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One area of controversy in evolutionary biology has been the 'choice', usually by females, of phenotypically extreme mates for the purpose of sexual reproduction. This 'choice' is thought to be responsible for the form of sexual selection called intersexual selection. 'Classic' laboratory studies which purport to provide evidence for intersexual selection are discussed. We suggest these experiments demonstrate that females fail to recognize as conspecifics, males which are deviant in their signalling systems. We argue that this is not evidence for intersexual selection. Results from field studies on a broad range of sexually reproducing organisms can be interpreted in alternative ways. We consider as other possible factors which affect an individual's ability to gain fertilizations: (1) chance; (2) competition between individuals of the same sex for mates; (3) ability to recognize high quality environments; (4) adequacy of reproductive structures and behaviours. We conclude that there is compelling evidence that factors (1) and (4) influence an individual's ability to gain fertilizations, but that to date, no compelling evidence exists for choice by individuals of phenotypically extreme mates.

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I. INTRODUCTION

Sexual selection, as defined by Brown (1975) is "the differential production of progeny by different genotypes as a result of competitive mating". That is, that part of the difference in reproductive success between individuals which is caused by the differential ability to acquire mates. The concept of sexual selection has attracted considerable attention since the process is thought to be of major importance in the evolution of reproductive structures and behaviours. Thornhill (1980d, p.405) for example, states "Sexual selection is apparently the form of non-random differential reproduction that has led to the evolution of courtship and mating behaviours as well as parental care patterns of many animals".

Sexual selection is generally assumed to operate in two ways:

1. Competition within one sex for mates of the other sex (this form of sexual selection has been called 'intrasexual selection' and 'male-male competition').
2. Preferential choice of mates by one sex (has been called 'intersexual selection', 'epigamic selection' and 'female choice').

In this paper we have not attempted a detailed review of the intersexual selection literature, rather we have discussed what we consider to be problems with the theory, and practical difficulties in identifying a possible role for intersexual selection.

2 INTERSEXUAL SELECTION : Theoretical problems

As pointed out by Trivers (1972, p.166) "... female choice can generate continuous male change only if females choose by a relative rather than an absolute criterion. That is, if there is a tendency for females to sample the male distribution and to prefer one extreme (for example, the more brightly colored males), then selection will move the male distribution towards the favoured extreme".

Certainly the phenomena which Darwin explained using the theory of sexual selection such as sexual dimorphism, elaborate mating behaviours, displays and structures used in male-male competition, would require such directional selection. These characteristics could not have arisen through stabilizing selection. We do not argue that stabilizing selection is not a feature of mating systems, but that it is inappropriate to use evidence for stabilizing selection as evidence for Darwinian sexual

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selection. That is, we feel that it is unjustified to extend the concept of sexual selection to include stabilizing selection since it is incompatible with Darwin's original proposition.

There is some debate as to whether the preferred, extreme males are 'fitter' or not. Some workers perceive sexual selection as a process analagous to natural selection, individuals preferentially mating with the 'fittest' mates available to them (e.g. Lack, 1968; Halliday, 1978; Alcock, 1979). However, others view it as a process which sometimes opposes natural selection (O'Donald, 1980). For the latter to occur, individuals must 'prefer' mates other than the highest quality mates available. Fisher (1958) attempted to explain how female preference for males of relatively low fitness could arise and be maintained in a population by selection. He postulated that once a female preference for a male characteristic had become established through the correlation of the characteristic with male fitness, the character could then become subject to selection simply for its attractive properties. Initially a female would increase her fitness by mating with an 'attractive' male, not only because her offspring would be fitter, but also because her sons would be attractive and thus more likely to reproduce. Fisher envisaged that the further development of the attractive character would proceed because of the advantage gained in sexual selection, even after it had passed the point at which its advantage in terms of natural selection had ceased. He did stress, however, that such a 'runaway' process would soon be counteracted and halted by natural selection. "If carried far enough, it is evident that sufficiently severe counter-selection in favour of less ornamented males will be encountered to balance the advantage of sexual preference; at this point both plumage elaboration and the increase in female preference will be brought to a standstill, and a condition of relative stability will be attained", and, "It is important to notice that the condition of relative stability ... will be of far longer duration than the process in which the ornaments are evolved" (Fisher, 1958, p.152-3). Fisher thus saw sexual selection as a process which could counteract natural selection, but only temporarily. Clearly, if a significant variation in male phenotype exists (which is necessary for female preference to develop), a female preference for a male character that does not correlate with genetic quality would be strongly selected against.

If, on the other hand, intersexual selection is to be seen as a process analagous to natural selection (i.e. individuals prefer 'fittest' mates), then it will be very difficult to distinguish the action of intersexual selection from that of other selective forces acting on reproductive structures and behaviours. In practice it would be very difficult to distinguish between the occurrence of intersexual selection and intrasexual selection in an experimental situation. For 'female choice' to be possible, a female must be given access to several males, and where more than one male is present, 'male-male competition' may occur.

Whether intersexual selection is seen as a form of natural selection or not, it involves 'choice' of mates based on relative rather than absolute standards and, at least for an initial period, these 'preferred' mates must be 'fitter' than other potentially available mates. Fisher did not discuss how this initial preference for extreme mates could come into existence. However, Trivers (1972) suggested two explanations as to how females might be selected to prefer extreme mates.

1. "When two species, recently speciated, come together, selection rapidly favours females who can discriminate the two species of males. This selection may favor females who prefer the appropriate extreme of an available sample" (Trivers, 1972, p.166).
2. "Natural selection will always favor female ability to discriminate male sexual competence, and the safest way to do this is to take the extreme of a sample" (Trivers, 1972, p.167).

Trivers' first explanation would seem unacceptable as a general theory, in view of the large number of species in which intersexual selection is claimed to have taken place, and the lack of evidence for speciation by reinforcement (e.g. Paterson, 1978, 1981; Futuyama & Mayer, 1980). The second explanation appears to be in conflict with widely accepted ideas about the function of mating behaviour. Courtship is generally seen as a heterosexual communication system leading to fertilization (Morris, 1972).

A universal function of courtship then in all sexually reproducing organisms is to find and fertilize a mate. Clearly, such a communication system must be the subject of stabilizing selection (Paterson, 1976, 1978, 1980, 1981), since a preference for mates with deviant courtship (for example A in Fig.1) is likely to lead to a failure to reproduce. Consequently, females which mate with males deviant in their courtship systems will be selected against. That is, if an individual produces an aberrant courtship signal due to mutation, or the pleiotropic effect of another gene for example, it is less likely to be recognized as a mate and the individual will achieve less fertilizations. Males such as C and D (Fig.1) are unlikely to gain any fertilizations.

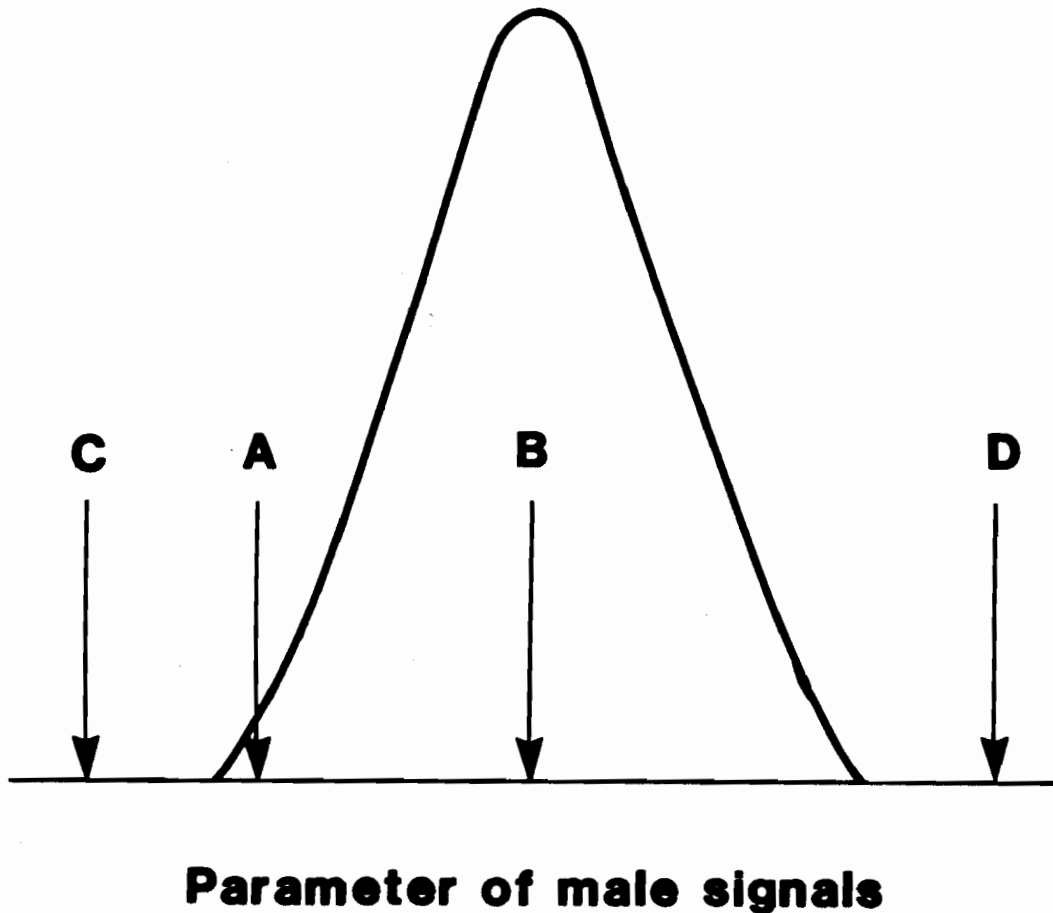


Fig.1 Signal characteristics of different males in relation to female recognition.

Similarly, a female which mates with male A, at the extreme of female receptivity, would be at a selective disadvantage because F_1 from such a cross will less successfully court mates and hence achieve less copulations. A female which mates with male B will produce a greater proportion of offspring that will successfully court females and hence obtain a relatively greater reproductive output. This will occur even if females which mate with deviant males have just as many offspring as those that mate with normal males, since males of type B will presumably inseminate many more females than will males of type A.

Females which are genetically attuned to respond to 'normal' males will produce both male and female offspring which are genetically likely to do the same. Even in species where males mate a number of times, those which respond to normal females will produce offspring (both male and female) which will have greater efficiency at gaining fertilizations. Certainly, in comparison to individuals which recognize

deviant mates, normal individuals will gain more fertilizations and produce offspring with a similar evolutionary advantage. This then results in stabilizing selection of the elements comprising a courtship pattern, and such stabilizing pressure would have a great influence on differential reproduction among males and females.

Some authors (e.g. West Eberhard, 1979, Thornhill, 1980b), argue that for selection to occur, it is not necessary that variations between individuals are genetic in origin. These authors distinguish between 'selection' and 'evolution by selection'. West Eberhard defines selection as 'differential reproduction' (1979, p.228), a definition intermediate between the everyday language usage of the word and the commonly used definition, 'the differential survival and reproduction of genotypes' (Futuyama, 1979). Clearly, to show that female choice actually results in evolution, it must be shown that the 'chosen' males differ genetically from those not 'chosen'. We feel that it is inappropriate and confusing to call such 'female choice' evidence for intersexual selection, and to use it as the basis for an evolutionary argument until the 'choice' can be shown to be made on the basis of genetic differences. Adhering to the commonly used definition of selection (sensu Futuyama, 1979) we argue that the case for intersexual selection rests on demonstrating that individuals consistently choose mates which differ genetically from those not chosen.

3. INTERSEXUAL SELECTION : the evidence

Attempts to provide evidence for intersexual selection have concentrated on two areas of research: firstly, manipulative studies carried out in the laboratory as choice experiments and, secondly, observations and experiments conducted in the field.

A. Choice experiments

These are generally characterized by a similar basic design; an individual of one sex is presented with two or more conspecific mates and the subsequent frequency of mating success of an individual is scored. 'Classic' experimental papers quoted in review (e.g. Trivers, 1972; Wilson, 1975) of this subject are Bateman (1948) and Maynard Smith (1956). These experiments were essentially of the same nature. Individual females were given a choice between normal or wild type males and those with inbred or deviant characteristics. Bateman (1948) used normal and mutant males of Drosophila melanogaster, e.g. bar eyed, while Maynard Smith allowed females of Drosophila subobscura to mate with either normal or highly inbred males. Both these authors have interpreted the higher mating success of normal males in such situations, as evidence for intersexual selection. For example, Maynard Smith (1978a) comments that a female is much more likely to reject a male which is inbred, old or injured. He then states that "the female is, therefore, extremely discriminating ..." and that "this seems a clear case of female choice". Recently, in a discussion of Maynard Smith's experiments Halliday (1978) explains that "... inbred males perform a particular step in the courtship less quickly than outbred males". Spiess (1970) comments further and with regard to the same experiments "... such lower mating success (by mutants) was not so much the result of lower intensity of courtship as inaccuracy and insensitivity to the female and lack of rapid reactivity to her movements ..." He then goes on to say, "... if females then can be said to discriminate between males that court 'properly' and those which court 'clumsily', there is some evidence that Darwin's sexual selection may be important in the evolution of the courtship ritual". Parsons (1973) makes similar comments in a discussion of this general subject. Sturtevant (1915) drew a radically different conclusion from his work on Drosophila courtship. He presented normal females with normal and mutant males (four different mutants were used), and observed a higher mating success of normal males. Similarly, where mutant females were presented with normal and mutant males, normal males were more successful. In both of the converse cases, where normal and mutant males respectively were given a choice between normal and mutant females, the mutant females achieved more matings. Sturtevant explained these data in terms of differences in activity between normal and mutant flies. The four mutants he used were all less active than normal Drosophila. He argues that the

normal males win competitive interactions due to their greater activity and 'vigor', while the mutant females gain more copulations as they are less likely to resist or escape from the male successfully if they are disinclined to mate. He concluded that "In general it is probable that, in Drosophila, neither sex exercises any 'choice' in the selection of a mate". (Sturtevant, 1915, p.365).

There is also evidence that some mutant males of Drosophila melanogaster have deviant courtship patterns (Spiess, 1970). Hence rejection by females of such males indicates only that stabilizing selection acts on these communication systems by selecting against individuals which are deviant in elements of their courtship patterns. Such a process certainly would not be responsible for a directional change in mating systems. If intersexual selection is responsible for many of the characteristics of male-female communication systems, such as sexual dimorphisms, directional selection would be expected to occur. We argue that these experiments provide evidence for stabilizing and not directional selection.

Another complication is the failure by workers to distinguish between male-male competition and mate 'choice'.

Partridge (1980) recently reported the results of an experiment designed to test whether Drosophila melanogaster females that have a choice of mates produce more offspring than females that do not. Adult females which had mated in a population cage where many males were present, were found to produce more offspring than females that were mated with a randomly chosen male from the cage. It was concluded that these results could be explained in one of the following ways :

- (a) "Fitter flies may be better at detecting or obtaining access to mates. Members of the other sex could then mate with a fly that was successful in some sort of competition with members of its own sex".
- (b) "Flies may be able to detect heritable fitness in members of the other sex. Fitter flies could then be actively chosen as mates".
- (c) "Flies with high levels of heterozygosity may have high fitness. In this case flies might produce fitter offspring by mating with individuals genetically unlike themselves, so that their offspring will have higher levels of heterozygosity". (Partridge, 1980).

We believe that this experiment failed to distinguish between 'male-male competition' and 'female choice' as possible explanations for the observed phenomena (Kingett et al. 1981). Similarly, in Borgia's recent paper "Mate selection in the fly Scatophaga stercoraria : female choice in a male-controlled system" (1981), no attempt is made to distinguish between 'female choice' and 'male-male competition'. Another apparently male-controlled mating system, and one of particular interest to us, is that of the endemic New Zealand mosquito Opifex fuscus. Larvae and pupae of this species live in salt water pools above high tide level, and males spend most of their adult life on the water surface searching for pupae. Pupae which are about to emerge are captured by the male using his large tarsal claws, and copulation commences while the female is emerging. A study of the mating system of this remarkable species is presently under way.

Another recent experimental approach (Burley & Moran, 1979) has claimed to demonstrate intersexual selection using feral pigeons Columba livia, by attempting to control for the important factor of male-male competition. This was accomplished by giving an individual access to two possible mates, while each of these was tethered to different nest boxes. The authors have succeeded in showing that individual pigeons are more likely to mate with partners which have been able to gain matings under normal mixed conditions. That is individuals which gain a number of matings when kept in a large cage with many other males and females of the same species, gain a greater number of copulations than individuals who have achieved less matings under the same conditions.

This is not to say that male-male competition has been completely eliminated. Dominance via auditory or visual communication is a common feature of most animals (Brown, 1975). Physical contact is only an extreme form of male-male competition.

Burley and Moran (1979) begin with the 'sociobiology story-telling' (Gould, 1978) that "There are (our emphasis) at least three important components of mate choice among species with biparental care". Burley and Moran's acceptance that there are at least

three components of mate choice because individuals should be able to choose a mate with these three characteristics is a good example of an adaptationist approach to the problem (Lewontin, 1978). They have assumed that if it is theoretically advantageous for any individual to choose a mate with a particular characteristic, then natural selection will have moulded this ability. The overwhelming evidence that the function (sensu Williams, 1966) of courtship is to ensure efficient fertilization is rarely considered or mentioned by authors.

B. Field studies

Many field studies have emphasized or concluded that intersexual selection is the major factor causing differential mating success. Examples can be found in work on bullfrogs (Emlen, 1976); toads (Davies & Halliday, 1977); fish (Warner, Robertson & Leigh, 1975); birds (Weatherhead & Robertson, 1977) and a variety of social systems (see Halliday, 1978, for a recent review).

Field evidence for intersexual selection requires the distinction between mate choice based on male genotype and recognition of high quality environments. For the American bullfrog (*Rana catesbeiana*) Howard (1978) makes this distinction by equating male size with genetic quality and territorial quality with embryo survival. He argues choice by females of specific males is based on an assessment of male size; an indication of fitness since size equates to age and hence survivorship (Wilbur, Rubenstein & Fairchild, 1978) and he equates optimal environmental conditions with oviposition site. Similarly, Searcy (1979a) concludes that in redwinged blackbirds (*Agelaius phoeniceus*) mate choice is based in part on territorial quality (the availability of food, vulnerability of potential nest sites to predation) and in part on an unknown component due to male quality. This is established by male-male competition for territories, i.e. females judge male quality by the ability of the male to succeed in male-male competition. In this situation he implies that not only does the female obtain the fittest male, she obtains conditions likely to produce maximum progeny survivorship.

However, the central assumption made in these studies is that females selecting males will maximize their relative fitness. These are males which are the oldest or who have attained the largest size. In these field studies it can equally be argued that females are recognizing conditions for maximum progeny survivorship and the mate associated with these conditions is an effect (sensu Williams, 1966) of this. Field situations where mates are removed from territories should provide a test between these alternative interpretations, i.e. that females are either choosing particular males or recognizing particular high quality territories. Where this has been done (e.g. Lill, 1974) females have been shown to remain and accept whichever male wins the territory in the absence of the previous male. This suggests that females recognize particular territories (i.e. portions of their environment) and will accept any male which occupies those territories provided that he exhibits normal courtship signals. Davies (1978) in his discussion of Lill's experiments comments, "This experiment may suggest that it is some characteristic of the territory that influences female choice, rather than some characteristic of the male itself", and further goes on to say, "Alternatively, it is possible that the new males who occupied the vacated territories were the 'next best' males, and females were choosing the best male possible".

Jones (1981) has recently discussed the results of male removal experiments with the protogynous wrasse *Pseudolabrus celidotus*. In this species terminal phase males defend territories which serve as both feeding and spawning sites. There is a great deal of variation in the reproductive success of different males. In Jones' experiments he removed the male which had the greatest breeding success. The territory previously occupied by this male was invaded by a neighbouring male which largely abandoned its old territory. This male, which had not been observed to spawn previously, began spawning at the new site only half an hour after removal of the previous male. Within a few hours, this male went from having a 0% spawning rate to the highest rate of 44%. The spawning rates of the other males in the area did not alter. Five males shared the remaining 56% of the spawnings and were intermediate in spawning rate between the removed male and his replacement. (Jones, 1981, Fig.9, p.136). Certainly, at least in this case Davies' hypothesis that the incoming male would be the 'next best' was not supported. If the intersexual selection argument is to have any credence, mates should be expected to 'reassess' the 'quality' of the new male with

that of its neighbour and move, if there is an imbalance, toward neighbouring males. Since this did not occur in either experiment, Davies' argument must be treated with caution. Moreover, since there was no correlation of territory quality with age or male size of *P. celidotus* (Jones, 1981) the occurrence of random or stochastic events in mating systems must be given emphasis.

In other field studies (e.g. Davies & Halliday, 1977; Wilbur *et al.* 1978; Sercy, 1979b; Garson, 1980; Greenspan, 1980; Lenington, 1980) there has been a tendency to conclude the occurrence of intersexual selection despite the compounding variables of site selection, male size and supposed intersexual selection. Davies (1978) clearly exposes the central problem. In a discussion of mating territories he writes, "... we have the problem of whether the females are selecting male quality or territory quality". We suggest that females choose specific areas of the environment because this choice directly affects the viability of their offspring. The identity of the conspecific associated with these environmental conditions may in fact be incidental. (See also McGregor, Krebs and Perrins, 1981).

In some mating systems, males present females with food items during courtship. This may represent an analogous situation to males offering use of territorial resources. In such situations, female preference for male quality and resource quality are difficult to distinguish. Thornhill (1976, 1980a, 1980b) has detailed an interesting mating system in the Hangingfly *Hylobittacus apicalis*. In this species 'mate choice' is based upon an arthropod gift that the male provides, and females discriminate against males which offer a gift below a certain size. However, no data is presently available concerning a correlation between gift size and male genotype. Thornhill (1980a, p.531-2) states that "... it is unknown whether males selecting prey smaller than 16 mm² differ genetically in regard to their predatory behavior from males selecting prey 16 mm² or larger". We agree with Thornhill (1980c, p.144) that "To show that female choice actually results in evolution, which is defined as changes in gene frequencies within a population, it must be demonstrated that the males chosen by the females differ genetically from those not chosen". It is our view that until this has been demonstrated for *Hylobittacus apicalis* we are reluctant to accept that intersexual selection is a necessary component of the mating system of this species.

We would suggest that nuptial feeding in *Hylobittacus* may have evolved to reduce the female's flight response so that copulation can occur. Thornhill's work shows that females will approach males with small nuptial gifts, and will feed on the gift. However, if the gift is below a certain size she will not copulate with the male at all, or will do so for only a short period (Thornhill, 1980a, c). This behaviour suggests a signal-response chain which, if the right signals and responses are given, will result in fertilization and egg-laying. If the male uses the wrong 'signal', a gift which is too small to satisfy the female, then she will terminate the interaction.

Discussions of intersexual selection have been restricted to monogamous or polygamous social systems where there are controllable factors or resources (Brown, 1975). In polygamous species and species with dominance hierarchies where there is no apparent difference in territory quality such as in elephant seals (Le Boeuf, 1972, 1974), ungulates (Jarman, 1974), primates (Clutton-Brock & Harvey, 1977) and insects (Thornhill, 1980d), social status determines access to females during their reproductive cycle, i.e. females have no choice as to the conspecific mate with which they copulate. Although Cox & Le Boeuf (1977) advocate that choice occurs in elephant seals *Mirounga angustirostris* by females inducing male-male competition, females may have no option under such social systems since the winner regardless of his status gains access to all females. There is no necessity to explain these observations strictly in terms of intersexual selection.

Lek mating systems have been an area of much controversy. In most situations females move through the male lek and mate with an individual which has gained a territory very close to the centre. This occurs in white-bearded manakins (Lill, 1974) the uganda kob (Floody & Arnold, 1975), the sage grouse (Wiley, 1974) and black grouse (Kruijt & Hogan, 1976), although it is not always the case (Shepard, 1975). Males are described as competing to gain access to central territories and hence maximize their

reproductive success. However, at least in the sage grouse (Wiley, 1978) this is closely correlated with age; older males being able to establish territories at the centre of the lek. Males move from the outsides of the lek as first year males, finally reaching the centre at three years of age or older. The great bulk of matings, therefore, are achieved later in life, and in this case there may be no consistent genetic differences between the males that are at the centre of the lek and those which are at the outside. Whether a male will eventually hold a territory at the centre will depend on how long he survives. Survival, in turn, will depend on the male's phenotype and chance. Wiley (1978) has presented good evidence for the role of chance in the final acquisition of a central territory and hence of substantial reproductive success.

Some authors argue that leks are, in fact, mechanisms (sensu Williams, 1966) for ensuring that females mate with the fittest males, i.e. that they evolved specifically for this purpose. For example, Bradbury argues, in a recent paper on the evolution of leks, that "If it is not generally advantageous for males to cluster, the fact that they do must arise from a preference for clusters on the part of females". (Bradbury, 1981, p.148). He gives three reasons why females should favour clusters :

1. "Clustering allows a female to examine a large number of males in the least possible time. This facilitates direct comparison of male phenotypes and may also reduce energy costs of moving between males".
2. "Males may be coaxed by females into aggregating at locations of maximal accessibility".
3. "Clustering of males allows females to monitor mate choice by other females".

The third factor is seen as advantageous in cases where "evaluation of male 'adaptedness' rests on experience" and where "the costs of mating with the 'wrong' male may be greater than the benefits of mating with the current favorites". Further, Bradbury quotes a suggestion by Sherman that "females may attempt to determine and modify the choices of other females and that clustering would facilitate this effort" (Bradbury, 1981, p.149).

In this paper, Bradbury develops a quantitative model based on the idea that an increasing ratio of female home-range size to male territory size should lead to a shift from resource defence to self-advertisement as the only viable male mating 'strategy'. He feels that the question of why lekking is adopted rather than some other form of self-advertisement is answered by proposing that lekking is advantageous to females. We feel that his argument, although plausible, must be treated with caution as it is based on some debatable assumptions. Firstly, the implicit assumption that leks must be advantageous, if not for males then for females; and, secondly, that males vary genetically in 'adaptedness' and that females are capable of comparing them and choosing the best male available. In our view it is far from certain that females have this ability. Indeed, it is the essence of this contribution that evidence for this is sparse. We would question whether lekking behaviour is likely to be an optimal solution for males and/or females. The 'problem' to be 'explained' seems to be why subordinate males frequent leks, as their chances of copulation would seem to be severely hampered by the presence of dominant males. Bradbury (1981) solves the problem by proposing that females are selected to prefer leks, therefore males which do not associate in leks are at a disadvantage. The advantage to the females is explained in terms of female choice and accessibility.

We would favour a simpler explanation and would suggest that leks are a mechanism for finding mates, rather than a mechanism for enabling females to choose. The behaviour of subordinate males, although it appears to be non-optimal, may well be the only option open to them. The forces which resulted in individuals coming together at a particular place and time for mating may have been the need to find mates when individuals are normally spread out over great distances. Thus, although subordinate males have a low probability of mating at the lek, their chances away from the lek may be close to nil. Alternatively, the lek may be a mechanism to overcome high predation rates while courting. For example, Wiley (1974) has reviewed the presence and absence of leks in grouse species and noted that species occupying open country habitats show lek mating behaviour whereas species occupying forest habitats do not.

4. CONCLUSIONS

Factors generally assumed to influence the ability of an individual to gain access to mates are:

- (1) chance;
- (2) competition with individuals of the same sex for mates;
- (3) the ability to recognize high quality environments;
- (4) the adequacy of reproductive structures and behaviours;
- (5) attractiveness to mates.

As has been pointed out by other authors before us (e.g. Thornhill, 1980b) most evidence for female choice is indirect, and female choice is often inferred merely when females mate with some conspecific males and not others (e.g. McCauley & Wade, 1978, Borgia, 1981). We feel that often alternative explanations are not considered. This is despite the fact that the biological existence and reality of factors (1) to (4) has been demonstrated in many cases.

We believe that the argument for the existence of intersexual selection is an example of the adaptationist programme (Lewontin, 1978, 1979; Gould & Lewontin, 1979). Such a programme maintains that natural selection is an optimizing agent, and that selection acts on all individual characteristics of organisms, competing selection demands being responsible for any apparent cases of non-optimization. (For a recent statement of "Optimization Theory" see Maynard Smith, 1978b). Provided an investigator can postulate an advantage in an individual's ability to possess some characteristic, natural selection will have moulded such a characteristic. Alternatively, if an organism exhibits a certain phenotype, e.g. a behaviour, a 'reason' for its existence in terms of natural selection is postulated. Such phenotypes are rarely postulated to be a consequence or effect (sensu Williams, 1966) of other processes.

Since it would be of obvious value for an individual to be able to recognize and mate with an individual of high genetic quality, it is assumed that individuals will possess mechanisms that allow this recognition. The only problem facing workers using this approach is how to properly illustrate this mechanism.

We agree with Thornhill that "Some very fascinating hypotheses have been put forth regarding how and why females may choose among males (Trivers, 1972, Zahavi, 1975, Alexander, 1975, Borgia, 1979, Downhower & Brown in press, and Lloyd, 1979); however, it has yet to be determined that females typically are discriminate of mates". (Thornhill, 1980b, p.14). We do not dispute that the practice of generating and testing falsifiable hypotheses is the basis of experimental science. We wish to point out, however, that hypotheses dependent on the assumption of optimization through natural selection are not falsifiable. (For an in depth discussion of this view see Lewontin, 1979, Gould & Lewontin, 1979).

Just as we reject the adaptationist programme approach to biology (although we certainly do not maintain that natural selection does not operate), we cannot accept the existence of intersexual selection until compelling evidence is presented. It appears that belief in the biological existence of intersexual selection has resulted in this concept being preferentially used in the interpretation of data on studies of laboratory and natural population of animals.

As in the field of population genetics where theory has far outstripped available data from natural populations, so too has theorizing in the study of mating systems been more popular than the collection of relevant information. We feel that there is a great need for carefully designed field studies which consider all factors which may influence the ability of individuals to gain access to mates.

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