possible combinations of mating preference and sexually selected male trait as evolutionary outcomes. The same feature holds in two- and three-locus models<sup>36,38,58</sup>. The expectation that evolutionary outcome will depend on initial conditions is one of the major contributions of Lande's<sup>45</sup> model and its descendants. Indeterminacy of outcome was alluded to by Fisher<sup>25,26</sup> but largely ignored in later discussions of sexual selection. When multiple characters are the focus of mate choice, the variety of possibilities at equilibrium is enormous with the equilibrium set forming a hyperplane<sup>45</sup>.

The family of sexual selection models illustrates a general rule for predicting the number of dimensions that constitute the equilibrium set. The dimensionality of the equilibrium equals the number of genetic degrees of freedom (the number of phenotypic characters with less than perfect genetic correlation) minus the number of independent selective constraints<sup>38,48</sup>. Thus in the sexual dimorphism<sup>43</sup> and sexy son<sup>37</sup> models with selection acting on both male and female characters, the equilibrium set is a point (dimensionality is zero). In the other models (table), selection does not act on one of the characters (female mating preference) and so the equilibrium is a line (dimensionality is one).

The existence of stable and unstable evolutionary outcomes is another major result from the models. The unstable case is of particular interest, because it corresponds to the runaway process first described by Fisher<sup>25</sup>, with accelerating evolution of male traits and female preference. The conditions favoring instability or runaway processes are identical or extremely similar in all the quantitative genetic models. Thus genetic variance in female mating preferences promotes instability as does stereotypy of mate choice and weak natural selection on the male trait. In many of the models, genetic variance in mating preferences, expressed as a genetic regression of mating preference on male trait, must exceed a critical ratio of mate choice stereotypy to strength of viability selection on the male trait in order to trigger the runaway. Homologous female traits may also evolve at accelerating rates during the runaway due to genetic correlation with sexually selected male traits<sup>48</sup>. Furthermore the runaway may occur over a broad geographic area<sup>46</sup>.

The need for empirical research in a number of areas is highlighted by the models. In particular we need new

information on the nature of mate choice, on the inheritance of mate choice and sexually selected traits and on the intensities of selective forces acting in nature. Estimates of critical variables in natural populations could tell us whether runaway sexual selection is plausible and whether mate choice acts on arbitrary male attributes, and could enable us to explore many other issues.

Typology has prevailed in past studies of mate choice, with a focus on average behavior rather than on variation within populations. Consequently we have a poor understanding of how individual females react to the spectrum of male phenotypes in natural populations and how females vary in those reactions. Such phenotypic studies are especially important because they lay the groundwork for genetical studies of mate choice, a virtually unexplored field. Promising starts at characterizing phenotypic variation in mate choice have been made by Boake<sup>7</sup> and Houck et al.<sup>32</sup>. The basic issue of the form of mate preference (e.g. absolute, relative or open-ended) is also critically important because the mode of choice also affects the possibility of a runaway process.

The importance of a series of genetical parameters is revealed by the models. Perhaps the most critical of these genetical issues is the existence and magnitude of genetic covariance between mating preference and sexually selected traits. This genetic covariance plays a critical role in predictions of both evolutionary trajectory and instability, yet no estimates of it have been made in either experimental or natural populations. The covariance is expected to originate and be perpetuated as a consequence of linkage disequilibrium arising from assortative mating<sup>45</sup>. Breeding designs of the kind usually employed to estimate such a genetic parameter<sup>23</sup> will impose a relaxation of normal assortative mating and so the linkage disequilibrium and genetic covariance will gradually decay from generation to generation. Thus special care must be taken to estimate the parameter soon after genotypes are sampled from nature and to correct for decay in covariance due to relaxation of assortative mating.

Decay in genetic correlation between the sexes during the evolution of sex-limitation is an unresolved empirical issue. The supposition of high genetic correlation between the sexes in homologous traits during the early stages of sexual differentiation is supported by genetic studies of species with slight or modest sexual dimorphism<sup>43</sup>. Pleiotropic gene action is undoubtedly responsible for the observed correlations between expression in male and female relatives. The correlation necessarily approaches zero as once one sex evolves to the point of not expressing the trait and presumably the correlation passes through intermediate values during the elaboration of extreme sexual dimorphism that precedes sex limitation. Remarkably, no genetical studies have measured the genetic correlation in traits with extreme sexual dimorphism. Thus we cannot make quantitative assessments of correlated female responses to sexual selection on males, as modeled by Lande and Arnold<sup>48</sup>, during the interesting phase when sexual dimorphism is pronounced.

Boake<sup>8</sup> has stressed the need for estimates of genetic correlation between male mating success and other components of fitness. Quantitative genetic theory provides a means of measuring male 'genetic quality' for it can be

viewed as the males' breeding value for fitness or its major components (e.g. viability), measured by scoring fitness in large samples of progeny as described by Falconer<sup>23</sup>. Thus a key test of the 'good genes' outlook is to seek correlations between breeding values for male mating success (or sexually selected traits) and nonsexual components of fitness. Genetic correlations are correlations in breeding values. Boake<sup>8</sup> outlines a strategy for estimating the critical parameters and illustrates it with an example.

Phenotypic correlation between male fitness components plays a key role in Kirkpatrick's<sup>37</sup> model for sexual selection when males provide parental care. Thus a negative correlation between male mating success (e.g. harem size) and the average fecundity of mates constrains the equilibrium state of paternal care to a value that maximizes male survivorship. Kirkpatrick<sup>37</sup> refers to this tradeoff situation as limited male reproductive potential. In contrast, when male reproductive potential is unlimited, mating success is not correlated with mate fecundity and paternal care equilibrates at a value that maximizes mate fecundity but that value may be maladaptive for male survival. Downhower and Armitage<sup>18</sup> pursued the critical tradeoff issue in a field study, but many subsequent studies of polygynous populations have neglected the issue. Arnold and Wade<sup>4</sup> show how the tradeoff can be measured as a weighted covariance that also represents part of the total opportunity for selection in the male population.

A balance between sexual and natural selection at equilibrium is a prediction of all the quantitative genetic models and one anticipated by Darwin<sup>15</sup>. I know of no quantitative test of this expectation in natural populations. A variety of studies have detected or measured sexual selection on male attributes, but studies documenting viability selection on sexually-selected traits are rare (nonexistent?). There is a great need for studies that measure sexually selected traits, mating success and survivorship in the same population so that the strengths of sexual and natural selection can be compared.

Lande's<sup>46</sup> model of sexual selection in a cline suggests that ethological isolation can evolve rapidly over a wide geographic area in the absence of postzygotic reproductive isolation. In many taxa postzygotic barriers do not accompany prezygotic isolation<sup>64</sup>, contrary to the view the ethological isolation is mainly elaborated by direct selection in secondary contact zones. Thus Lande's results suggest that conspecifics exerting sexual selection, rather than sister taxa, may be the main selective agents in the evolution of reproductive isolation. The Fisher-Lande model for stasipatric speciation points to the need for clinal studies of sexual selection, an almost entirely neglected field of enquiry.

A number of sexual selection processes have never been analyzed with formal genetic models and might be the focus of future theoretical work: 1) Sexual selection arising from male contest or combat is an unexplored area. Models of sexual selection via mate choice suggest that male-male interaction could cause the elaboration of weapons deleterious to the survival of the weapon-bearing male. 2) Male-male interactions commonly consist of offensive and defensive tactics<sup>2</sup>. The joint evolution of such tactics might involve complicated dynamics. 3)

Fisher<sup>25</sup> suggested that the male displays might intimidate rivals as well as impress females. He predicted that a process of 'war propaganda' among males might lead to the evolution of displays but that these would not be as elaborate as the products of selection via mate choice. Borgia<sup>9</sup> has discussed this possibility but the process has not been formally modeled. 4) Many authors have proposed that females should evolve preferences for attributes used by males in sexual combat. A formal model would involve episodes of viability selection, combat and then sexual selection via mate choice. 5) Many species possess epigamic characters that appear to be sexually selected but with no sexual dimorphism<sup>33,34</sup>. Darwin<sup>15</sup> and Huxley<sup>33</sup> proposed a process of *mutual sexual selection* for such species, with each sex exerting mate choice on the other. Could such a process lead to runaway sexual selection? 6) Fisher<sup>26</sup> proposed that evolutionary elaboration of sexually selected traits would occur suddenly with periods of stasis between epochs of rapid evolution. Rapid development of one trait might be followed by sudden elaboration of another trait in the next epoch, perhaps with deterioration of the traits that were sexually selected in the early epochs. A multivariate model of mate choice might test Fisher's idea of an uneven tempo for evolution by sexual selection.

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