

A Critical Review of Sexual Selection Models

G. Borgia

**Department of Zoology
University of Maryland
College Park, MD 20742, USA*

Abstract. The evolution of extreme sex-limited male display traits is a poorly understood process. Here I suggest that the claims for acceptance of some runaway models of sexual selection are not supported by the available data. Moreover, there exist other plausible models for the evolution of male display characters that have not been considered in detail. Many of the models discussed as alternatives are not necessarily in conflict and may help explain the same phenomena. I discuss constraints on the evolution of display characters, especially the effect of competition among coevolving male trait and female choice genotypes, and how such effects can influence the predictions of models. It is suggested that an understanding of the evolution of male display characters requires detailed empirical studies. Methods for evaluating models for the evolution of male display characters in natural populations are considered.

INTRODUCTION

A strong divergence of opinion has recently developed over how female choice can shape patterns of male sexual display. Most attention has focused on species in which males have no role in parental care and cannot directly control female mating decisions. It is in these species, such as peafowl and many birds of paradise, that some of the most extreme sex-limited male displays have evolved. A variety of models have been proposed that attempt to explain the evolution of these male display traits, but two have received the most attention: the 'good genes' models and runaway models.

Fisher (1980) initiated the modern discussion of the evolution of extreme male display characters when he proposed the 'runaway process.' According to his model, a consistent mating preference by even a small proportion of females in a population in which males initially show no strong sexual dimorphism can lead to (a) a spread in the choice pattern among females, and (b) continued enhancement of male characters chosen by females to the point of extreme sex-limited development. It predicts no enhancement of offspring

Moreover, current versions of these models are relatively simplistic and are based on numerous unproven assumptions (e.g., O'Donald 1983; Seger 1985; Andersson and Charlesworth, both this volume). It is possible that none of the currently popular models is correct and that other mechanisms are operating. There are numerous other plausible models for the evolution of extreme characters that have not yet been explored in detail. This is coupled with an almost complete ignorance of the basic life history of species with extreme male sexual displays and no measurement of quantitative genetic and other parameters that have figured prominently in the discussion of recent models. So, while recent models have fueled an interesting and often intense debate over the plausibility of various explanations for the evolution of exaggerated male display traits, given their limitations and our lack of knowledge about what happens in nature, it is clear that this problem is far from resolved.

My objective in this paper is to discuss some distinguishing features of current models of sexual selection, present some plausible alternatives, and consider promising methodologies for testing these models. Our sparse knowledge of how sexual selection operates in species with extreme male display makes it difficult to determine how these male characters evolved. Without more information, we are left to determine if different models are plausible and to devise tests that might distinguish among these models in future studies. Solving the difficult problem of the evolution of extreme display will require an open-minded search that carefully evaluates the full range of theoretical possibilities and has a solid basis in the biology of species with extreme male displays.

GOOD GENES MODELS

There are several types of results supporting the possibility that selection for good genes occurs. Maynard Smith (1956) has shown that in *Drosophila*, females discriminate against inbred males based on the vigor of male display. He interpreted this as female choice for avoiding poor quality sires and, in an extreme version, this may be viewed as selection for good genes. If selection has favored females who choose males with vigorous displays, it is also possible that males have morphological characters with similar function.

There are currently no solid demonstrations of good genes effects. Mayr (1963) and others have suggested that male display characters often arise as species identification characters. It is costly for females to produce hybrids so there is selection on females to choose males with characters distinctive of their own species. Although this can be viewed as an extreme version of selection for good genes, it is not the same as demonstrating that finer within-species discriminations are also beneficial. Partridge (1980) has shown that females able to choose among males have higher fitness than females who are assigned mates. It is not clear if the observed effect was due to male interactions or to

fitness outside the context of sexual selection. Recent modelers (Lande 1981; Kirkpatrick 1982, 1986) suggest that characters with negative effects on the fitness of offspring may evolve by processes similar to that first described by Fisher.

Good genes models of female choice propose that female discrimination among males can lead to heritable viability gains for offspring. Extreme male display traits are commonly envisioned to have evolved as indicators that enhance the females' ability to select high quality sires. Currently popular models propose that male traits are expressed conditionally, that males with the fullest expression are the most likely to produce vigorous offspring. Different models focus on different qualities that male characters are supposed to indicate. Some of these are the ability to survive to old age (e.g., Howard 1979; Halliday 1978), disease resistance (Hamilton and Zuk 1982); overall vigor (e.g., Trivers 1972; Andersson 1982, 1986), and male dominance in aggressive encounters (Borgia 1979; Borgia et al. 1985).

Apart from these two types of models there exist additional alternative explanations for the evolution of extreme male display characters. Parker (1983) proposed that extreme displays evolve because they enhance male advertisement and allow displaying males to be more readily discovered. LeCroy et al. (1980) suggest that male plumage displays evolve in the context of inter-male competition and that female choice is unimportant in their evolution. Finally, there may be instances where male displays provide some immediate proximate benefit to choosing females. For example, female bowerbirds may prefer males with bowers because it gives them a safe place from which they can observe a courting male (Borgia et al. 1985).

Advocates of the runaway model have been particularly outspoken in asserting the correctness of their views. For example, Davis and O'Donald (1976) argued that there is no other suitable model for the evolution of these characters, and there are no important criticisms of the runaway model; concluding with the view that '... the evolution of extreme sex-linked characters is fully explained by Fisher's model.' In a critique of what he calls the 'Panglossian view,' Arnold (1983) claims that good genes models cannot work because '... there is no direct force of selection on mating preferences.' This conclusion is based on the assumption that '... the number of progeny produced by the female is unaffected by mate choice.' More recently Kirkpatrick (1986) subsumed all good genes models under the term 'handicap' and, when the specific model failed, asserted that none of these models work.

The extreme certitude of these statements belies our ignorance of how exaggerated male displays evolve. Recent models have established the plausibility of the runaway process (e.g., Lande 1981) and good genes models (Andersson 1986) as mechanisms for the evolution of extreme male display characters. Even so, evidence that either of these processes is the exclusive or even a contributing cause for the evolution of exaggerated display is lacking.

display traits, but they do not produce the coevolutionary escalation in display and choice that was described by Fisher (1930). Hence, these models are not really equivalent as has been claimed (Arnold 1985). Moreover, the differences raise questions about the usefulness of these particular models as explanations for the evolution of extreme male displays.

O'Donald and Majerus (1985) have shown in studies of ladybird beetles that only a few loci are responsible for controlling female choice and male traits selected by females. This simple genetic system would prevent the ongoing type of selection envisioned in quantitative genetic models and because few-locus models do not explain extreme elaboration of male characters, it is not clear that the evolution of extreme male displays can be explained by available models if display and choice traits are not polygenic.

EXAGGERATION WITHOUT A GENETIC CORRELATION

Recent quantitative genetic models have assumed that a genetic correlation between the male trait and female preference is required to produce extreme male displays. This is not necessarily so. Consider the case in which as open-ended (supernormal) female preference is established in a population where the choice trait is controlled by only a small number of loci that become fixed. At the time the preference is established, no males show extreme displays, but with time sufficient mutations occur among males to allow this persistent preference to select for males with exaggerated displays. This result will be an elaborated male character without any coevolution of the female preference with the male trait. Unlike the claims of quantitative genetic models (e.g., Arnold 1983), the nature of female preferences can have a dramatic effect on evolutionary outcomes. The female preference that selects for extreme male character development could evolve in a variety of contexts. For example, it may be a result of selection for a character that allows females to obtain immediate benefits or from the evolution of a female preference as described by Kirkpatrick (1982). The key point is that the ultimate elaboration of the male character in this model is dependent on the type of female preference that is already established and not on the existence of a genetic correlation between the female choice and male display traits.

INITIATING THE SELECTION PROCESS

Fisher envisioned a preference initially linked to real benefits where a genetic correlation developed and led to a runaway process that produced extreme male characters. Female preferences that initially provide some real benefits may have a slight advantage over other less advantageous preferences. This may occur because a rare beneficial preference would be less subject to loss by drift and because benefits associated with these choice patterns may be

female choice, and Schaffer et al. (1984) were unable to replicate the original effect.

A theoretical difficulty seen for good genes models is the possibility that heritable variation in the benefits for choosing males is exhausted (Williams 1975; Borgia 1979; Charlesworth, this volume). Zahavi (1975) pointed out that for these models to work, they should be based on assessment of genome-wide characteristics of males. Given this, it is possible that shifting (Borgia 1979; Andersson 1986) or cycling (Hamilton and Zuk 1982) conditions can maintain sufficient variability in males so as to produce heritable gains for discriminating females in each generation (see also Charlesworth, this volume).

Selection for good genes in models of polygynous populations has usually been overshadowed by Fisherian runaway selection for the male trait (Maynard Smith 1985). Andersson (1986) circumvented this problem by modeling a monogamous population where the male advantage from polygynous matings could be eliminated. However, the most interesting cases of elaboration of male characters occur in polygynous populations, so it is reasonable to ask if the type of selection Andersson modeled has any important effect on the male display characters that evolve in polygynous species? Fisher (1930) suggested that what I call 'good genes selection' may be important in initially increasing the number of preferred traits. Good genes selection may partly determine the types of traits that evolve, but it may have little effect on the extent to which they are elaborated.

RUNAWAY MODELS

Much attention has been directed at demonstrating Fisher's premise that extreme male displays evolve as a result of a coevolution of male display and female choice. These models differ from Fisher's in not assuming an initial advantage for these traits. Both quantitative genetic (e.g., Lande 1981) and two-locus models (e.g., Kirkpatrick 1982) have been used to determine if the runaway process can operate. Most attention has focused on Lande's quantitative genetic model in which he was able to show that the self-reinforcing pattern suggested by Fisher could develop between female preference and male display characters. In the model, female choice is neutral and propels changes in male display characters until they are checked by the costs of extreme displays to males. The model produces a line of equilibrium that represents a balance between the effects of female choice and the cost of male characters.

These models differ in two important respects. The quantitative genetic models require that female choice and male display characters be highly polygenic; under this condition the models can explain an elaboration of male traits and female preferences as suggested by Fisher. The two-locus models describe the increase in frequency of genes coding for female choice and male

sufficient to overcome the costs of choosing that might otherwise halt the evolution of the female preference. In recent genetic models (e.g., Kirkpatrick 1982), the evolution of preferences is typically frequency-dependent. New choice traits must reach a threshold frequency in the population before they can replace an established alternative. So while it is possible that these traits reach threshold frequencies by drift, it is more likely that differences in the initial benefits produced by traits affect their success in becoming established as suggested by Fisher (1958; see also Heister 1984). This implies a bias in which the display traits most likely to evolve are those that have, at least at some time in their evolution, proven advantageous to choosing females.

ARE MALE DISPLAY CHARACTERS ADAPTIVE?

Much of the interest in the evolution of extreme male display traits results from the suggestion that runaway selection can lead to nonadaptive female choice (e.g., Lande 1981; Kirkpatrick 1982). Such treatments emphasize that a female preference for elaborated male traits can produce characters that lower the survivorship of sons and decrease the vigor of daughters. While this is not a necessary result, it has been used to distinguish these models from adaptive (good genes) models. This prediction of nonadaptive outcomes contrasts with empirical observations of well studied resource-based mating systems where females consistently evolve to choose males who provide real benefits (e.g., Thornhill 1976, 1980; Downhower and Brown 1980; Borgia 1982; Pleszczyńska 1978). Possibly, selection is so different in these two types of mating systems that one produces adaptive outcomes while the other does not.

The prediction that the runaway process produces nonadaptive outcomes is based on an assumption that male display traits that characterize populations are those that are established first. Thus, models for extreme male displays differ from most other recent evolutionary models in not comparing a full range of competing alternatives and allowing invasion of qualitatively different female preference patterns. If this were done, then the predicted outcomes of runaway models might be very different (but see Kirkpatrick 1982). Competition among alternative female choice patterns should lead to replacement of patterns without beneficial effects for females' offspring by patterns with beneficial effects. A consistent pattern of selection of this type should lead to adaptive patterns of mate choice. This argument implies that our expectations concerning the degree of adaptiveness of female choice will be related to how easy it is for novel, advantageous female choice patterns to replace established, less advantageous alternatives. If replacement is common then female choice will be adaptive, but if replacement is rare then choice will be nonadaptive and arbitrary.

This result suggests a format in which runaway and good genes selection can work together to shape sexual selection. The issue of competition among

female preferences is critical in understanding which male display characters evolve and deserves much more attention that can be given here. Competition among female preferences might influence the outcome of sexual selection in several contexts.

1) Preference curves describe the intensity of individual female preference relative to the degree of male character development. Above I suggested that differences in preferences can affect the outcome of sexual selection. However, if some types of female preference curves have consistent advantages in direct competition with others, then the same dominant types of preference curves may characterize female choice in most species. The result might cause widespread evolution of extreme male characters. The recurrent evolution of elaborated male displays in non-resource-based mating systems might reflect this pattern of selection. Of course, if the success of different female preferences is situation-dependent, then a wider array of outcomes might be expected.

2) Male display traits that have sex-limited expression will be favored over those that are fully expressed in both sexes. Even partial expression of male display traits in females can be expensive to them, so selection should favor females who choose male traits that are expressed only in males. This pattern of selection emphasizes the female preference and male trait as coevolving characters. The cost of the display trait as expressed in both daughters and sons will affect the success of these characters in competition with other coevolving female preferences and male display traits.

3) Polygenic display traits lose in competition with similar single gene traits. A substantial substitutional load may occur with rapid changes during the runaway process. Arnold (1985) notes that this load is due to pleiotropic effects of the substitutions of many alleles associated with the evolution of polygenic male display characters and female choice traits. Where replacement of traits can occur female choice traits, which evolve with less load, should have an advantage. Thus, there should exist a bias in favor of male display and female choice traits that are not highly polygenic, thereby creating less of a substitutional load. Load could affect evolution of display in other ways. If display and choice traits were polygenic, perhaps resulting from selection for modifiers once the choice trait was established, then the effects of substitutional load may make large qualitative evolutionary changes less likely to occur. These effects may make it more difficult for new choice patterns to invade or to drift along the line of equilibrium (see Lande 1981).

A central issue that appears to separate these models is the extent to which competing alternatives can be replaced. In the "no genetic correlation" (see above) and current runaway models, the persistence of a choice trait favoring extreme males requires that choice traits are not easily replaced by a more advantageous competing alternative. The opposite is true for models allowing competition between alternatives; extreme characters are maintained precisely

because they are the most successful of the competing alternatives. The first case predicts sexual selection for nonadaptive, arbitrary male display characters, whereas in the second, fitness-maximizing traits are expected.

TESTING MODELS

Several distinct models have emerged that give very different predictions about the outcomes of sexual selection. In order to determine which of these alternatives provides the most realistic view of sexual selection we need to determine if there is an important role for invading preference traits, if female choice is characterized by the type of preferences that are initially established, or if some intermediate condition obtains. Modeling can show which of the above-mentioned scenarios provides realistic possibilities for the evolution of exaggerated displays and if the parameters defined in the model are consistent with properties of real organisms. However, we must depend on empirical tests to determine if particular models actually work for living organisms and if they describe the process that caused the evolution of a particular extreme male display. Two general types of tests have been proposed.

The first involves measurement of parameters described in sexual selection models to determine if the conditions stated in the proposed model are met under real conditions. This is a potentially important test of models, but it may be exceedingly difficult to carry out. Species with the most extreme male character development, such as birds-of-paradise, tend to be long-lived and have complex mating behaviors that are difficult to observe in nature. Individual females may mate only once a year in situations that cannot be easily duplicated in the laboratory. This complicates attempts to measure variables such as genetic covariance between males and females and heritability of fitness which must be measured with exceedingly large sample sizes. Deviations from the assumptions of models may require more difficult measurements of parameters. For example, a deviation from the assumptions of mutation-selection balance would require that variance and covariance for choice and display characters be measured not as point estimates but as functions of the intensity and duration of selection. Even with these difficulties attempts should be made to measure factors affecting the models we have discussed including the degree of polygyny of display and choice traits, the amount of load incurred in attempts to select on these characters, the degree of sex-limited expression (and causes for its expression in females), the shape of female preference curves, and the heritability of fitness.

The second option for testing models for the evolution of extreme male characters is the detailed study of species with male display characters to determine which of the available models best predicts observed patterns of male character evolution and display. Specific versions of the indicator, proximate benefit, and advertisement models make distinctive predictions that

can be tested. For example, the male dominance model predicts that male display characters should be good indicators of dominance. The model can be falsified by tests to determine if females choose males with the indicator and if the indicator can be used to predict dominance (see Borgia 1985a,b). Similar predictions can be tested for indicators of age, vigor, or disease resistance. Proximate mechanism models can be directly tested to determine if male displays provide some immediate benefit. This is not so with current versions of runaway models that predict arbitrary or indeterminate results. Models that predict all possible outcomes cannot be directly falsified. However, indirect tests can be made to determine if male displays show a consistent pattern in relation to the habitats where they occur. For example, bower of bowerbirds appear to differ in relation to the habitat where a species lives (Borgia et al. 1985). In open habitats, bowers offer more cover to females. This is consistent with a hypothesis that the bower functions to protect visiting females and suggests that the bower display is not arbitrary. However, there are several alternative possibilities.

The interpretation of results and attempts to use them to evaluate models will not doubt be controversial. Consider Arnold's (1983) prediction from Lande's model suggesting that there should be high intraspecific geographical variation in male display characters among polygynous species with extreme male character development. This hypothesis has not been systematically tested for any species with extreme display. However, the most extreme cases known of intraspecific variation in male display traits occurs in monogamous sparrows in which the function of the display song appears to have little to do with female choice (Baptista and Morton 1982). This result emphasizes the need for careful tests and interpretation of results.

In most instances the hypotheses lead to straightforward predictions about the types of male display traits and associated behaviors that are expected to evolve. An exception, however, are the runaway models which, in some versions, can lead to almost any outcome (Lande 1981; Kirkpatrick 1982, 1986). Predicting the outcome of the runaway process is further complicated because Fisher's original version of the model included the elaboration of a male character through female choice for adaptive characters.

Comparisons of male displays in closely related species provide an opportunity to evaluate predictions about the stability of display traits. If display traits are unstable then large differences in male display characters among closely related species should be common, whereas a model of stable sexual selection would predict the species differentiate and develop different display patterns in a bifurcating pattern with few evolutionary reversals. If male display traits are commonly stable (and the conditions for male display are not grossly different), then the degree of differentiation in male traits should follow a pattern very similar to a dendrogram based on genetic overlap among species. Shifts in patterns of male displays should be associated with changes in

conditions that can qualitatively change the display. The Fisherian mechanism should give a more irregular pattern, often with closely related taxa showing little similarity in their sexual display traits. Frequent shifts in male display patterns that are not associated with any obvious adaptive cause, e.g., a shift in habitat, would support Fisherian runaway models.

The discussion of the evolution of sexually selected traits has taken on a much wider focus than a mere comparison of models. At issue is a whole complex of ideas of how selection works in a complicated social environment. Lande's model for runaway selection requires that characters be highly polygenic, that there be a mutation-selection balance, that male display characters are arbitrary and have no impact value to the female or her offspring, that initially established characters be resistant to invasion by new competing types, that selection for male display characters is rapid rather than gradual, that the results of sexual selection be unstable and subject to drift in small populations, and that drift in small populations be responsible for the evolution of species-identifying characters. These assumptions need to be tested.

Not all models for the evolution of extreme characters incorporate Lande's assumptions, and these models may provide more realistic views of how extreme characters evolve. Even so these models still rely on important simplifying assumptions (e.g., haploidy) that may have important and unrecognized effects on their conclusions. Efforts must be made to produce models that are more faithful to the genetic system being described. This may require an emphasis on simulation rather than analytic models. It is critical to explore the significance of competition among qualitatively different female preferences. Arnold (1985) and others have drawn attention to the nonadaptive aspects of sexual selection, but this appears to depend on the assumption that competition between preferences does not occur.

Very little real progress on these issues will be made with only theoretical arguments. We are in need of empirical tests of assumptions of current models so that we can make preliminary tests of hypotheses and eventually build a more refined set of models. As Arnold (1983) points out, 'Models should be viewed as guides for field and laboratory work: only empirical work can produce generalizations about the natural world.' A large body of data on the behavior, ecology, and genetics of mate choice in species with extreme displays is needed to resolve current issues. Collection of such data should be the focus of an intensive effort by behavioral and evolutionary biologists.

Acknowledgements

I thank the many attendees at the Dahlem Workshop for their helpful comments. Additional suggestions came from A. Houde, C. Loffredo, and J. Lauridsen.

REFERENCES

- Andersson, M. 1982. Sexual selection, natural selection and quality advertisement. *Biol. J. Linn.* 17: 375-393.
- Andersson, M. 1986. Evolution of condition-dependent sex ornaments and mating preferences: sexual selection based on viability differences. *Evolution* 40: 804-816.
- Arnold, S. 1983. Sexual selection: the interface of theory and empiricism. In: Mate Choice, ed. P. Bateson, pp. 67-107. Cambridge: Cambridge Univ. Press.
- Arnold, S. 1985. Quantitative genetic models and sexual selection. *Experientia* 41: 1296-1310.
- Baptista, L.F., and Morton, M.L. 1982. Song dialects and mate selection in montane white-crowned sparrows. *Auk* 99: 537-547.
- Borgia, G. 1979. Sexual selection of the evolution of mating systems. In: *Sexual Selection and Reproductive Competition*, eds. M.S. Blum and N.A. Blum, pp. 19-80. New York: Academic Press.
- Borgia, G. 1982. Experimental changes in availability of oviposition sites: effect on mating success of male *Scatophaga stercoraria*. *Evolution* 36: 307-312.
- Borgia, G. 1985a. Bower destruction and sexual competition in the satin bowerbird (*Ptilonorhynchus violaceus*). *Behav. Ecol. Sociobiol.* 18: 91-100.
- Borgia, G. 1985b. Bower quality, number of decorations, and mating success of male satin bowerbirds (*Ptilonorhynchus violaceus*): an experimental analysis. *Anim. Behav.* 33: 266-271.
- Borgia, G.; Pruett-Jones, S.; and Pruett-Jones, M. 1985. The evolution of bowers as markers of male quality. *Zeit. Tier.* 67: 225-236.
- Davis, J., and O'Donald, P. 1976. Sexual selection for a handicap: a critical analysis of Zahavi's model. *J. Theor. Bio.* 57: 345-354.
- Downhower, J., and Brown, L. 1980. Mate preferences of female mottled sculpins, *Cottus bairdi*. *Anim. Behav.* 28: 728-734.
- Fisher, R.A. 1930. *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.
- Fisher, R.A. 1958. *The Genetical Theory of Natural Selection*, 2nd ed. New York: Dover.
- Halliday, T. 1978. Sexual selection and mate choice. In: *Behavioral Ecology: and Evolutionary Approach*, eds. J.R. Krebs and N.B. Davies, pp. 180-213. Sunderland, MA: Sinauer.
- Hamilton, W.D., and Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? *Science* 218: 384-387.
- Heisler, I.L. 1984. A quantitative genetic model for the origin of mating preferences. *Evolution* 38: 1283-1295.
- Howard, R.D. 1979. Estimating reproductive success in natural populations. *Am. Natural.* 114: 221-231.
- Kirkpatrick, M. 1982. Sexual selection and the evolution of mate choice. *Evolution* 36: 1-12.
- Kirkpatrick, M. 1986. The handicap mechanism of sexual selection does not work. *Am. Natural.* 125: 788-810.
- Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. *Proc. Natl. Acad. Sci. USA* 78: 3721-3762.
- LeCroy, M.; Kulipi, A.; and Peckover, W. 1980. Goldie's bird of paradise: display, natural history, and traditional relationships of people to the bird. *Wilson Bull.* 92: 298-301.
- Maynard Smith, J. 1956. Fertility, mating behavior, and sexual selection in *Drosophila subobscura*. *J. Genet.* 54: 261-279.

- Maynard Smith, J. 1985. Sexual selection, handicaps and true fitness. *J. Theor. Bio.* 115: 1-8.
- Mayr, E. 1963. *Animal Species and Evolution*. Cambridge, MA: Harvard Univ. Press.
- O'Donald, P. 1983. Sexual selection by female choice. In: *Mate Choice*, ed. P. Bateson, pp. 53-66. Cambridge: Cambridge Univ. Press.
- O'Donald, P., and Majerus, M.E.N. 1985. Sexual selection and the evolution of preferential mating in ladybirds. I. Selection for high and low lines of female preference. *Heredity* 55: 401-412.
- Parker, G.A. 1983. Mate quality and mating decisions. In: *Mate Choice*, ed. P. Bateson, pp. 141-166. New York: Cambridge Univ. Press.
- Partridge, L. 1980. Mate choice increases a component of offspring fitness in fruit flies. *Nature* 283: 290-291.
- Pleszczyńska, W. 1978. Microgeographic prediction of polygyny in the lark bunting. *Science* 201: 935-937.
- Schaeffer, S.W.; Brown, C.J.; and Anderson, W.W. 1984. Does mate choice affect fitness? *Genetics* 107: 94.
- Seger, J. 1985. Unifying genetic models for the evolution of female choice. *Evolution* 39: 1185-1193.
- Thornhill, R. 1976. Sexual selection and feeding behavior in *Blattica apicalis* (Insecta: Mecoptera). *Am. Natural.* 110: 529-548.
- Thornhill, R. 1980. Competitive, charming males and choosy females: was Darwin correct? *FLA Entomol.* 63: 5-30.
- Trivers, R.L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man*, ed. B.G. Campbell, pp. 136-179. Chicago: Aldine Press.
- Williams, G.C. 1975. *Sex and Evolution*. Princeton: Princeton Univ. Press.
- Zahavi, A. 1975. Mate selection - a selection for a handicap. *J. Theor. Bio.* 53: 205-214.

Sexual Selection: Testing the Alternatives
eds. J.W. Bradbury and M.B. Andersson, pp. 67-82
John Wiley & Sons Limited
© S. Bernhardt, Dahlem Konferenzen, 1987.

The Evolutionary Forces Acting on Female Mating Preferences in Polygynous Animals

M. Kirkpatrick

*Department of Zoology
University of Texas
Austin, TX 78712, USA

Abstract. A framework for discussing the forces responsible for the origin and evolution of female mating preferences is developed. Although preferences can arise as adaptations to enable females to discriminate between prospective mates, they may often arise as side effects of biases intrinsic to the sensory system used by females. Once established, these biases may often evolve in response to selection pressures unrelated to mating. This is illustrated by an example from hylid frogs in which ecological factors can cause body size to evolve, which causes female auditory tuning and hence mate preference to change as a byproduct. The forces involved in the evolution of established mating preferences can be organized into three categories: (a) direct selection, in which preferences are selected because of their effects on female survival and fecundity; (b) indirect selection, in which preferences evolve as a correlated response to selection on other traits (such as male secondary sexual characters); and (c) other forces, such as group selection and genetic drift. The qualitative effects and relative importance of each of these are discussed. The final section of the paper presents a model for the evolution of preferences when females experience costs while searching for mates.

INTRODUCTION

There is now widespread, though not universal, acceptance of Darwin's (1859, 1871) hypothesis that female mating preferences have been responsible for the evolution of secondary sexual characters in the males of many species of animals. In contrast to this consensus, there is little agreement about what forces are important in the evolution of the preferences themselves.

This paper develops a framework for the discussion of evolutionary forces that give rise to and cause the subsequent evolution of mating preferences. The topic is developed in three sections. First is an examination of how preferences may originate. It is emphasized that observation of the effects of preferences on male characters can mislead the search for what caused their origin. Second, a