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SEXUAL SELECTION AND THE EVOLUTION OF MATING SYSTEMS

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INTRODUCTION

A precise understanding of the manner in which mating associations between individuals develop is essential for generating a comprehensive model of social interactions. Not only is mating behavior a key social event in any species, but it may have important effects on patterns of parental behavior (Trivers, 1972), parent-offspring interaction (Trivers, 1974; Alexander, 1974), the evolution of sociality (Trivers and Hare, 1976), sex ratios (Fisher, 1958; Hamilton, 1967), and the population genetics of breeding units (Williams, 1975). In spite of the central role of mating behavior, our ability to predict patterns of matings in any population is relatively limited.

Darwin (1871) noted two patterns by which mating associations are formed. He considered (1) "a constantly recurrent struggle between males for the possession of females" (p. 213) and (2) choice by females in which they "select those (males) which are vigorous and well armed, and in other respects most attractive" (p. 214). He also recognized the relationship of extreme sexual dimorphism to high variance in male reproductive success or "polygamous marriages." However, he did not explicitly relate patterns of mate choice to sexual dimorphism and variance in reproductive success. From his discussion of male elephant seals physically controlling harems of females (p. 523), he seemed aware of the relationship of large male size to success in controlling females, but this idea was not developed further.

For some time after Darwin's work, mating systems were classified into types without concern for how natural selection might cause observed differences. Various criteria for classification have been used (see Selander, 1972, for review), but the significance of these factors as causes of observed variation in mating type has seldom been considered in detail.

ISBN 0-12-108750-6

Important departures from this kind of analysis were provided in salient papers by Orians (1969) and Trivers (1972). These authors refocused analysis of mating systems on fundamental problems of mate selection and placed particular emphasis on individual behaviors designed to maximize reproductive gain. However, models developed in each case tended to minimize differences in types of male-female mating relationships and gave little detail relating how such variation might evolve.

The approach taken here is to emphasize differences in patterns of sexual selection. Four different types of male-female mating relationships are considered in relation to (1) how each pattern influences reproductive success of individuals and (2) what conditions are likely to cause each of the different patterns of mate selection. A critical part of this analysis is to evaluate genetic and material, or non-genetic, benefits described by Orians (1969) as an important criterion for mate choice by females.

PREDICTING PATTERNS OF MATING SUCCESS

Types of Male-Female Interactions

Bateman (1948) provided both experimental and logical bases for an understanding of the operation of mating systems. In a series of experiments with *Drosophila,* he showed that males' reproductive success varied over a wider range than that of females. Males were able to gain added reproduction with increased numbers of matings, but similar opportunities for multiple matings by females led to no increase in the output of offspring. Two important conclusions from the results of these experiments seem to apply to most mobile outbreeding species. First, female gametes are rare relative to those of males. Under all but lowest density conditions, females should have little difficulty in obtaining sufficient sperm to fertilize eggs. Second, under no conditions should all males (who provide only sperm) realize their reproductive potential. High levels of mating success of some males necessarily come at the expense of other males. Low reproductive variance simply describes a situation where all males have unsatisfied reproductive capabilities.

These relationships have been used in constructing various mating system models (Maynard Smith, 1958; Orians, 1969; Trivers, 1972). Each of these models suggests that the relative shortage of gametes produced by females places the female in control of the mating circumstance. It is stated or implied that the ability of females to control male access to gametes allows them to choose mates who give them or their offspring the highest return on investment in calorically expensive eggs.

Criteria females use in selecting mates may be exclusively based on the *genetic quality of mates* (Fisher, 1958; Williams, 1966; Orians, 1969; Alexander, 1975; Ghiselin, 1974; Trivers, 1972; but see Williams, 1975; Davis and O'Donald, 1976). Presumably, female choice of some males leads to advantageous heritable differences in offspring. Males may use energy and effort not spent or not likely to be spent in producing sperm to demonstrate their relative genetic quality. (See section below on the mechanism of "genetic choice.")

Males may spend available reproductive effort on other types of behavior which may be effective in attracting females. Such effort may include attempts by individual males to enhance their prospects for reproduction by *providing females and their young with material benefits,* such as food, nests, or protection, in exchange for the opportunity to mate. Such alternative types of mate attraction are especially important to individual males who are otherwise not likely to mate successfully because of the relatively low quality of genetic benefits that they offer. Genetic benefits such males can offer are fixed, and their ability to provide material benefits can serve as the only effective inducement to alter female mating decisions in their favor.

In many situations, unrestricted female choice is the primary mechanism for determining male-female mating relationships. However, males may evolve to remove some degree of freedom for females in their mating decisions and, in some cases, completely dominate females in determining viable patterns of reproduction. A male may *make genetic representation in a female's offspring a prerequisite for the use of resources that he controls.* The female tendency to invest heavily in gametes often commits females to a strategy of high levels of resource utilization. Such a commitment may allow males to use resources that are otherwise abundant and easily exploitable to force female mating decisions in their favor. Females are then forced to choose a particular male as their mate, whereas another male would have been chosen had the females been unconstrained in their access to resources.

It is worthwhile to contrast this pattern of mate choice with one in which males collect needed resources and offer them to females in exchange for matings. If *collected* resources are used as inducements, a female may choose to forego contributions offered by a male, as she may be able to rear some offspring by herself. However, if one male should *control* all available resources, every successfully reproducing female would have to choose him as a mate, regardless of the qualities of other males. Control and collection also differ in their effect on the reproductive output of females. Male delivery of material benefits should result in a net increase in absolute reproductive output of offspring by a female.

Control of resources needed by females may lead to reduced output, since females may be forced to sacrifice genetic gain from choosing males in order to gain access to resources controlled by other males. Male ability to attract mates through either the control or collection of resources will be considered in terms of individual ability to provide material benefits. In initial considerations, differences in the quantity of offspring produced through the use of these different types of benefits will not be important because comparisons are restricted to males using similar means for attracting females.

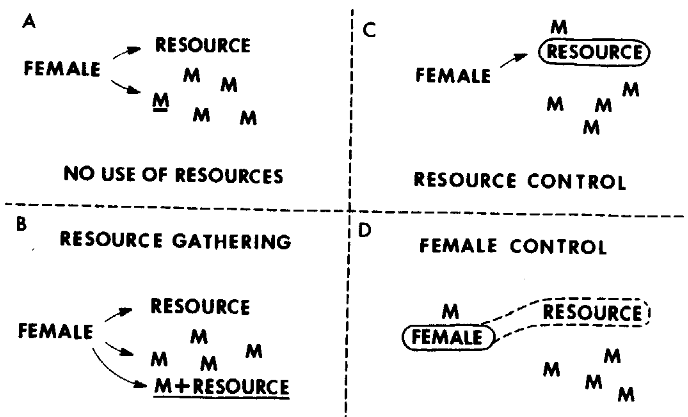

Fig. 1. Four male strategies in mate procurement and the use of resources by males to enhance mating prospects. (A) Females have free access to resources and presumably choose among males on the basis of differences in genetic benefits that they offer. (B) Males gather resources to enhance their attractiveness to females. The female is free to choose among all males, but may compromise gain from genetic benefits in order to obtain needed material benefits in excess of those she can collect herself. (C) If males control resources, female options for mate choice may be severely limited. To obtain needed resources, she mates with a male who has established control over resources. (D) Males who directly control females deny them the opportunity to freely choose a mate. Although resources are not a necessary ingredient in the capture of females, they may serve as a focus for capture; in addition, success of the capture strategy depends on male ability to allow females unmolested access to needed resources.

Direct control of females by individual males represents a fourth pattern for determining male-female mating interactions. A male may capture a female and prevent her from mating with individuals other than himself (Darwin, 1871; Ghiselin, 1974; Emlen and Oring, 1977). Such capture denies females the opportunity to demand material and genetic benefits as a prerequisite for mating. As in the case of resource control, such capture may be most easily accomplished near limited resources required by females. Male control may not be complete, since a female may exert some level of choice in mates by selecting her own capture site. The relation of each of these patterns of establishing male-female matings and the value of resources in determining these associations are described in Fig. 1.

The very different patterns discussed here suggest that in order to develop a predictive model of mating systems, two questions must be answered:

1. How can individual and "populational" patterns of reproductive success be predicted within each system of mate choice?

2. Under what conditions is each of the four patterns of male-female interaction likely to occur?

Predicting Variance in Male Reproductive Success

Patterns of male reproductive success for conditions in which females choose their mates only on the basis of the genetic benefits that they offer have been described by Williams (1975). He predicts high levels of variance in success among males. This may occur for two reasons. First, females are likely to use the same criteria in choosing males. If females are unimpeded in their ability to choose, this should lead them to a small set of males who have been able to demonstrate fitness in some significant way. Second, Orians (1969) points out that males offering high quality genetic benefits should rarely be limited in their ability to fill female needs. Males provide rapidly renewable sperm at a relatively low caloric investment, and a male should be able to mate with as many females as choose him.

Material benefits offered by males typically differ from genetic benefits in that they may be used up as males mate successively with different females. Matings in which males use material benefits to attract females reduce the residual value of benefits that they can offer to other females. Devaluation of the amount of benefits held by some males increases the opportunity for other individuals to father offspring. The high variance in mating success, typical in genetic choice systems, may be rare where material benefits are the primary basis for mate choice and may be restricted to conditions in which one or a few males hold all or nearly all material benefits.

The allocation of benefits a female is likely to receive is determined by her value to males as a mate when compared to other females. Similarly, males must compete to attract females. In each case, depletion of a male's benefits with successive matings is a key element in understanding patterns of individual success. Males who offer too few benefits may not successfully attract mates; those who offer too many rapidly exhaust their supply of expendable benefits and allow other males, who spend less per female, an opportunity to attract mates. If material benefits limit female reproduction, then female demands may be fashioned around an equilibrium value as they shop among males for those who offer the best deal. Those females making excessive demands are passed over by males in favor of other females who require a guarantee of fewer benefits as a precondition for mating. Females demanding too few benefits may be very attractive to some males, particularly when the number of benefits a male contributes only partially determines the number and quality of offspring he fathers. Even so, these females reproduce at a lower than average rate over their lifetime because of the more limited assistance they receive from males.

If material benefits are the sole basis for mate choice by females, then male reproductive success should be proportional to the share of all material benefits that an individual male can defend or deliver. This prediction follows the pattern of mate choice outlined by Orians (1969). The relationship may not be exact in all cases because female benefits, and male gain derived from them, come in discrete packages which may not exactly match the amount of benefits that individual males have to offer. In large populations it is more likely that males and females of nearly equal value can find each other and mate. Females may also split broods, allowing several males--each with a probability of leaving offspring in proportion to the amount of benefits he delivers--to father their offspring.

Female Compromise and Patterns of Mate Selection

The delivery of genetic and material benefits and their effect on mating patterns have been considered in cases where males provide each kind of benefit separately. Genetic benefits may be offered where they are the sole basis for mate choice. However, in cases where males offer material benefits, it is unlikely that males selected as mates are

identical in genetic quality. Females who gain most in mating decisions are those who discriminate among males on the basis of differences in genetic quality, in addition to evaluating the material benefits offered by these males. The need for females to simultaneously consider two kinds of benefits may force them to compromise gain through one or the other of the types in order to maximize the number of descendants that they can produce. For example, males of highest genetic quality may be somewhat limited in their ability to provide material benefits. Females choosing males other than the one offering the highest level of genetic benefits may be sacrificing some prospects for genetic gain in order to secure material benefits which may be more valuable to them.

Placing females in situations where they must compromise gain from different sources suggests that they may develop some means of evaluating each kind of benefit a prospective mate may offer. Patterns of female mating decisions and male reproductive success are then based on (1) the relative value females assign to the two kinds of benefits and (2) the degree of correlation in the quality of benefits a male may offer (that is, are males who have high levels of genetic benefits likely to hold high levels of material benefits?). These two factors, combined with variance in genetic quality and distribution of material benefits among males, should be sufficient to develop a simple model of mating systems in which females have the opportunity to compare and choose among males who offer varying levels of material and genetic benefits.

The Equilibrium Model of Mate Choice

A mating system model can be developed which applies to conditions in which males collect or control resources. Consider the case involving two males and F_t females who are of equal quality and who mate once with the male offering them the greatest share of benefits. These matings invariably lead to the production of offspring. For the nth male, G_n represents the value of genetic benefits he is able to offer prospective mates, $\emptyset_n$, the fraction of all material benefits he controls of the total controlled or collected by all males, and F_n, the equilibrium number of matings received by the nth male. A constant, R, describes for each mating system the absolute value of material benefits males can offer to females. Females are assumed to value resources at a constant rate not dependent on the value of R. Where males attempt to control resources, R is proportional to the fraction of all resources controlled by males. If males provide resources, R is proportional to the level of assistance given to females or their offspring relative to that given by females.

Patterns of matings can be approximated using the following set of relationships:

$$G_1 + \frac{\emptyset_1 R}{F_1} = G_2 + \frac{\emptyset_2 R}{F_2}. \qquad (1a)$$

where F come in? # of females mated with

And if $\Delta G = G_1 - G_2$, Equation 1a can be reduced to

$$\Delta G + \frac{\emptyset_1 R}{F_1} = \frac{\emptyset_2 R}{F_2}. \qquad (1b)$$

This relationship compares the genetic and material benefits offered by the two males. Material benefits are devalued by the number of matings a male accomplishes, while the genetic benefits he can offer a female remain constant. If the number of females and quantitative relationships between material and genetic benefits are specified, predictions can be made about the distribution of matings among males. The number of variables does not permit an analytic solution, but by restricting the level of genetic benefits to low values (see below) and by considering end points in the range in variation in material benefits, a picture of mating patterns in different situations involving two males and two females can be developed. These results then will be generalized for large numbers of males and females.

Consider the case in which each male has equal amounts of material benefits, $\emptyset_1 = \emptyset_2$; Equation 1b will reduce to

$$\frac{2\Delta G}{R} + \frac{1}{F_1} = \frac{1}{F_2}.$$

The number of matings obtained by male #1, F_1, can be graphed as a function of R and ΔG, a constant (Fig. 2a). At low R, male #1 gets all of the matings due to differences in genetic quality. As R increases and becomes more important in female decisions, male #2 gains opportunities for matings.

In systems where resources are not distributed equally among males, there are two limiting cases in which one or the other of the males controls all resources. Genetic and material benefits may be negatively correlated between males or held by different males. In this case $\emptyset_1 \rightarrow 0$, $\emptyset_2 \rightarrow 1$, and $G_1 > G_2$, Equation 1b reduces to

$$\frac{R}{\Delta G} \simeq F_2$$

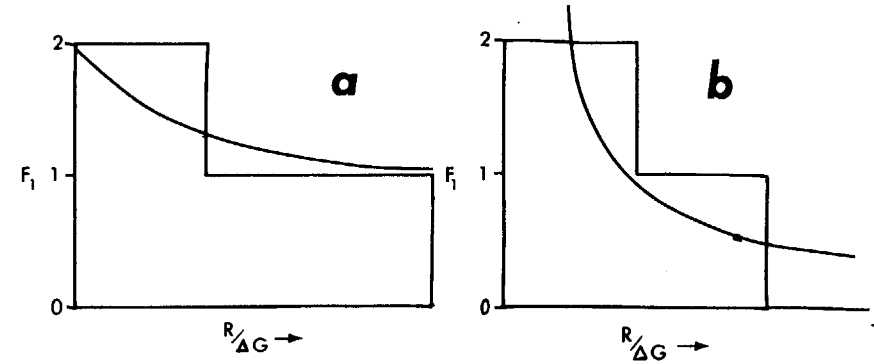

Fig. 2. (a) Pattern of male mating success with changing male ability to provide material benefits. In this case, both males have equal ability to provide the available material benefits. (b) Same as a, but males have unequal ability to provide benefits. Here, male ability to provide material and genetic benefits shows an extreme negative correlation.

and F_1 is directly related to R, so that when R is large, so is F_2, and vice versa (Fig. 2b).

If material and genetic benefits are held by the same individual or are positively correlated ($\emptyset_1 \rightarrow 1$, $\emptyset_2 \rightarrow 0$, and $G_1 > G_2$), male #1 will win at all values of R since $F_2 \rightarrow 0$.

Having shown patterns of mating success under changing conditions of R for three different relationships of $\emptyset_1$ and $\emptyset_2$, these results can be combined in order to develop a more general model for predicting patterns of mating success. Cases in which one or the other of the males receives all or nearly all of the resources represent end points on a scale of changing levels of evenness in apportionment of material benefits among males. Using these two end points as limiting values, together with results from the case in which $\emptyset$s are equal, and assuming simple relationships with changing levels of evenness, patterns of mating success can be predicted for conditions where resources are positively and negatively correlated with male genetic quality (Fig. 3).

Increasing unevenness in resource distribution has, not unexpectedly, the same effect in both cases--increasing differences in the level of success among males. In the case in which genetic and material benefits show a strong positive correlation, a consistently high level of success for male #1 is maintained for all values of R. In the case in which the two types of benefits are negatively correlated, there is a reversal in the type of male which wins. Male #1 wins at low values of R and male #2 wins at high values. The significance

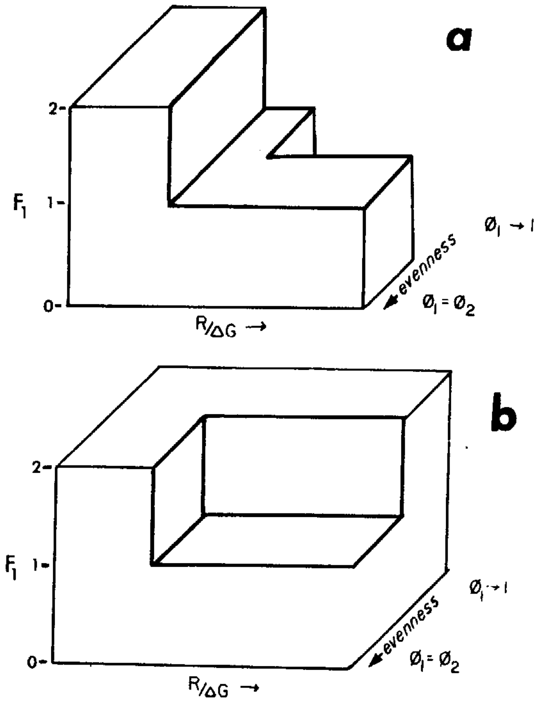

Fig. 3. (a) Pattern of male mating success determined by differences in the ability of individuals to collect from or control resources and differences in the relative importance of genetic and material benefits. There is a positive correlation between ability to deliver material and genetic benefits. (b) Same as a, but with a negative correlation between male ability to deliver material benefits and the genetic benefits offered by that male.

of differences between these two cases lessens if variance in reproductive success is considered instead of which male wins. The depression in variance at intermediate levels of R in cases in which benefits are negatively correlated is likely to disappear when mating systems involving multiple males and females are considered. This occurs because transitions in success of particular individuals may have little effect on population-wide variation in mating success, and distinctions between male success based on the different benefits they provide may be difficult to establish.

The two-male equilibrium model can be extended to deal with n males and varying conditions of R and distributions of resources. Such an equilibrium relationship for multiple mates might appear in the form

$$\Delta G + \frac{\emptyset_1 R}{F_1} = \frac{\emptyset_2 R}{F_2} = \cdots = \frac{\emptyset_n R}{F_n},$$

when it is assumed that $G_2 = G_3 = \ldots = G_n$. The pattern of matings under these conditions with equal sex ratios might appear as in Fig. 4. Increased proportions of females will

tend to enhance the importance of differences in genetic quality. The degree of change in male mating success with variation in the value of R depends on the pattern of differences in the values of genetic quality among males. Where all differences in genetic quality of males involve one male who is better by an equal amount over all other males, a sudden steep change in variance in mating success at some intermediate level of R is expected. More variable differences in quality among males allow a more gradual response.

Patterns of variance in reproductive success shown in Fig. 4 can be related to mating systems in different species. High variance in mating success at low values of $R/\Delta G$ is related to the use of male genetic quality as a primary criterion in female mating decisions. This may be common in typical breeding leks of birds (Snow, 1962; Robel, 1966, 1969; Scott, 1942). In these leks males apparently give no material benefits to females. Territories may exist, but there is no necessary relationship between territory size and male mating success; relative position seems more important.

High variance in ability of males to control resources leads to a second type of polygyny. Resources held by a male may be present in such abundance that use by one female does not strongly affect the residual value of benefits a male can offer to subsequent mates. In such cases, females choose males primarily for the material benefits they provide. This pattern of choice may be independent of the genetic quality of males who control available resources, although in most circumstances it is likely that these two male qualities are positively correlated. These types of polygyny really represent end points on the high variance plateau in which genetic and material benefits are both important in allowing high variance in success.

High levels of success due to high variance in the quality of material benefits a male can offer are likely restricted to situations in which males control resources. Success of

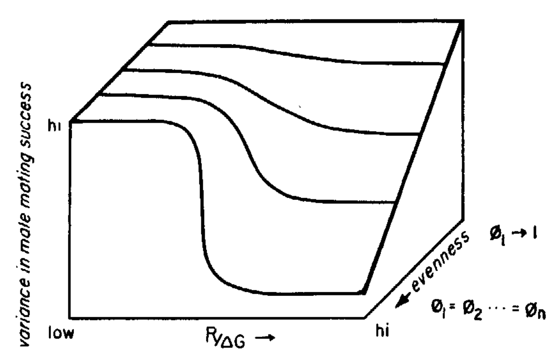

Fig. 4. Changes in patterns of male reproductive success due to variation in the value of material benefits and in individual male ability to provide these benefits. See text for further explanation.

an individual male in collecting from resources is extremely time and energy dependent. Time and energy constraints seem to limit even the most able individuals from collecting more than a few times the amount of benefits gathered by the average male.

Review of Assumptions of the Equilibrium Model

Constancy in Value of Benefits

In the preceding model, it was assumed that the two types of benefits maintained a constant value to females independent of the amount they had already received. However, females may often be limited in their ability to utilize benefits. Given the choice of two males, one of whom offers material benefits in excess of her needs, a female may choose the male of higher genetic quality, even though he may be able to provide fewer total benefits. The effect of placing limits on female needs, especially if females mate only once, is to lower the value of material benefits and shift choice in favor of males of high genetic quality, even when resources are distributed equally among males. Male gain from offering genetic benefits faces no parallel limitation since relative and not absolute value of benefits is important to females. In other instances, females may require a minimum commitment of material benefits in order to successfully reproduce. The only source of such benefits may be males offering overall fewer benefits than high quality individuals. Effect of such limits will be to lower the value to females of differences in male genetic quality.

Are Females Always Limiting?

Male-female patterns of interactions in the pattern of resource utilization are generally based on male interest in maximizing the number of matings they achieve with females. Assuming this behavior in males generally leads to an accurate description of mating patterns because males commonly profit from exploiting high levels of investment already made by females in eggs. However, a strategy of attracting as many females as possible onto a territory may not be effective in cases in which males control, but do not directly provide, a resource that limits the overall reproduction of females. In these cases, a female's success depends on getting onto breeding areas that are controlled by males. When pairing takes place, a female may have little investment in gametes. All investment on her part must come from exploiting limiting resources controlled by a male. The territorial male is

essentially "hiring" the female to turn resources he owns into offspring. A shortage of resources may present a condition in which there are more females than can effectively convert resources into offspring. Males may limit the number of females on their territories to that which yields the highest output of offspring, even though this may be below the maximum number of mates the individual males could attract. Such relationships may be common in marmots (Downhower and Armitage, 1971) and in species in which nonreproducing females are common in the breeding season.

Availability of females and their eggs in excess of resources needed to mature these eggs may be important in the development of polyandry as a dominant reproductive mode in some birds. Females in these populations may evolve to control resources in order to guarantee for themselves access to suitable sites where young can be raised. In jacanas, Jenni (1974) describes not only resource control by polyandrous females but also large numbers of nonreproducing females during the breeding season. This is a relatively uncommon occurrence in most species and suggests that suitable habitats for raising young are in short supply. Ability to relate polyandry and female territoriality to the shortage of resources seems important since a pathway for the evolution of high variance in female reproductive success, which may even surpass that of males, is not apparent from Bateman's (1948) model and its more recent derivatives.

Effects of Variance in Female Quality

The assumption of equal value of females in the equilibrium model may not be realistic in most situations and, in certain cases, may strongly influence predictions relating to the pattern of mating success. Such incongruities may commonly occur in cases where individuals pair with mates of their own relative quality, as was considered by Darwin (1871), Fisher (1958), and O'Donald (1974). They point out that where such pairings occur, nearly all males may be able to obtain matings, but there still may be high levels of variance in reproductive success. For the equilibrium model, prediction of patterns of mating success depends on the assumption of equal quality among females. However, ability of males to discriminate among females suggests that, under most conditions, variance in the quality of females should have little effect on patterns of male reproductive success, since gain through choice of a few very good females or many poor females should generally give similar levels of genetic gain for males.

Variation in the quality of females may also influence mating patterns if a significant interaction between male and female quality effects the quality of their offspring. A multiplicative relationship between the quality of parents and offspring will lead to selection for females who seek out high quality males and forego possible gain derived from paternal investment in offspring. High quality males should certainly be able to supply receptive females with contributions of sperm. Males need only choose among females if it is likely that they might run out of sperm. It is unclear if this kind of multiplicative relationship exists. The prevalence of monogamous pairs in situations in which it is possible for females to rear their broods alone suggests that, at least in some instances, this is not the case.

Females who vary in quality may not be able to demand benefits according to the relative quality of offspring that they produce--the expected basis for determining an individual's market value. Consider the case in which one of two males who offer material benefits if of high relative genetic value. The male of high genetic value may favor mating with low value females. Selective matings with low quality females allow him to utilize his entire complement of genetic benefits to attract females while using only a small amount of his material benefits. His ability to secure additional matings is thereby only slightly reduced. Preference for low value females by these males may allow selected females to bargain for higher levels of material benefits than they might otherwise expect to obtain.

Male Commitment To Deliver Benefits

In the equilibrium model, males were assumed to be able to deliver material and genetic benefits to females with equal ease. Trivers (1972) points out some of the problems associated with the transfer of material benefits in relation to mating. The model he develops focuses on apparent instances of deception, such as "desertion" of females by males and cuckoldry of males by females. In this analysis, the relative likelihood of "desertion" is considered important in determining patterns of male-female interactions. He argues that desertion becomes a theoretical temptation for the partner that has made the lesser investment, particularly if the difference is great. Later, in discussing the profitability of the desertion strategy, he states, "The balance between these opposing forces should depend on the exact form of the cumulative investment curves as well as opportunities for further matings." This view has been criticized by Dawkins and Carlisle (1976), who note correctly that parents are concerned with maximizing gain from their future opportunities to invest, and, in some cases, the past history of investment in individuals may be of little importance in influencing future patterns of parental contribution. However, situations

in which past investment and future ability to invest are correlated must be common. Under these conditions, past investment may define opportunities for further investment by both parents.

Another, and perhaps more important, problem common to both of these explanations of male-female behavior in benefit transfer comes from the attempts of Trivers, and Dawkins and Carlisle, to describe patterns of parental investment in terms of desertion by one or the other of the parents, usually the male. Desertion is defined as "abandonment without consent or legal justification of a person, post, or relationship and duties and obligations therewith" (*Webster's Third International Dictionary*). Obviously, most animal species have no legal system, but opportunities to make agreements and for partners to develop expectations about levels of benefit a partner will contribute seem to exist. In the equilibrium model discussed above, choice of a mate based on his expected delivery of benefits that are not at hand may be interpreted as requiring the development of an obligation or agreement supported by some guarantees. However, that model and the one offered by Trivers differ in the manner by which females develop expectations about the amount of material benefits they can demand. The amount of benefits demanded by females and delivered by males in the equilibrium model depends on the market value of each individual at the time of mating. By contrast, Trivers assumes that each sex's obligation to its mate should be equivalent to the amount that its partner contributes, and he thus calls individuals who contribute less to offspring than their partners "deserters." Similarly, Dawkins and Carlisle do not seem to view commitments made near the time of mating as having any significant role in mate choice.

The definition of desertion suggests deception of the nondeserting parent by its mate. The common tendency for one parent to leave the other with their offspring, and the suggestion of these authors that attributes all bias in parental commitment to desertion, leads to the prediction that deception occurs on a large scale. By contrast, in the equilibrium model I assume that males meet female expectations for the delivery of material benefits in the great majority of cases. Female tendencies to choose among males offering different levels of benefits suggest that long-term success in deception by males is rare. In cases where successful tendencies to deceive females spread, selection may favor females who devalue material benefits according to the level of deception and favor males who provide high quality genetic benefits. Deception in benefit transfer is unlikely among males chosen for their ability to provide genetic benefits, since such males will rarely lose in supplying females with sperm that they are likely to use. Females might also select males who offer the best assurances for the delivery of material benefits. The ability of males to offer material benefits may allow many males their only means of attracting a mate. Shifts in female preference toward choice based on genetic characters would strongly reduce these males' prospects for mating. Such shifts in preference should cause selection among these males so that they strive to provide the best possible assurance that obligations established at the time of mating will be met.

Females must commonly adjust their expectations for receiving benefits according to their own quality, the availability of benefits, and the likelihood that benefits will be delivered. Successful deception by males, although important in determining the amount of benefits delivered through its effect on male ability to guarantee benefits, is likely to exist for only short periods, i.e., up to the time when a female adjusts mate choice patterns so as to maximize gain from her alternatives for choosing mates.

Other than desertion, there are several reasons why males may commonly contribute fewer material benefits than females to raise a brood. These might include: (1) lower confidence of genetic relationship for males than females to offspring, which may lead males to alternative investment patterns with higher payoff (Alexander, 1974); (2) females may prefer genetic benefits offered by some males over material benefits offered by others; and (3) males may be unable to collect and/or guarantee material benefits at the time of mating. Consistent lower investment by males, resulting from the operation of one or more of these factors, may give the appearance of deception or desertion when, in fact, males are satisfying all commitments they are able to make at the time of mating. For example, in instances when females appear to prefer genetic benefits offered by males, behavior in which the male leaves before the female's contribution to the brood is complete may not result from "maltreatment at the hands of one's mate" (Trivers, 1972), but because females are victims of their own decisions. The "deserted" female may have passed up the opportunity to mate with a male who offered a full complement of material benefits and who would have stayed with her through the whole nesting period. In his place she may choose a male who offers higher levels of genetic benefits but who is likely to contribute fewer material benefits to offspring. Presumably the choice of this second male leads to an overall higher payoff in descendants even though her selected mate will leave before she finishes rearing her brood.

The importance of understanding behaviors effecting the transfer of material benefits is underlined by the treatment

of mating patterns in fish by Dawkins and Carlisle. They invoke Trivers' notion of the "cruel bind" to explain typical male behavior in guarding eggs and sometimes hatchlings. Using this concept, they suggest that males are stuck in the parental role because females who lay externally fertilized eggs have the opportunity to "desert first." The cruel bind these males find themselves in is one in which any tendency for them to leave after the female has departed would lower their reproduction to below what it would be if they stay. It is suggested that the deserting female gains from having her eggs guarded at a much lower cost than if she tended them herself.

In fishes in which males are parental, the pattern of mating and investment by parents seems to be less haphazard and largely determined before the eggs are laid. Male protection of eggs is preceded by nest building and territorial defense (sticklebacks: Assem, 1967; sunfish: Keenleyside, 1972). The territorial behavior of males commits them to stay with eggs, since territories are important in attracting future mates and may be difficult to reestablish (J. Taylor, pers. comm.). Protection of eggs probably adds little cost to the male if considered in relation to his other reproductive activities, but it may be important to the female in allowing her to leave the oviposition site to feed and produce more eggs. The ability of males to guarantee some level of protection to eggs is probably a key element in allowing males who are inferior in genetic quality the opportunity to attract mates.

Reliance on an individual's relative opportunity to abandon its mate to predict patterns for the transfer of benefits ignores (1) the effect of one sex's consistent failure to contribute benefits to their mates in long-term mating patterns, and (2) the importance of limiting investment, usually controlled by females, in influencing the amount of postmating benefits delivered by a prospective mate.

If males are consistently left by females, there should soon be a shortage of unmated males, since most are committed to the care of offspring. In response to these conditions, females may either start a new brood, for which they provide all necessary benefits, or forego reproduction until males become available. In either case, females may be forced to compete for opportunities to mate with rare, available males. The latters' rarity gives them leverage to make demands on females which in turn enhance the reproduction of the individual male.

The material benefits that males offer in exchange for matings may be of little value in affecting mating decisions unless females can be assured of their delivery. A female can only value male commitments to deliver benefits if they occur before fertilization of the eggs--in which she has made a large investment, or commitment of parental effort. Assurance of delivery is most certain in cases of nuptial feeding (reviewed by Thornhill, 1976a) in which males provide benefits as a precondition to mating. Probably, males most often provide guarantees which give the female a high degree of confidence that promised benefits will be delivered.

Several means exist by which males might guarantee delivery of benefits to females after they have mated. A male may commit himself to a situation which would lead to a net loss in offspring if he were to attempt to deliver to other females benefits his mate expected to receive. As suggested, a high quality territory may be difficult to reestablish; even when new territories can be formed, all or most females may have already mated. Trivers (1972) recognizes that the male's investment after copulation may be increased by the indirect force of female choice exerted before copulation. While this statement agrees with the views suggested here, it is inconsistent with his attempts to relate the amount of committed parental investment to tendencies to desert. Prefertilization indices of aid-giving behavior and actual contributions of benefits directly to the female may have no direct effect on individuals' tendencies to leave their mates, since, according to Trivers' definition, neither represents parental investment. His notion of the cruel bind, if generally applied (as by Dawkins and Carlisle, 1976), further complicates the development of a clearcut view of male-female relationships, since its operation allows for no important premating agreements.

Females often must recognize tendencies to give benefits by simple contextual cues. After some point in the reproductive season, it may be difficult for a male to obtain a high quality mate, so with limited alternatives for reproduction, a female is guaranteed her mate's assistance. Prolonged courtship could function to force males in seasonal mating systems to wait until the critical point at which their interest in leaving has passed (Wiley, 1976). If this is so, females who have lost a courting male should mate rapidly after spending reduced time in courtship with a new male. These females would be expected to mate at approximately the same time as other females of the same quality. High quality females may also mate first, since male expectation of subsequently finding a better female is low. Waiting need not occur if females cannot raise offspring without male assistance. Under these conditions, males should not begin matings unless it is likely that they will remain with their first mate, since all effort devoted to abandoned females is ultimately lost.

Installment mating may be important in some species in which females allow a male to mate repeatedly. Each mating gives that male a low probability of paternity of a female's offspring. Between matings, the male may provide benefits. The sum of benefits may equal that contributed by a single parental male, and total copulations lead to a high probability of success for some males (see Cronin and Sherman, 1977).

Female Promise of Paternity

Successful reproduction by males involves not only mating with females but successfully fertilizing eggs. Males chosen primarily on the basis of genetic characters are assured of some level of success if females control matings, since benefits to females are only gained when sperm from these males is used to fertilize eggs. By contrast, males who provide material benefits face the possibility of reduced or even no reproduction if they are unable to tie the delivery of benefits and sperm to females with a high confidence of paternity.

Cuckoldry is most likely to be profitable for females when they are forced into conflicts resulting from their attempts to maximize gain in benefits from different sources. One such conflict arises from choosing among mates who differ in the material and genetic benefits they are able to offer. Females who mate exclusively with males who deliver material benefits may outgain those who mate with males who provide only genetic benefits. However, increased material gain from these matings comes at the cost of reduced gain in the genetic quality of offspring. If females can deceive males into providing a full complement of material benefits, but use the sperm of males providing genetic benefits, they can simultaneously enjoy the benefits of both types of matings. For males who rely on material benefits to attract mates, this female behavior will lead to severe reductions in fitness and possibly complete loss of reproduction. We must ask whether females commonly are able to deceive benefit-providing males, or if selection will work on males to suppress apparent instances of deception.

Existence of females who vary in detectable levels of confidence offered may allow males the opportunity to bargain for high confidence by offering extra material benefits to females who offer high levels of confidence. Competition among males for high confidence matings gives truthful females the ability to demand and receive material benefits at levels above those that would occur if there were no attempts to deceive males. Increased levels of offerings to these females come at the expense of females who attempt to cuckold. If material benefits are highly valued, as indicated by female tendencies to include them in mate-choice decisions, preferential treatment of truthful females by males should lead to an increase in the proportion of females who assure high levels of confidence. Selection by males should favor rewarding demonstrations of confidence by females to levels approaching (but usually below) those in which material benefits are accorded their true value (the value if males had complete confidence) relative to genetic benefits. In cases where males can bargain for higher confidence, reduction in the value of material benefits may come from costs in determining variations in confidence and rewards to pay off truthful females.

Male success in offering benefits to females in return for higher confidence of paternity depends on (1) how females value added benefits relative to the amount they have already received from males, and (2) ability of individuals to evaluate differences in benefits provided by members of the opposite sex. If females value new benefits as much as those received when they had less, the prospects for male success in bargaining for high confidence in offspring are quite good. Competition among females for these added benefits may be strong, and females would be expected to guarantee high levels of confidence at relatively low cost. However, if female interest in benefits diminishes in relation to the level of material benefits already received, then added contribution of material benefits in exchange for higher confidence will have little effect on female decisions to share paternity of a brood with other males.

In cases where males have evolved to contribute material benefits, there are two reasons to suspect that males providing valued benefits may often win in conflicts over confidence in paternity of offspring. First, the material benefits they offer outweigh the value of the genetic benefits, and, as I have attempted to show, they are often in a position to use them to control female mating decisions. Second, males suffer a greater loss in being cuckolded. Under the best conditions, females gain only the difference between the genetic quality of the male who provides them with material benefits and that of the male who eventually fathers their offspring. A deceived male loses his entire reproduction. This asymmetry in the potential for gain suggests that benefit-providing males will be more inclined to invest effort and resources in preventing cuckoldry than females will in attempting to carry it out. For these reasons it is suggested that cuckoldry may be rare, but other factors must be considered in determining its actual level of occurrence. In the model which discussed males exchanging benefits for increased confidence of paternity, it is assumed that females can demonstrate high male confidence at a low real cost. However, if these costs are high, as may occur when females must forage over large areas

for food, it may be impossible for males economically to provide sufficient benefits to cause females to raise the guaranteed level of confidence beyond very low levels. Selection should work to reduce these costs where possible, since females would stand to gain increased shares of resources. But there may be limits to how far this type of selection can go, and where these limits appear, the real value of material benefits to a male in attracting mates shows a related decrease.

In cases where females are not able to demonstrate differences in levels of confidence in paternity, there may be several outcomes. The simplest of these may involve males not changing their behavior. Reductions in confidence given by females may leave those benefit-providing males who offer less than the highest level of genetic benefits with few options but to continue to provide their benefits, even if these are severely devalued in their effectiveness for attracting females as mates. Formerly benefit-providing males may adopt entirely new strategies, including devoting energies to the direct control of females. Even if these only generate a low payoff, they may be more profitable than collecting and providing resources and getting little or no return on genetic representation in offspring. Alexander (1974, 1977) has pointed out that if male confidence in paternity is low, individuals may contribute to full sisters' and even half-sibs' offspring, related to them by 1/4 and by 1/8, instead of to those who, on average, may be related by a lower fraction.

Several males may be involved in the fathering of offspring in one brood in blackbirds (Bray et al., 1975), but it is unclear whether this results from deception or female attempts to balance benefits received from males with some expected level of confidence in offspring. Multiple matings by females with males who provide different amounts of material benefits do not necessarily mean that males are being deceived. For instance, a female may have only limited need for material benefits that males contribute. Such a female may compromise when confronted with the choice of mating with the highest genetic quality male, who offers no material benefits, or with a male offering material benefits important to her reproduction. She may mate with both males, apportioning confidence among them according to the relative worth of the benefits they provide. One male would be offered fractional confidence of parenthood in her brood for his supply of material benefits, while sperm derived from the male of highest genetic quality was used for the remaining eggs. If there is a population-wide change in the rate of female gain from material benefits per unit of confidence delivered to a male, the material benefits would be revalued according to this change in need. Fractions of females won in the equilibrium model are significant in this context. The payment to males in probability of fathering offspring relative to the value of benefits they provide may give a false appearance of deception. Such opportunities to split broods may allow males of low genetic quality their only opportunity to gain any offspring.

Splitting paternity of broods between males who contribute material benefits at different rates, e.g., one male contributes all material benefits and other none, may complicate a male's problems of assessing a female's relative value. In these cases, benefits of resources contributed by males are shared by all offspring. No problem exists if males are utilizing only previous female investment, as apparently occurs in Mecoptera (Thornhill, 1976b) in which a male's contribution is not directly associated with his offspring. If the quality of offspring is dependent on the level of male contribution, then males contributing material benefits may suffer a relative loss in mixed broods. The genetic benefits females acquire go only into specific offspring, but material benefits go to all and perhaps even more to those of high genetic quality; therefore, males of high genetic quality enjoy the gain in their offspring though they contribute no benefits of their own.

Because a male's interest in the disbursement of benefits differs from that of his multiple-mated mate, males should avoid direct contribution to her. One strategy may be for males to deliver material benefits directly to their offspring, provided they can discern those likely to be their own. Another may be for males to place a premium on females who mate exclusively with them.

MALE CONTROL OF FEMALES

Up to this point I have focused attention on systems in which choice by females, although sometimes restricted, is the key element in determining patterns of mating associations. Male capture of females, or sequestering or otherwise denying them access to other males in order to force copulations or severely restrict their reproductive alternatives, provides an interesting contrast. Since males who embark on a female control strategy commonly have much more uncommitted reproductive effort available than females, presumably, this effort can be directed to capture of females.

For females, effort to avoid capture must be deducted from investment in offspring. Differences in quality between males chosen by a female and those who might capture and inseminate her must be sufficiently large so that costs of avoidance, paid in reduced reproductive output, are justified. It might appear that males have a distinct advantage over females, but female proximity to eggs and differences in difficulty of capture and escape suggest that there is no simple way to compare male effort spent in attempts to capture females and the effectiveness of females in avoiding capture. At best, situations can be noted in which such capture and control are more or less likely.

Male success in control must be most common when differences in the genetic quality of the male an uncontrolled female might choose and the male who actually controls her are small. In harems of sea lions (Gentry, 1970) or ungulates (Jarman, 1974), successful males gain their position by winning many intense fights, and these triumphs are probably a good indicator of genetic quality. Since in these cases it appears that males have not been able to provide or control any valued material benefits, the real cost to females of establishment of control by males may be small. In some cases such control may actually enhance female reproduction. If males who are unlikely to attract females even occasionally are successful in "stealing" a copulation, females may submit to control and protection by a male of their choice. Cox and Le Boeuf (1977) point out that harem females often call out when sexually harassed by an invading male. The harem master recognizes the call and responds by chasing away the invader. In the dung fly *Scatophaga stercoraria*, Parker (1970b, c) has suggested that a female may gain from a male's postcopulatory guarding, since he fends off would-be copulators while she oviposits. Female *Scatophaga* actively choose large males with whom they are most likely to rapidly complete copulation and oviposition (Borgia, in prep.). In addition, females begin to display rocking motions when held away from the oviposition site by males for more time than is commonly required for copulation. These rocking motions cause an increase in attack rate and increase the probability of male replacement. Notably, it is generally small males who hold females for long durations, up to three times the average copula duration. The female signal and consequent replacement of the guarding male may reduce the time needed to place her eggs into the oviposition site, which decays rapidly in quality as it ages.

In a variety of insect groups, females fly into aggregations of males, are grasped, and the pair falls to the ground where they mate (see Downes, 1969). Choice of timing and pattern of approach may give females a high degree of control over which males capture them. Differences in genetic gain lost between this pattern of choice and one in which females can more facilely reject males may be minimal.

High costs to females in resisting control in some contexts seem the most common basis for establishment of this mating strategy. In ungulates and other mammals, group formation by females is considered predominantly a defensive response against predators (Hamilton, 1971; Alexander, 1974). However, such an adaptation may restrict the ability of herd members to freely express mate choice, since attempts to leave the herd are likely to severely increase the risk of predation. Grouping by females may not be as costly as being captured by random males, since females in groups are commonly controlled by a dominant male who has "earned" his position and may, therefore, be considered to be a good choice as a mate in most contexts.

Male control may also be effective when the time and space in which reproductive functions are carried out are restricted. Male *Scatophaga* (Hammer, 1941; Parker, 1970a) capture females as they attempt to oviposit on restricted sites. Male dragonflies also capture females and then guard them from above as they oviposit (Campanella and Wolf, 1973). As Parker (1970c) has suggested, male control may simplify and speed the mating and oviposition process for females, but initial tendencies to control must have been encouraged by female tendencies to group around oviposition sites.

Long-term success of a strategy in which males attempt to control females is dependent on male ability to limit access of sperm from other males to a female's eggs between ovulation and fertilization. Without this extended control, internally fertilized females who are captured and then released may move to a preferred male and mate with him. Selection on females should work to increase their control over which male's sperm actually fertilize their eggs.

Males able to directly control females save on expenses associated with collecting and/or defending resources in order to obtain benefits to exchange for matings. However, the absence of a tendency to contribute resource-based benefits removes the leverage males might have in rewarding females who offer high confidence of paternity with extra material benefits. This may not often be a problem for highly successful males if ability to control females and gene quality are highly correlated. However, if there is no bias in terms of which males can control females and consequently no correlation between control and gene quality, some investment in avoidance of males and attempts to choose controlling males is likely.

Female tendencies to clump may strongly affect the variance in male reproductive success in cases where males capture females. In these instances, females can be treated as resources controlled by males, and the analysis below can be used to predict patterns of male mating success if the relationship between timing of copulation and its effect on mate success in fertilizing eggs is understood.

HIERARCHY IN TYPES OF MATING ASSOCIATIONS

Predicting which of the four mate selection strategies will occur in a given instance requires knowledge of (1) habitat conditions sufficient for each of the patterns of mate procurement and (2) some means of specifying outcomes in cases where sufficient conditions exist for more than one of the four patterns. Conditions necessary for establishment of each mating pattern have been discussed, and relationships among resource control, resource collection, and genetic choice strategies mentioned. This discussion suggests that a hierarchy exists among strategies which defines which is likely to prevail for cases in which more than one might occur.

A strategy in which males can control the resources which females must have to reproduce would seem to be dominant over those in which males either collect resources or provide high quality genetic benefits. Arguments presented earlier which suggest a low expected value of genetic benefits can be used to define typical relationships among the remaining subordinate strategies. Low value of genetic benefits implies that whenever material benefits are available, they will be the primary criteria used in mate choice decisions by females. Pure genetic choice systems can then occur only where males are unable to collect any substantial amount of items from the habitat that are of value to females. Choice involving males offering material benefits might then be considered dominant over a pure strategy in which mate selection is based only on genetic benefits offered. However, consideration of genetic benefits offered by a prospective mate is involved in both of the strategies discussed here.

Strategies involving male capture of females also dominate over some other mate selection patterns. The other types of mate choice generally involve a high level of control by females over which males will be their mate. However, any demands a female might make in the mate selection process are voided if a male offering no material benefits can force a female to use his sperm to fertilize her eggs. Therefore, when males can control females, strategies involving collection of benefits and pure genetic choice by females are likely to be ineffective. The relationship between female control and resource control is less clear, since both females and limiting resources may be necessary for successful reproduction. Males who capture and release females away from oviposition sites may be able to fertilize the eggs of a female in a way which cannot be detected by a resource-controlling male. Males using a resource control strategy will likely lose in sexual competition if these female-controlling males capture a sufficiently large share of females who have not yet reached areas where males hold territories. Alternatively, a mate-capturing male may only be able to insure successful fertilization of eggs with his sperm by guarding a female after copulation (Parker, 1970d). Success in mating may demand males capable of both controlling resources and of capturing and holding females who come to utilize these resources.

In the hierarchy of mating strategies, male control of resources and ability to capture females share the highest rank; male contribution of collected benefits, a lower position; and when no other strategy is effective, a pure strategy of genetic choice by females will occur. The hierarchy system can be used for determining the likelihood of a strategy in a given context by asking if sufficient conditions exist for the highest ranking strategy to occur. If so, that strategy should characterize the behavior of individuals fertilizing the majority of eggs in the population. If not, then the same procedure is carried out for the strategy of next highest rank. This testing is continued until genetic choice represents the only remaining strategy. If this type of selection is limited, as by a high density of predators, then we might add an even lower level of "choice" onto the hierarchy. This new level would involve a tendency for females to mate with the first male that they encounter.

It is implicit in the categorization of strategies presented here that the last male to attempt to mate with a gravid female fertilizes the largest share of her eggs. This relationship is typical of cases in which a female's eggs are fertilized externally. Development of internal fertilization, particularly in cases in which females store sperm, allows females more control over the process of mate selection. As discussed above, control of sperm by females may reduce the rank of some strategies, particularly those involving direct control of females.

Interspecific comparisons of breeding systems in Central American hummingbirds illustrate dominance effects in patterns of mate selection (Stiles and Wolf, 1977). Males of large species commonly hold territories around inflorescences where females feed; acceptance of copulations from controlling males is apparently a precondition for feeding by the females. Males of smaller species are effectively excluded from holding territories around flowers by males of the larger species. In these excluded species leks are the common type of breeding systems.

Dominance relationships also occur in the mating systems of flies which use cow dung as oviposition sites (Borgia, in prep.). *Scatophaga stercoraria* is a predator on adult flies of other species and is the only one of at least ten large species in which males come to the oviposition site and control this resource to influence mating decisions. Costs of predation on males from other species by *Scatophaga* may have

prevented them from evolving and maintaining a resource control strategy. In two small dipterous species, males do come to the oviposition site. Males of one species cannot be held and eaten by *Scatophaga*, and those of the other, which are eaten but do not appear to be a preferred food source, mate in crevices underneath the dung when *Scatophaga* is present in abundance.

GENETIC CHOICE

The Lek Paradox

Understanding mechanisms of genetic choice is critical to developing mating system models if, as I have suggested, genetic choice consistently forms an alternative to mate choice systems based on other criteria. However, Williams (1975) has pointed out a problem in assuming that variance in genetic quality is a likely basis for mate choice. He states, "High heritability of fitness from father to son must be maintained in order to explain mate choice based only on genetic criteria." The problem Williams (pers. comm.; see also Davis and O'Donald, 1976) alludes to is that of maintaining the levels of genetic variation necessary to form the basis for mate choice if only a small fraction of males breed successfully. Though this criticism appears valid, there should be an explanation for those behaviors of animals which suggest that differences in genetic quality are sufficient to provide the basis for mate selection. Perhaps the most convincing evidence for genetic choice occurs in what Alexander (1975) calls nonresource-based leks. These have been studied in greatest detail in birds (Robel and Ballard, 1974; Lill, 1974a, b, 1976; Wiley, 1973) and in some mammals (Buechner and Roth, 1974) in which single males achieve large proportions of observed matings. Several aspects of the behavior of animals in these systems characterize the pattern of mate choice: (1) no vehicle for female benefit appears to be transferred other than sperm, (2) females reject numerous males capable and seemingly willing to fertilize them, (3) females seem to exhibit unrestricted choice which is directed at particular males, (4) males fight for positions which affect their success, (5) no obvious postcopulatory assistance is given by males. Although the gene-quality hypothesis may have problems, no alternative appears to explain lek behavior better. It is the unique behavior associated with lek-breeding systems which causes the separation of what appears to be pure genetic choice systems from the continuum of systems that rely on material benefits and perhaps other male attributes.

In what might be called the lek paradox, there is apparent contradiction in theoretical predictions about (1) disappearance of genetic variance, the necessary basis for heritable variation in mate choice, and (2) suggested advantage to females in choosing males of high genetic quality in the lek system. Resolution of this paradox is important if we are to understand the operation of nonresource-based leks and related systems.

Alternative explanations for the selective basis of leks have been proposed, but none seems to fully explain the very specific behavior which occurs in breeding leks. For example, Lack (1968) and Trivers (1972) suggested that breeding leks in birds speed mating by females. Abundant data suggest that females may spend much more time around the lek, displaying to and surveying different males, than one might expect if females were attempting to minimize time devoted to mating (Lill, 1976; Brandler, 1967). Lack (1968) also suggested that lek behavior may reduce predation. Although he provides no specific mechanism, we might assume systems similar to those described by Hamilton (1971) in which individuals who join groups enjoy reduced likelihood of attack or, as suggested by Pulliam (1973), are capable of enhanced detection of predators. By itself, this hypothesis seems inadequate to explain complex displays by both sexes; repeated female displays with different males (Lill, 1976; Robel and Ballard, 1974); and behavior likely to attract predators, including the bright coloration, loud calls, and odors that invariably accompany male lek behavior.

As might be expected if predators were unimportant in lek evolution, reports of behavior near leks either scarcely mention activities of potential predators or suggest that they are only infrequent visitors. For example, Lill (1976), having observed manakin leks, states, "During nearly 2000 hours of observations made from partially enclosed blinds at arenas, I saw neither actual nor attempted predation." However, if leks have been effective in predator defense, it may be improper to eliminate the predation hypothesis only on the basis of this type of observation.

The lek paradox might be resolved in several ways that would allow females to base their mating decisions primarily on the quality of genetic benefits that a male might provide. One way is to consider the actual levels of polygyny in populations where genetic choice appears to occur. Supposed reductions in fitness in lek-breeding populations are based on assumptions of high levels of polygyny. However, in many cases, these supposed levels of variance in male success are not achieved; therefore, expected reductions in genetic variance may not occur. Lill's (1976) work on the manakin *Pipra erythrocephala* provides some of the rare data on behavior of marked males and females on leks. On the four leks he observed, my calculations, using his data, show that 39.8% of the males copulated more than the average. In addition, 45.7% of the males on leks copulated with the average number, or more, different females.

Large numbers of leks provide an additional barrier to the rapid depletion of genetic variance. Snow (1962) estimated approximately 1,700 individuals of *Pipra erythrocephala* on Trinidad, and using Lill's data on sex ratio of adult males and mean lek size, I calculate that there may be approximately 45 leks on the island. Similar results appear to characterize other lekking birds (e.g., Patterson, 1952).

Levels of genetic variation are probably maintained at or near some equilibrium value, and variance in male mating success is only one of several factors likely to affect this equilibrium. Shifts in selection patterns may provide the main source of genetic variation. In eukaryots, which contain large numbers of loci, it is probable that changes in selective coefficients which affect the relative success of alleles at the same locus occur at the rate of one such shift per generation. With some slowdown in the loss of variance, as occurs in manakins, it may be possible for males to offer females significant levels of genetic benefits. Linkage disequilibrium may act as another barrier to the rapid loss of variability.

Another, but not exclusive, explanation for the maintenance of heritable gain from mate choice based on genetic characteristics is dependent on advantage for heterozygotes. Heritable advantage for females can be maintained even when there are extreme levels of polygyny if it is assumed (1) that females have no effective means of assessing the type of alleles that they carry and (2) that a substantial number of male characteristics which affect male vigor are dependent on heterosis. Dominance on the lek of males possessing the greatest level of heterotic loci should cause females to favor whatever pattern of mate choice yields offspring with the highest probability of having high levels of heterozygosity. Denying females information about their own genetic make-up prevents potential advantage from complementation by matching specific alleles that they carry with alternatives that occur in males. Even with information about their own genetic qualities, difficulties in attempts to complement large numbers of loci should make such behavior ineffective (Alexander and Borgia, 1978; and see below).

Choice of the dominant/heterozygous males offers one route to greater than average expectation of producing heterozygous offspring. At any one locus, all matings involving heterozygous males or females will produce one-half heterozygous offspring, regardless of the genotype of the female. However, probability of homozygotes producing heterozygotes depends on the frequency of alleles in the population. If two alleles are present in equal frequency among potential mates, a female's success in producing heterozygous offspring will be the same whether she picks randomly among homozygotes or heterozygotes. But, if the two alleles are not present in equal frequency and are unequal by relatively constant proportions in both sexes, there is a payoff in choosing dominant males. Most matings in which females mate with males other than those showing high levels of heterozygosity will lead to a greater than average expectation of producing only homozygous offspring; frequency of the common allele in one sex is correlated with a high frequency of the same allele in the other sex. Some matings will lead to whole broods of heterozygous offspring, but these will occur at a lower rate than those producing only homozygotes.

The success of this pattern of mate selection is dependent on overdominance as a common pattern in genetic systems. High levels of genetic variation are known to occur in a wide variety of species (see Powell, 1975), and heterozygous advantage has been suggested (Fincham, 1972; Johnson, 1976) to account for much of this observed intraspecific variability. Even in overdominant systems, deviation of allelic frequencies from equality should be common because of unequal fitness in homozygotes. In fact, the fitness values of homozygotes must rarely be exactly equal. Females' ability to base mate choice only on relative dominance of males presents them with an opportunity to pick genetic characters without any need to identify particular alleles in males. While dominant males will probably rarely come near to being heterozygous at every overdominant locus, the dominant male presents the best average choice, considering all loci, for females.

I have suggested that genetic choice by females is most likely directed at some genome-wide indication of gene quality. Three reasons for this view are (1) difficulties may arise in carrying out assessment of individuals where several favored alleles may occur, but not in the same individuals; (2) females who use generalized characters in choosing mates have the greatest opportunity for gain in mate choice because they can take advantage of variation at each locus; and (3) selection on genomic elements is likely to oppose consistent patterns of identification and control of choice by individual alleles when these deny the full potential for success in reproduction to other alleles (Hamilton, 1967; Alexander and Borgia, 1978).

The notion of genome-wide selection of characters in males by females might be questioned because of results of mate choice experiments with *Drosophila* (reviewed by Petit and Ehrman, 1969). Females show convincing tendencies to choose

males of rare phenotypes in laboratory experiments in which differences in traits are based on differences of single mutation or chromosomal inversion. This type of experiment commonly has been cited as strong evidence for genetic choice in which females are programmed to select males based on a difference of a single gene, which is suggested to complement alleles in their gametes (Sheppard, 1953; Anderson, 1969; Ford, 1971; Trivers, 1972; Charlesworth and Charlesworth, 1975; Ehrman and Parsons, 1976; and many others). Surprisingly, in more recent publications these interpretations have not taken into account experiments by Ehrman (1970) which show that by introducing the odor from a colony of the rare type into the mating chamber, the pattern of mate selection can be regularly reversed so that common alleles are favored. This suggests that characters used in mate choice by females are not those initially selected by investigators. Biases favoring rare types apparently occur because these types are correlated with odors derived from the different genetic backgrounds of the test animals or nongenetic differences related to the different growth conditions. Females may have evolved to prefer "rare-smelling" males because, on average, these males are from different habitats and are not close genetic relatives. Maynard Smith (1956) has described the severe costs associated with inbreeding which females commonly appear to be programmed to avoid. Males from different habitats may also offer females the opportunity for gain from genome-wide complementation, which is quite different from hypothesized gain based on complementation of individual alleles. Even if foreignness is indicated by differences in single genes, odor may be only the first element in a hierarchy of criteria used in mating decisions. There appears to be ample evidence for the importance of other criteria in mate selection by *Drosophila* (Ewing and Manning, 1967), and these may give better indications of genome-wide differences in male quality.

Sheppard (1953) points out that olfactory cues may also provide a basis for instances of supposed complementation in the moth *Panaxia dominula*. He describes experiments in which when the characters he used to separate moths of different genotypes were concealed, females were able to maintain a biased pattern of mate choice. Since we are not told of the procedures for collecting and rearing moths for these experiments, the possibility of inbreeding avoidance patterns must be considered. These might occur if tests were carried out using adults reared from a small number of broods or from larvae which developed proximate to each other in the laboratory--as might occur in nature among siblings. Interestingly, the calculations of Haldane (1954) from field data on these moths suggest that in natural populations moths mate randomly with regard to the characters investigated by Sheppard. The choice based on the presumed gain from complementation of single alleles appears to be less common than Sheppard (1953) predicted would occur.

Mechanisms for Genetic Choice

Male-Male Fights

Direct interactions between males provide perhaps the best composite indication of relative overall quality. Male success in fights summarizes lifetime success in collecting food, resisting disease, and avoiding predators and injury. Conspecific males perform the most rigorous tests when matched head-to-head, and even small differences in performance are likely to be significant. These tests are always of considerable relevance since males tend to evolve together, and it is often in their interest to challenge attempts at deception by other males. In cases in which there is extensive maternal care, fights are likely to indicate not only quality of the chosen individual male in development and fighting ability, but the quality of those genes carried by the male which affect maternal parental care, as Alexander (1975) points out. Fighting by males, especially in systems in which structured dominance relations exist, leads to unambiguous results. Females with even limited abilities are likely to quickly and inexpensively discern differences among males based on fighting ability, especially if the loser is chased away or leaves. For lek organisms, fighting has been associated with obtaining central positions (Ballard and Robel, 1974; Wiley, 1974; Buechner and Roth, 1974), which are generally correlated with mating preference by females.

Large mating leks should be most common when females are able to move freely through the habitat and are not forced to compromise choice in the genetic quality of males to gain material benefits or to avoid predation. Females may generally favor mating with males in aggregations because such groupings (1) allow inexpensive, direct comparisons of physical attributes of many males, (2) facilitate tests by males of competitors because of nearness of potential opponents, and (3) provide indicators which females may use to judge the outcomes of past aggressive encounters. Each of these conditions should cause females to generally favor males in groups. If females can fully control sexual access of mates, then males must respond to female demands to mate successfully. Alexander (1975) pointed out that acoustical displays, luminescence, olfactory signals, and other cues generated by females, which have been considered to have the exclusive function of

attracting males to insure fertilization, may often be important in assisting females to institute "private leks" at which a female may encourage aggressive interactions among males, the outcomes of which may aid her in mate choice (see also Cox and Le Boeuf, 1977).

Lek-like aggregations are common in insects as well as vertebrates. Instances occur in a wide variety of groups (Lepidoptera: Shields, 1967; Scott, 1972; Hymenoptera: Zmarlecki and Morse, 1963; Diptera: Downes, 1969; Spieth, 1974a, b; Coleoptera: Lloyd, 1971). Among mammals (Le Boeuf, 1974; Gentry, 1970; Jarman, 1974) and some insects (Lin, 1963; Alcock, 1975; Alcock et al., 1976; Parker, 1970b-e, 1974a), males commonly control females. Even so, their behavior may strongly resemble a lek situation in that males commonly fight for access to females or places where females can be controlled (see discussion of *Scatophaga* behavior below).

Alexander (1975) has also suggested that fighting is important in mate choice as an indicator of the "prowess" of males (see also Waage, 1973); and on this basis, he explains lek formation. Alexander's argument differs from the one proposed here in that he suggests that females choose males because of the males' ability to fight. The suggested gain from this mate choice pattern arises from the assumption that females have been selected to choose fighting males as mates in order to have sons who fight well and are preferred in mate choice. Although it is clear how such a system might be maintained once started, this explanation does not provide a mechanism to explain why females who are unconstrained in mate choice are initially programmed to choose fighting males. No such problem exists if male fighting ability is correlated with greater average genetic quality among offspring of both sexes; then a net genetic gain should be expected among females who initially tend to choose aggressive males.

"War Propaganda" and Courtship Patterns

On "true" leks, private leks, or even when males are offering benefits derived from a territory, females are expected to test males through courtship displays. In some instances, females may encourage males to send out highly developed signals, which are often associated with aggressive interactions among males. Here I suggest that males willing to advertise their presence are either dominant and winners in previous combat or will soon be tested if they have not established such dominance. The greater the commotion a female can force a prospective mate to raise, the more effective is his advertisement to other potential suitors with whom she might mate. Males who can develop extravagant displays from a particular mating territory or perch, yet remain undisturbed through the whole courtship bout to be dominant over other nearby males. Such displays evince that the courting male is not a short-term intruder temporarily occupying a position or territory of a higher ranking male. If courtship is interrupted, a female's interests may be best served by leaving that male and searching for another who can maintain his position even after having provided a high quality display. Courting queen butterflies may leave the territory of a displaying male if chased by more than one male (Brower et al., 1965). Robel and Ballard (1974) describe female tendencies to avoid matings with males in leks without stable dominance relationships.

Most courtship structure and behavior has been commonly related to interspecific recognition of males by females. However, these characters may have a primary function in intraspecific communication among males. Fisher (1958) hinted at the relationship between characters which influence other males' aggressive tendencies and those which attract females. He stated, "As a propagandist, the cock behaves as though he knew that it was advantageous to impress the males as well as the females of his species, and a sprightly bearing with fine feathers and a triumphant song are quite as well adapted for war propaganda as for courtship." Wynne-Edwards (1962), in considering a very different hypothesis, recognized the same relationship when he noted, ". . . adornments used in epidectic (which includes fights among males) and amatory displays are frequently the same." He continues, "The converse development of adornments used solely for courtship and never for aggressive display seems at best to be relatively uncommon: examples probably exist, though I have not succeeded in finding a clear case among birds." In general, vivid and active displays which most accurately show a male's dominance should be favored by females not seriously threatened by predators during the mating process. I will refer to structures and behaviors which evolve in this context as products of selection under the war propaganda model.

Evolution of "Extravagant" Characters

Zahavi (1975) recognizes the need for female choice of males to be based on a wide array of genetic characters. However, the mechanism he proposes for how females might make these decisions has received extensive criticism (Dawkins, 1976; Davis and O'Donald, 1976; Maynard Smith, 1976). Based on Zahavi's "handicap" principle, females are expected to choose males based on the existence of characters likely to *decrease* males' fitness. Zahavi reasons that males who survive despite these recognizable handicaps are likely to

otherwise carry a better overall genetic complement than those who have failed or have not carried the handicap. He maintains that this model provides an alternative to the "runaway selection" model suggested by Fisher (1958) to explain the evolution of what Fisher called "extravagant" characters.

However, both Maynard Smith (1976) and Davis and O'Donald (1976) develop genetic models which suggest that the type of mechanism described by Zahavi is not effective. (A simulation by Maynard Smith showed no condition where genes responsible for the handicap and others for its selection by females could be favored. In their model, Davis and O'Donald found that handicaps could be favored only under extremely high intensity of selection against the handicap, a condition they considered extremely unlikely.)

It is my view that the structure of male characters used by females in mate selection does not correspond to what might be expected if the "handicap" principle were operative. Characters in species in which mate location is not difficult appear to be of two types--those of high signal value and those which are effective weapons. In each case, they seem extremely effective at carrying out specific functions. Deer antlers (Lincoln, 1972) and beetle horns (see Eberhard, this volume) realistically cannot be considered handicaps since they have a very apparent role in helping males to directly control conspecifics of both sexes. Exaggerated characters, such as brightly colored feathers and scales, acoustical signals, and odors, appear almost invariably to function in signaling male dominance both to females and to other males. According to the "war propaganda" hypothesis, a female who chooses a displaying male is choosing one who has earned his right to display. Nondominant males who attempt to court through displaying are promptly interrupted by dominant males. A female's encouragement of behavior which tests a male's dominance should include not only extravagant displays but sufficiently long courtship to insure that the behavior of her prospective mate has not gone unnoticed by other males.

Gilliard (1969) describes behavior among birds with the most extravagant displays, such as the Greater Bird of Paradise, which has dominance territories. Males of the Magnificent Bird of Paradise also appear to hold territories in trees (Rand, 1940). Most of the species described in detail by Gilliard have "loud, police whistle calls" and, in some cases, plumes are raised when a male approaches a territory-holding male's space. Male courtship displays commonly involve extension of plumes and loud noises from wing flapping.

Peacocks, which provide perhaps the most exaggerated display, are identified by Zahavi as an example of handicap. They also use their feathers primarily as a signal device.

Beebe (1926) states that

> Cockbirds, before they begin to fight, will often erect their tails about one another, although when the first actual threat is made these ornaments are folded away as compactly as possible . . . .
>
> There is no doubt about severe battles taking place, however, judging from the circumstantial evidence of sturdy legs and sharp spines, and actual evidence of fierce encounters between captive birds. As I said these are usually preceded by the display on the part of both birds.

In domestic fowl (Lill, 1966) and wild grouse (Kruijt et al., 1972; Kruijt and Hogan, 1967), frequency of display correlates with mating success. Ballard and Robel (1974) found that prairie chickens show the same trend. In addition, they present evidence that dominant males prevent subdominants from giving displays associated with courting.

Audubon (1831) says that male turkeys

> immediately fly towards the spot when a female calls from the ground. [Males then erect their tails, strut, quiver, and vocalize.] While thus occupied, the males often encounter each other, in which case desperate battles take place, ending in bloodshed, and often the loss of many lives, the weaker falling under the repeated blows inflicted on their head by the stronger.

While it is clear that displays used by males fit the "war-propaganda" function described by Fisher, they seem inappropriate in the role of handicaps, as suggested by Zahavi. In most cases, most or all of the plumage can be folded and concealed from the view of predators outside the mating season. Such structures seem designed to maximize signal value for a minimum of caloric cost. A true handicap needs to be demonstrably expensive to its bearer. Females should be generally unimpressed by males with the ability to conceal the handicap, as is common for most secondary sexual characters which are not weapons. Contrary to this prediction, display of such ornaments seems to strongly influence female mate choice.

Davis and O'Donald (1976) present several additional criticisms of the "handicap" principle which not only are relevant to that model, but also to the analysis of selection based on female preference for males able to demonstrate dominance. They suggest that models in which females are presumed to gain by choosing males of high genetic quality are ineffective in explaining long-term patterns of mate selection. Using an argument similar to the one attributed to Williams (1975, see above), they state that "When the combination of characters is as near the optimum as it can get, there can be no advantage in mating with a more highly selected male since no benefits can be received in an increase in fitness in offspring." Davis and O'Donald imply that the disappearance of genetic variability and associated benefits in mate choice are the expected condition. This conclusion is predictable considering their reaction to Zahavi's insistence that selection is based on the composite of characters in the whole genotype. They state, "The number of characters that are being selected as a result of mating preferences appears quite irrelevant to us, for different phases in a polymorphism are being selected, each phenotype of which is usually a combination of several characters." The apparent disregard for the female's need to consider effects of selection on alleles throughout the genome calls into question their assertion that genetic variance and consequent gain from mate choice are unimportant. Models relating to this problem have already been discussed. These, considered together with changes in selective coefficients likely to involve some of the vast number of alleles in the genome in each generation, suggest that gain is available for females from choice among males of a given generation. In addition, long-term gain from even occasional substitution of beneficial alleles may be sufficient to maintain a constant mate selection pattern among females.

The concluding remark made by Davis and O'Donald is that "Zahavi offers no substantive criticisms of Fisher's theory of evolution of mating preferences." These authors consider the absence of such criticism important since "This theory provides a sufficient explanation for difficulties that led Zahavi to put forward his own theory." Even though Zahavi has failed to put forward any suggestion of problems with the "runaway process," as it is called by Fisher (1958), important difficulties do exist with it. The general acceptance of this model (O'Donald, 1967, 1973; Brown, 1975) suggests that further discussion is warranted.

Generally unstated implicit assumptions in Fisher's model are necessary for the pattern of character development he describes, e.g., females must employ an open-ended preference whereby the greatest extreme in a character present in a group of males is favored. This requirement leads to problems with the model. Fisher and later O'Donald (1967, 1973) suggest that the "runaway process" will continue until balanced by disadvantage, presumably through male mortality. However, they do not state exactly how this equilibrium is established.

Two types of "equilibrium" outcomes might occur. One type is stable and is expected when male mortality due to the development of an exaggerated character is constant or nearly constant between generations. Under these conditions, directional selection should produce a situation in which only one or a few males survive to breed in each generation. If, for example, tail length is the character of concern, males with shorter tails never reproduce so there is little value in producing them.

The other "equilibrium" condition often may be unstable and is associated with variable male mortality between reproductive periods. Under this condition, short-tailed males may reproduce in seasons when all of the long-tailed males die. If mortality is unpredictable, there may be disruptive selection for the character of concern. However, this may also affect the pattern of female choice. Since tail length of males is heritable, females who choose short-tailed mates will produce sons that are more likely to live under all conditions. These females who choose short-tailed males will not lose, even in years when long-tailed males are available, since they may mate within their own type and, barring any differences in female mortality associated with type and/or random events, should persist to the same degree as females who have chosen long-tailed males. In bad years, short-tail-choosing females have an advantage. Sons of long-tail-choosing females die, and these females are forced to mate with short-tailed males. The relative frequency of short-tailed males and females who choose them should increase. If choice of short-tailed males is open-ended, as was choice of long-tailed males, then selection for the "runaway" character should be reversed. This will be fueled not only by the open-ended selection process as described by both Fisher and O'Donald, but by added gain for females who produce males with a greater than average life expectancy.

It can be argued that within-type mating may lead to inbreeding and consequent reductions in fitness (Maynard Smith, 1956) and may cause such lines to decrease in frequency. However, when the limits of male survival are reached under variable conditions, many females are likely to produce short-tailed males; hence, inbreeding may be avoided.

Two kinds of information suggest that the "runaway process" may be of limited significance. First, outbreeding populations with extreme shortages of males in which polygyny is common do not exist. For example, Selander (1965) describes biases of 2.42 females per male in the great-tailed grackle, but even at these levels many more males are present than females need in order to be effectively fertilized. In this instance, the "runaway process" appears not to have stabilized at a condition in which available males are limiting female reproduction. Second, the "runaway process" suggests that females would choose males based only on physical characteristics. Typical lek behavior, in which females appear to choose males based on their position, would only be predicted

from the "runaway selection" model if differences in tail length could account for male position on the lek. However, males fight for position, and since there is no *a priori* reason to suspect that fighting ability is enhanced by exaggerated characters, it appears that female choice based ultimately on male fighting ability does not support the "runaway selection" model. One might argue that dominant males keep other males from displaying and thereby limit female ability to survey other males. However, if females were only interested in the size or intensity of display, subordinate males with high quality displays should leave the lek and females should seek them out. Lill (1976) describes male and female manakins feeding together during the mating season with little suggestion of attempts by males to display off the lek. This also seems to be true for other lekking species in which males show more highly developed dimorphism.

Mate choice based on selection of dominant males, according to the "war propaganda" hypothesis, provides perhaps the most likely explanation for the evolution of Fisher's "extravagant characters." This model also may have some significance in territorial species in which males control material benefits. A display, perhaps not as well developed as might occur in a genetic choice system, could show that a male present on a territory is the true owner and not simply visiting while the owner is temporarily away. Certainly, various modes of signaling are well known for most species with resource-based territories (crickets: Alexander, 1961; grasshoppers: Otte and Joern, 1975; birds: Howard, 1974; fish: Assem, 1967; lizards: Evans, 1938). Even in these cases, the signal may not only indicate possession of resources and consequent ability to disburse material benefits, but may also serve as an indicator of the genetic quality of an individual male.

Although Fisher (1958) recognized the essence of the "war-propagandist" model, he clearly did not intend for it to be used to describe the wide variety of characters outlined here. This is shown in the sentence concluding the discussion of this model: "Male ornaments acquired in this way might be striking, but could scarcely ever become extravagant." Information presented on the behavior of cocks who display "extravagant" characters, as well as problems with the "runaway" model he apparently favored in explaining these cases, suggest that a revision in thinking of how sexual selection operates may be in order.

RESOURCE STRUCTURE AND MALE ABILITY TO INFLUENCE FEMALE MATE CHOICE

The Effect of Resource Structure on Male Control of Resources

In the equilibrium model presented above, knowledge of male variation in ability to control resources appears as a key element in predicting patterns of mating success. Two factors are important in determining this ability: (1) success of an individual male in dominating conspecifics in aggressive encounters and (2) structure of resources used by males to influence mating decisions by females. Brown (1964) considered variation in aggressive ability of individuals as central to their ability to hold territories. Trivers (1972) discussed the evolution of male size and provided data to show its relation to reproductive success. A more general model which discusses strategies of individual males in holding resources has been discussed by Parker (1974b). He models male decisions to fight in a habitat in which resources are subdivided into units of equal quality. Differences in male ability to win fights are considered in terms of varying physical characteristics, which are valued according to their ability to confer "resource holding power."

Resource structure, defined as the spatial pattern and richness of resources along spatial and temporal axes, has been considered to a more limited extent. Verner (1964) discussed the relationship of male territoriality and actual levels of benefits males could provide and thereby affect female mating decisions. He compared his own and Kale's (1965) work with marsh wrens and suggested that the different degrees of polygyny enjoyed by males in the two studies would be related to territory shape. Kale's birds bred along a canal and territories had long, lateral dimensions. The territories of Verner's birds were in swamps and were more nearly circular. It was suggested that the oblong shape of territories belonging to Kale's birds limited the effective area a male could defend (see review by Emlen and Oring, 1977).

Fretwell and Lucas (1969) developed a model which related aspects of resource structure to male ability to control resources. Male success from aggressive behavior was tied to variance in the quality of habitats occupied by males. They predicted that males fill various levels of habitat quality in accordance with their ability to displace lower-ranking males. The best males gain the best habitat sites, while males of lowest ability obtain low quality sites which would otherwise be unoccupied.

An attempt is made here to develop a more general model. However, predicting patterns of male control of resources directly from resource structure is difficult because of the large number of spatial configurations possible under conditions where resources are unevenly dispersed. It is unlikely that each specific configuration could be conveniently described. In addition, males with differing abilities to move may react differently to a given pattern of resource distribution. Classification of resource structures into types thus appears as the only feasible approach to using resource characteristics and predicting how they affect male ability to set territories. The approach used here is not to consider resource structure directly, but to deal with resources as seen by males who control them. Changes in structure can be viewed in terms of their relevance to males. Aside from reducing the number of resource configurations which must be considered, this approach avoids variations in level of male control due to interspecific differences in males' abilities. With minimal knowledge of the physical capabilities of males attempting to control resources, resource structure can be used to predict the distribution of material benefits among males.

Consider a situation in which all resources available for females of a population for successful rearing of offspring are condensed into a minute clump. A dominant male exists who is able to exclude other males and unreceptive females from these resources. If females are fully dependent on the resources he controls, such a male would father most, if not all, offspring of the next generation. Expanding the area over which resources are distributed is likely to handicap the dominant male in his attempts to control resources. Defense of a larger perimeter results in increased energetic costs and, together with physical limitations on movements, should lead to a maximum *defense perimeter*. A spread of resources beyond the maximum perimeter which a male can effectively defend leads to an automatic increase in prospects for matings by subdominant males.

Males who have escaped the influence of the dominant can establish their own territories and influence the pattern of female mating decisions in their favor. Where strong dominance relationships exist between males, an increase in the area over which resources are distributed should cause a reduction in population-wide variation in reproductive success. High levels of dispersion may allow all males some access to resources and may even reduce variance in success to zero, especially under conditions in which mating decisions are based solely on the amount of resources controlled by an individual.

A similar shift in resource structure can be considered under conditions in which males are more nearly equal in their ability to control resources. Inability of any one male to control all resources will lead to either temporal or spatial subdivision of the resource. Although males may have equal overall ability, males may focus risk and energetic expenditure into a small time segment so they can control the resource and gain exclusive matings over a short period. Alternatively, males may subdivide the resource into small territories, all contained within the perimeter of one individual, since, over long periods, it is unlikely that a male can be continuously excluded by another of equal ability.

Effects of changes in the degree of dispersion of resources can also be considered in cases in which an increase in the variance in the pattern of resource distribution accompanies the spread of resources. The initial condition may be similar to the first case in which the dominant male controls all matings. As resources spread, the situation becomes identical to the one described by Fretwell and Lucas (1969) and the same results are predicted. The aggressive ability of males is correlated with the quality of the position they win.

If resources vary in quality, but males are of constant ability, prediction is more difficult. Males in good habitats are likely to be challenged at various intervals by others of very similar aggressive ability. If movement between territories and fights are low cost, and owners of good territories do not have a consistent advantage, then replacement should be common. Individual males may spend nearly equal amounts of time in the various quality habitats.

These models involve three of four variables important in determining patterns of male control. Two of these deal with resources and are defined by the limits of male ability to control resources. By assuming that males have a maximum diameter that they can defend, the *number of defense perimeters* can be used as a measure of the total area over which resources are spread. *Variance in quality among perimeters* can be used to measure the degree of clumping of resources relative to a male's ability to cover some limited area. An accurate measure of resource clumping requires several parameters, among which is *variance among perimeters*. However, by assuming homogeneity of resource quality within perimeters and by establishing a protocol to standardize the positioning of perimeters on resources, e.g., establishing the first perimeter so that it covers the richest area and successively placing subsequent perimeters on the highest quality area that remains uncovered, this one measure may give reasonable estimates of variance in resource distribution.

Males competing for control of resources are rated in terms of *variance in aggressive ability* as measured by differences between individuals in their ability to win conflicts over resources valued by females. *Number of males* has not been dealt with, but changes in this variable parallel those in which the number of resource perimeters changes. Increase in

the number of males is equivalent to reducing the number of perimeters if in each case variance in quality of resources among perimeters and in aggressive abilities among males remains unchanged.

Resource Structure and Resource Defense

The variables which describe the proportion of individually held resources are also important in determining the value of the resource control strategy. If the number of defense perimeters in which resources occur exceeds the number of territorial males, then females and nonterritorial males are free to use uncontrolled resources. Females not limited to controlled resources can avoid compromises based on the need for resources in choosing a male. The presence of resources outside the control of males allows other males the option of collecting on resources when benefits derived from this behavior represent an effective attractant to potential mates.

The success of both females and nonterritorial males in using these unprotected resources is also affected by variation in resource quality. High variance in resource quality will allow territorial males to concentrate resource defense efforts on high quality areas. These hot spots reduce the rate at which males lose control of resources as the resources become spread over an increasingly wide area (see Fig. 5).

A decrease in the percent of all resources controlled by all males may lead some individuals to abandon resource control as a strategy for attracting mates. Alternatives for these males include (1) collecting on resources and then using the items collected to attract mates or (2) abandoning efforts to use resources in mate attraction and becoming subject to genetic-based evaluation by females. Transition from resource control or resource collection was dealt with in the equilibrium model above. The first of these two kinds of transitions is most likely if the formerly defended resource is not easily collected, at least in terms of the immediate physical abilities of the animal being considered. Examples of such non-collectable resources are oviposition sites of odonates and nest sites for birds. Alternatively, food--or time and energy to obtain it--is commonly a limiting resource (Lack, 1954) for which collection and control may be important in determining male success in attracting mates.

Successful initiation of resource collection must be related to conditions where some male-female pairs are able to collect more resources useful to the female than she can obtain being paired to a territorial male and using resources collected and defended by him. At least six variables are likely to affect the value of collection and control strategies

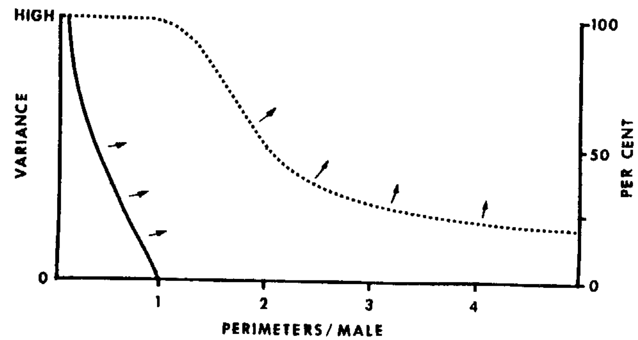

Fig. 5. Change in number of defense perimeters per male and its effect on variance in the proportion of resources held by individuals (solid line) and the percent of resources controlled by all males (dotted line). Spreading males out over the available resources reduces the effects of dominant males on individual ability to hold resources. Consequently, variation among males in the share of resources held by individuals decreases. This spreading may also reduce overall male ability to control available resources. Some variation in the aggressive abilities of males is assumed; lines in the figure show relationships when all perimeters are equal in value. Increased variation in the quality of perimeters causes a shift in curves resulting from a higher variance among males in the proportion of resources controlled and a smaller percent of any uncontrolled resources.

to males. These include (1) variation in control of resources among males, (2) percent resources controlled by all males, (3) ability of males to guarantee benefits, (4) correlation of control with genetic quality, (5) efficiency of resource collection both on and off territories by both sexes, and (6) the degree of contribution of collected benefits by territorial males.

A decrease in the proportion of resources controlled by males is likely to favor attempts at resource collection, but predicting the level at which such a transition is likely to begin is difficult. If females are very inefficient in collecting resources that are valuable to them and there is low variance in the quality of resources, then collection may become an important strategy with only a small fraction of the resources beyond the control of males. However, if females need as much foraging space as possible and are very efficient in collecting available resources, then males need to control only a little more than 50% of all resources for resource control to remain as a dominant strategy. Additional difficulties for prediction of the relative importance of

resource control and collection strategies come from our inability to evaluate the effect of high levels of variance in the amount of resources controlled by individual males. High variance may suggest a decreased tendency for territory-holding males to assist individual mates in resource collection, especially since such efforts by these males might detract from their ability to hold territories needed to attract additional females. However, high variance in control implies clumping of resources within a few defense perimeters and perhaps greater efficiency for females in collecting resources in these defended areas. The first effect would tend to devalue the controlling male, while the second is likely to enhance his attractiveness.

Resource Structure and Male Fighting Ability

In dealing with the evolution of characters in males which enhance their aggressive ability, Trivers (1972) identified two primary patterns for the expenditure of reproductive effort by males--those involving "appreciable male parental investment" and those in which males have "little or no parental investment." Individual success among noninvesting males is suggested to be strongly dependent on the level of effort made by other males. Males who are able to dominate others are more likely to enjoy frequent matings. Success in male-male encounters is correlated with the amount of effort spent by males on characters which enhance their ability to dominate others. In systems in which some males gain from heavy investment in characters which enhance their ability to win fights, Trivers (1972) predicts that the mating success of individual males remains low until there are very high levels of effort in reproduction. A sharp increase in success is expected to follow this effort (see also Gadgil, 1972). Trivers suggests that competition in "investing" males is likely to be less severe. As a result, no escalation of effort is predicted to occur; expenditure of effort by males is not directed toward the high degree of development of specialized structures common in males who frequently engage in combat. Although Trivers did not tie the evolution of these characters to resource structure, these relationships are easily developed.

Although the suggested dichotomy in reproductive competition by investing and noninvesting males is often true, exceptions occur which make a more detailed understanding of evolution of patterns for expending reproductive effort important. Among noninvesting males, those who do not use resources to influence female mating decisions may commonly be involved in direct physical encounters with other males (but see below). Dominance in such conflicts was understood by Darwin (1871) to be important in determining levels of mating success and selection of males for development of structures which aid in winning sex-related combat. However, use of resources by males may cause expenditure-of-effort patterns to be most closely tied to resource structure. Resources distributed in a small number of clumps, relative to the number of males, provide dominant males with the opportunity to gain from their ability to exclude nearby competitors. Areas which individuals might defend overlap, and males successful in excluding sexual competitors within the contested area gain control of a large share of the available resources. The potential to achieve control provides strong selection for increased expenditure of effort in resource control. Spreading out resources leads to a reduction in male opportunity to gain from extreme investment in characters required for success in aggression; there is a smaller payoff from winning which does not justify diversion of parental investment or added risk to the developing juvenile. Reduced prospects for gain from winning fights favor adjustment of potential investment, which may be devoted to characters useful in allowing some males to dominate other males.

Benefits delivered to females before mating may serve to attract mates and detract from a male's ability to provide investment. In some cases, these contributions may constitute the total items delivered by males to either females or their offspring and reduce male ability to invest directly in offspring. Although such contributions are not considered parental investment by Trivers, their effect on female success and male ability to attract mates is quite similar. By considering patterns of male effort which include premating contributions of benefits by males (see Alexander and Borgia, this volume), the suggested dichotomy in male strategies can be extended to explain most common patterns of male behavior.

In examples discussed so far, only two real alternatives have been considered for spending reproductive effort. Another context in which noninvesting males are not likely to devote effort to activities or structures related to combat may occur at extremely low population densities. In this context males searching for females may exhaust themselves in the search for mates. Scarcity of competitors suggests very limited need to commit effort to the development of fighting ability and little residual ability to invest in mates when they are found.

Resource Structure and Male Mating Success: Experimental Support

Other studies besides that of wrens (Verner, 1964) correlate polygyny with the quality of male territories (Zimmerman, 1966, 1971; Haartman, 1969; Verner and Willson, 1966; Verner and Engelsen, 1970). Although these studies support suggested relationships between resource structure and variance in male success, they do not correlate characteristics of males with the ability to supply females with items from the habitat that they need. Also, the correlative nature of these data leaves some question as to the true nature of cause and effect in these relationships.

Experiments involving changes in availability of resources used by females as oviposition sites have allowed me to test the effect of these changes on the mating success of males of various size classes in the fly *Scatophaga stercoraria*. In these experiments, cow dung, which is used as an oviposition site by females, was placed in two levels of abundance under conditions of high and low fly density in an isolated cow pasture. Male *Scatophaga*, which are highly variable in size, hold territories and/or patrol oviposition sites. These behaviors enhance their ability to capture females who come to the dung pat to oviposit. After males capture females, they copulate and then guard them during oviposition (see Parker, 1970b). Availability of oviposition sites was controlled by removing all fresh dung pats deposited by grazing cattle. Fresh dung of constant quality was put out under two conditions--high (two hundred pats) and low (six pats) availability. Each pat was 15 cm in diameter. Fly density was controlled by running experiments at times during the mating season when numbers of breeding flies are known to differ (see Hammer, 1941; Parker, 1970a). Mating success of males was measured by counting frequency of copulations by males in each size class. Results suggest that under conditions of both low and high fly density, an increase in resource availability lowers the mean size of the copulating male. In addition, the mean size of males who can obtain positions on the dung pat shows a similar decrease (Fig. 6).

These data support the notion that the spreading of males over a resource tends to reduce variance in mating success, a prediction one might make if females used only resources in mating decisions. Observations suggest that females choose pats for reasons other than the males who occupy them and that males capture the majority of females in the vicinity of the pats.

Large males influenced the mating success of small males in at least two ways. Attacks by large males caused small males to move off fresh dung pats. Large males also successfully stole females from copulating or guarding smaller males.

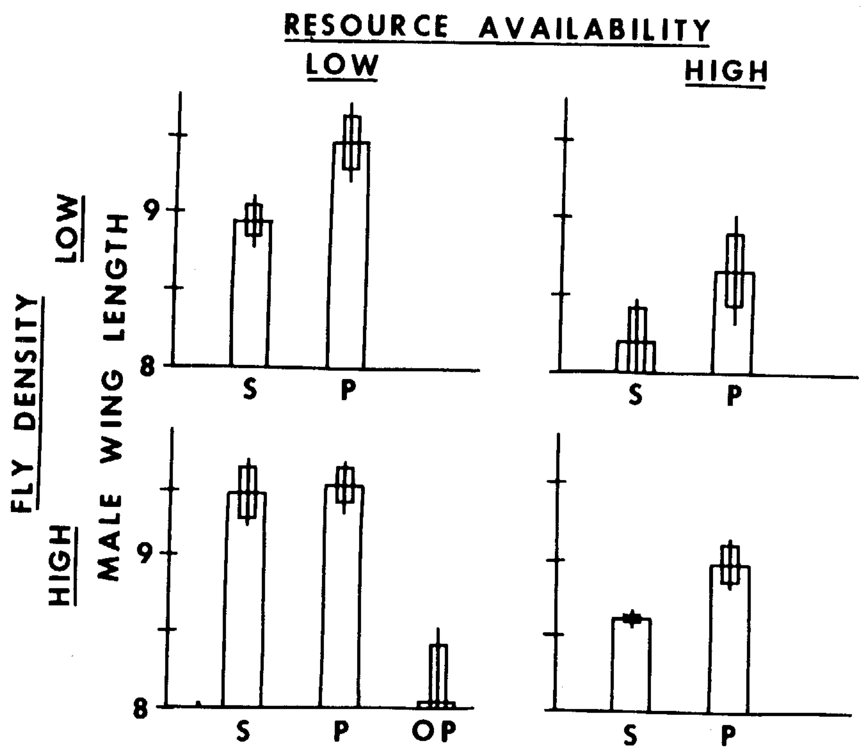

Fig. 6. Results of resource manipulation experiments performed at high and low male density conditions. S represents the mean size of unpaired males who are on pats, P is the mean size of males paired to copulating or ovipositing females, and OP is the mean size of males not in the immediate vicinity of pats. Bars and lines represent 95% and 99% confidence intervals, respectively. Under both conditions of male density, shifts in resource availability appear to cause significant changes in the mean size of copulating males.

At low densities of males per pat, small males chased from pats by large males could move to unoccupied pats and capture any females that came to these pats. As the number of pats was decreased, males were forced onto fewer resources and interactions with large males caused smaller males to leave the dung pats.

Territories were common at low male densities per pat, but as density increased, males scrambled to capture females without obvious attempts to remove conspecifics from the dung. Small males apparently avoided these pats because of (1) the high probability of being replaced by larger males while guarding females, and (2) costs from being attacked by large males searching for females in the vicinity of the pat.

In the models presented above, it was assumed that females choose males on the basis of the resources that they offer. Increasing the males per unit area of resource was predicted to cause a reduction in territory size, much like the model proposed by Huxley (1934). In *Scatophaga*, females have limited ability to choose mates, and it appears that the primary function of male territories is to aid males in capturing females. As male density increases, defense of small areas becomes ineffective if, as appears to happen, nonterritorial males can capture females before they reach areas where males' territories are formed at low density. Ability of large males to control females during and after copulation, and their inability to effectively remove other large males from the available resources, eliminate opportunities for gain through attempted resource control at high male densities per pat.

The relationship of sexual dimorphism to resource structure and the effect of each on male-male combat are supported by these experiments with dung flies. If males are forced onto a few pats, advantage to large males is shown by their increased mating success. The spreading of resources and increased relative success of small males suggest a reduction in the advantage gained from large size. Maintaining low density conditions should commonly cause selection for reduced average size among males. Apparently, increased size comes at some cost in terms of mortality, and when it provides no net gain in reproduction, selection would favor individuals who avoided additional growth.

A convincing comparative study also points out the relationship between resource structure and the development of sexual dimorphisms. Alexander et al. (1978) correlate the degree of sexual dimorphism with harem size for four mammalian groups. In this case, groups of females may be considered resources, and harem size a direct measure of the number of females per diameter containing resources.

Variation in Male Ability To Control Resources

Variability in adaptations related to defense of resources might be best considered by comparing growth strategies of individuals placed in habitats of different quality. Considering size as a typical sexually selected character, males must make a "decision" as to how much risk of mortality to take in order to reach a size which enables them to most effectively compete with other males. Particularly in organisms in which growth is restricted to larval habitats, and which receive no parental assistance, risk due to mortality during growth can be related to the length of time an individual spends in its larval habitat (Wilbur and Collins, 1973). Larger adult size also results from a longer larval growth period. Male gain from large size must be weighed against increased risks (Williams, 1966; Wiley, 1974) to determine the best size at which to leave the larval habitat. In cases in which parents are the primary source of resources needed for growth, there may be a similar time-dependent growth rate. However, the decision lies with both parent and offspring. For both parent and offspring, increased commitment must be considered primarily in terms of decreased parental ability to contribute to other offspring (Trivers, 1974).

Such relationships are considered in Fig. 7, in which gain from the male decision to grow to a larger size is compared to the cost derived from increased mortality and delayed or lost reproduction. Slope of the benefit curve is determined by the added payoff in reproductive success for a mature male about to reproduce who shows an infinitesimal increase in size. He competes in a population in which all other males are the same size and have not experienced this same tendency to grow. The cost curve shows the effect on mortality and reproductive rate related to the same change in male size. Successive instances of directional change in size are predicted to occur until the difference between costs and benefits reaches a maximum.

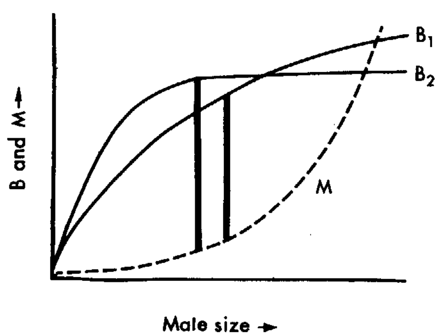

Fig. 7. The effect of increased male size on costs of growth (M) and associated benefits of increased size. B_1 shows a relatively constant increase in gain for males with additional size, which could be related to conditions in which resources are clumped. Males under conditions which show the B_2 pattern of gain probably occur where resources are spread far apart and increased size leads to little measurable gain in mating success.

The pattern of gain from changes in male size depends upon resource structure. Extreme clumping of resources allows a consistent gain from increased size, particularly in populations with many males. Spreading of resources causes a limit in gain from size and a flattening of the gain curve. Assuming the same association of mortality with size, the predicted size for males when resources are spread is much smaller than when resources are clumped.

Populations in which equilibrium male size occurs in a flat portion of the gain curve may be considered to have realized the full potential for developing dimorphism as determined by the structure of resources. In other cases in which males can only control territories smaller than they can effectively cover, limits on the development of characters needed for defense are, at least theoretically, determined by conditions of growth.

The growth conditions for all individuals within a population may not be identical. This is likely to have important effects on male patterns of competition. Insects which develop in suboptimal host plants, or in ponds of different temperatures or prey density, must adjust accepted levels of risk to reach a competitively successful adult size. Parents may also differ in the amount of effort they are able to devote to sons (Trivers and Willard, 1973). Open sexual competition among adult males will force growth "decisions" of a developing male in any habitat to be weighed against those made under the best prevailing conditions for juvenile development.

Developmental strategies of growing males in three habitats that differ in quality are considered in Fig. 8. Those that grow in the lowest quality habitat, even when taking maximum risks, may not be able to attain the level of aggressive ability of males who grow up in the best habitat. Males in the habitat of intermediate quality can equal the quality of males produced under the best conditions, but only with high levels of risk. Under conditions in which there is little predictable variance in the quality of resources controlled by adults, there may be few, if any, opportunities for reproduction by males who develop in low quality habitats. However, variance in resource quality, the number of males, and the spread of resources may allow males who develop in low quality habitats to occasionally hold resources. In a system with two states of resource dispersion, males who grow in low quality habitats may only be able to gain access to resources under conditions of high resource dispersion. All growth and behavior of males in low quality habitats are keyed to success under conditions in which resources are highly dispersed when these individuals are adults. If there is some possibility of added reproduction by these males when

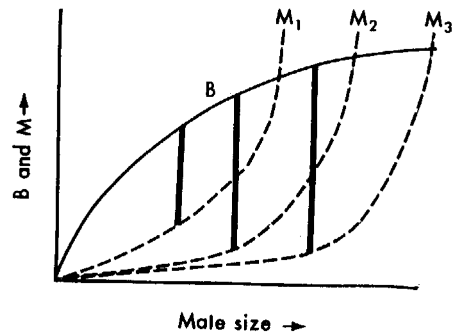

Fig. 8. Variable growth conditions lead to different costs to males in obtaining a sufficient size for effective sexual competition. Males growing under the worst conditions (M_1) cannot, with any level of risk, equal the optimal size of males who grow in the best habitat (M_3). Males growing under intermediate conditions (M_2) can reach that size, but only with high levels of risk. Decisions about size for males who grow under the best conditions may change with an increase in the number of males from other habitats who attain what might otherwise be their optimal size.

resources are condensed, individuals may evolve to take added risks so as to exploit the preferred habitat. Males' strategies for development will generally depend on the commonness of each condition of sexual competition and the costs to males of each of the growth strategies. Developmental models discussed here are designed for organisms, such as insects, in which growth is complete before sexual maturity. Similar kinds of decisions must be made by vertebrates and other organisms with less determinate patterns of growth if growth is less efficient at different stages of the life cycle, such as after sexual maturity.

A constant pattern of variation in resource structure may allow the development of genetically determined polymorphisms for male size and other sexually selected attributes. Genetic variation in males necessary to cause polymorphisms is most likely maintained in a frequency-dependent fashion. The balance of genetic alternatives is adjusted in relation to (1) the proportion of resources to which morphs are best adapted and (2) the relative cost of growth to produce the ideal phenotype for each condition of sexual competition. This form of polymorphism may be most likely where there is little variation in juvenile growth conditions which might predispose individuals to certain strategies of resource

acquisition. Despite the plausibility of these genetically determined polymorphisms associated with resource structure, their occurrence seems limited (Charlesworth and Charlesworth, 1975; but see Gadgil, 1972; Gadgil and Taylor, 1975), while there is abundant evidence for occurrence of polymorphisms apparently based on varying growth conditions (Wynne-Edwards, 1962).

SUMMARY

It is unlikely that a single model of sexual selection can be developed which is sufficient to explain all mating associations. Four typical patterns of male-female pairing are discussed. These show varying degrees of participation by members of each sex in mating decisions. Differences apparently result from variation in the relative ability of members of each sex to gain control of conditions in which mating occurs. Outcomes of intrasexual shifts in control may be largely determined by ecological conditions.

Of the different types of mating associations, female choice based on male ability to generate both material and genetic benefits is given special attention. This is done because of difficulties in (1) female attempts to weight the value of each type of benefit and (2) effective transfer of benefits between the sexes. A model is developed in which females shop among males to maximize gain from the combination of benefits received. Patterns of male mating success are predicted on the basis of (1) distribution of each type of benefit among males, (2) female need of the two types of benefits, and (3) the effect of previous matings on male ability to discharge both types of benefits. Transfer of material benefits in this model assumes that members of each sex can effectively guarantee delivery of benefits before mating. Such an approach implies that (1) the use of the term "desertion" by Trivers (1972) and others is inappropriate for most conditions in which males leave before nesting is complete, and (2) males may often be able to bargain through the control of benefits to avoid instances of cuckoldry.

The four patterns of male-female interactions can be organized into a dominance hierarchy. If conditions are sufficient for the development of more than one of these strategies, then the relative position of the strategies involved in this hierarchy predicts which one will occur. Strategies in which males have the highest relative influence in mate choice tend to be more dominant.

Strategies and implications resulting from the use of genetic and material benefits in mate attraction are considered in detail. In apparent genetic choice systems, the "war

propaganda" model is developed to consider the evolution of what Fisher (1958) called "exaggerated characters" and common patterns of courtship. Success in fights among males (Alexander, 1975) is seen as a key character for females in making appropriate mating decisions about the genome-wide quality of their prospective mate. Fisher's "runaway selection" model is criticized and suggested to be inferior to the "war propaganda" model. The key elements of the "war propaganda" model are extended to explain courtship patterns, particularly in species in which males generally transfer only genetic benefits.

Problems of the genetic choice model are discussed and plausible explanations consistent with the effective functioning of that model are presented. Two models for the maintenance of genetic variation at levels sufficient to allow for females using genetic criteria to gain through nonrandom mating are presented. Interpretations of experiments on mate choice which suggest selection of mates based on single alleles are questioned.

Aspects of male population and resource structure are used to describe (1) the overall importance of material benefits to females and (2) the relative ability of individuals to provide benefits. Experimental data are provided which support the hypothesis that changes in resource structure can have important effects on patterns of resource control by males and on male reproductive success. The relationship of resource structure to the ability of males to control versus provide benefits derived from resources is related to patterns of male population and resource structure. Factors affecting variation in male ability are also considered and these are reviewed in Fig. 9.

ACKNOWLEDGMENTS

I thank the following people whose helpful discussions aided me in developing this paper: M. Feaver, M. Hirschfield, J.L. Hoogland, R.D. Howard, C. Kagarise, L. Kirkendall, K. Noonan, R.B. Payne, D. Ruby, P. Sherman, R.W. Storer, R. Thornhill, D.W. Tinkle, and, especially, R.D. Alexander. J.L. Hoogland, L. Blumer, and R.D. Alexander read the paper and improved it in many ways. Support for field research has been provided by the following groups: Theodore Roosevelt Memorial Fund, Sigma Xi, The University of Michigan, and the National Science Foundation (BM575-17806). Diane B. de Forest gave technical and financial support. This paper is dedicated to the late Jasper Loftus-Hills, who greatly stimulated my interest in problems relating to sexual selection.

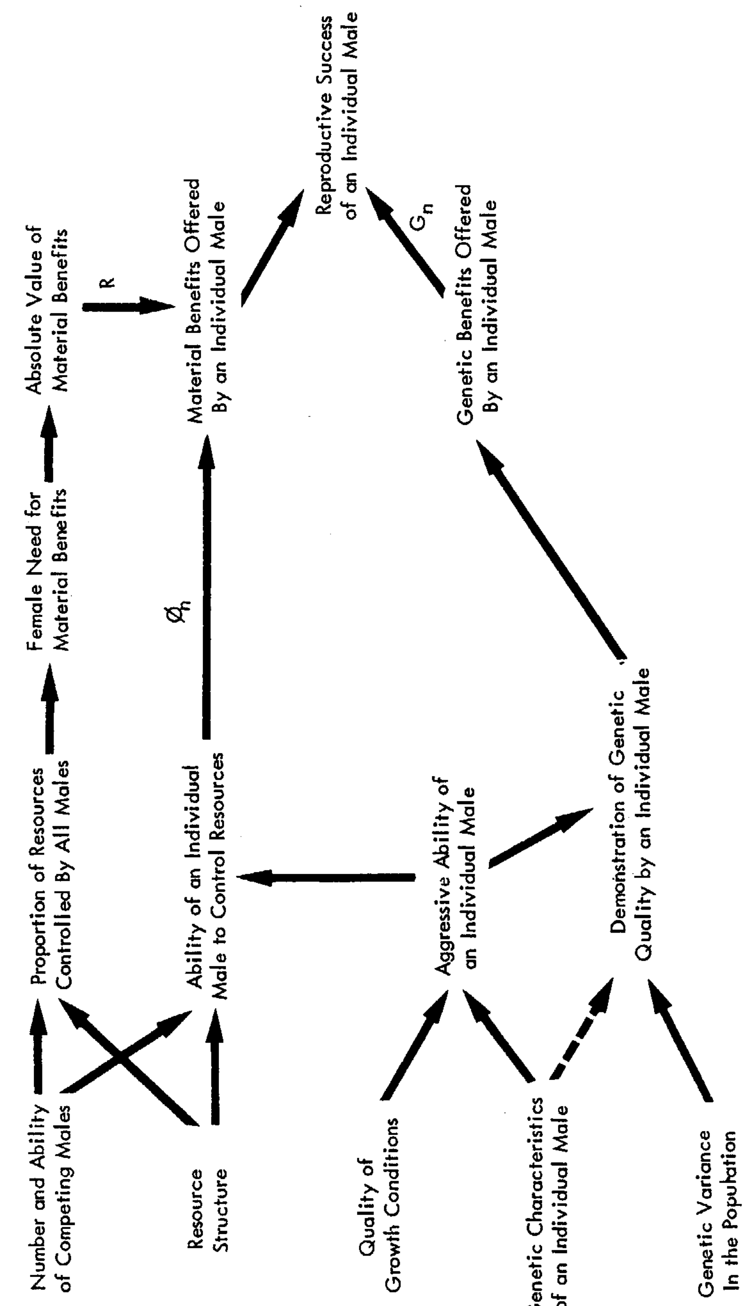

Fig. 9. Summary of relationships among variables influencing male reproductive success in situations where benefits males offer originate from defended resources.

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MALE AND FEMALE SEXUAL SELECTION AND THE EVOLUTION OF MATING STRATEGIES IN INSECTS

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INTRODUCTION

The concept of sexual selection, formulated originally by Darwin (1871, 1874) in *The Descent of Man, and Selection in Relation to Sex,* has received less attention from evolutionary biologists than the concept of natural selection. Early opposition to some of Darwin's ideas on sexual selection (e.g., Huxley, 1938; Grant, 1963) probably discouraged investigators. Also, some authors writing on the subject of sexual selection seem to have difficulty in distinguishing between natural selection and sexual selection as envisioned by Darwin (e.g., Richards, 1927; Mayr, 1972). Recently, however, there has been a reevaluation of the importance of sexual selection as shown by the increasing number of publications on the subject (e.g., see papers in Campbell, 1972). Part of the change in attitude must be attributed to a relatively recent realization by evolutionary biologists of the potency of selection acting at the level of the individual organism rather than at a supraorganismal level (Lewontin, 1970; Williams, 1966, 1971; Wilson, 1975; Alexander, 1974, 1975). An investigator must consider the severe reproductive competition between individuals of the same species in order to understand sexually selected attributes.

Darwin proposed his theory of sexual selection to explain certain characteristics of organisms not explicable in terms of survival or natural selection. Sexually dimorphic attributes in insects played a prominent role in the development of Darwin's ideas on sexual selection. He cited numerous insect examples to support his ideas on how such attributes might be favored by selection even though they increased the chances of individual mortality. For example, the elaborate and cumbersome mandibles of male stag beetles and dobsonflies were cited as characteristics that primarily function in sexual combat

ISBN 0-12-108750-6