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Conflicts between and within the Sexes in Sexual Selection
Group Report

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INTRODUCTION

Sexual conflict began with the primal divergences in size and function of gametes — with the origin of anisogamy. Since that moment competition between and within the sexes has produced a wondrous array of forms and behaviors in both plants and animals, seeming to manifest every conceivable permutation of male vs. female pursuit, manipulation, cooperation, and control. This report summarizes our brief and stumbling efforts to canalize our own verbal conflict and cooperation in a way that might illuminate pattern and cause in the diversity of sexual competition.

CONCEPTS AND DEFINITIONS: RECOGNIZING THE PHENOMENA

Sexual selection is differential reproduction that is the result of competition between the members of one sex for mates. The mating success of an individual can be measured in terms of the number of zygotes formed by unions of his or her gametes with those of the opposite sex, a definition which allows for the possibility of post-copulatory gamete competition. Following Darwin, we recognize that there are two major forms of sexual competition: one involving direct interaction (e.g., combat) of competitors and one involving "choice" (differential mating) following comparison of competitors, or of resources produced or controlled by competitors (e.g., nuptial gifts or territories). These two categories are often referred to as "intrasexual" and "intersexual" competition, respectively. However, all sexual selection fundamentally involves competition among the members of a single sex and thus could be called

"intrasexual" competition, whether via direct interaction or comparison of competitors. "Choice" means differential responsiveness to potential mates.

Since females are often the limiting sex, sexual competition is often strongest among males. In this report, therefore, we will often refer to "male-male competition" and "female choice" even though female-female competition for mates, male choice of females, and mutual sexual selection can occur.

We found it useful in theoretical discussions to make the following distinctions regarding female choice.

Active versus passive choice (Lloyd 1979; Parker 1985).

Active choice involves some comparison or scanning activity by females which reduces the possibility that they are responding differentially to different males due to biases of perception rather than to differences in the male phenotype (the signal or resource itself). Passive choice is a differential response without bias-reducing comparison. For example, in a species where the female is choosing on the basis of song loudness, a passively choosing female would go to the male with the loudest apparent song but might thereby choose a song that seemed loud simply because the singer was nearby. A female exercising active choice, on the other hand, might move about or evaluate distance in order to compare the relative loudness of songs actually being produced by males. Passive choice is analogous to male-male "scramble" competition, with the loudest or best located (with respect to females) males capturing more females in their sonic traps. The terms "active" and "passive" to refer to this distinction may be confusing, since "passive" could be "active" in the sense of involving a decision accompanied by some movement or energy expenditure.

Sexually selected preference versus preexisting preference.

Female choice may involve discrimination evolved in the context of sexual selection (sexually selected preference) or it may involve female responses evolved in other contexts, which males exploit during courtship (preexisting preference). For example, male mimicry of an infant cry might prove an effective courtship signal by causing females to pause or become less aggressive, and a maternal response might then serve as a sort of "preadaptation" yielding differential responsiveness to males differing in their ability to imitate infant cries. Preexisting preference (or transfer of responses to the sexual context) could conceivably produce either passive or active choice, since preexisting responses (such as that to babies' cries) could be preadapted for discrimination of phenotypic (e.g., signal) differences.

Sexual reproduction can give rise to both cooperation and conflict between the sexes. Obviously, the interests of both male and female are served by mating and zygote production. However, conflict between the sexes arises

from purely sexual competition when members of the competing sex manipulate the responses of potential mates in ways that are costly to them (e.g., forcing prolonged copulation in sites exposed to predators, producing deceptive signals of resource superiority, or successfully bypassing signals of true phenotypic of genetic quality). The "battle of the sexes" arising from sexual manipulation can come to include conflict over parental investment if females select mates on the basis of resources or behaviors benefiting offspring. The conflict over parental investment can then begin to affect sexual selection, with males selected to give deceptive signs of costly donations and females selected to detect deception and choose truly endowed males. We will discuss conflict between the sexes over parental investment only as it affects competition for mates.

MATING GAMES: WHAT SETS THE RULES?

One of the most striking aspects of sexual conflict, aside from its spectacular effects on the phenotypes of males (plumes, antlers, pheromones, and other accoutrements and antics of courtship and battle), is the very great diversity of arrangements under which sexual competition occurs. The mating behavior of a species can be synchronized or sporadic and can occur in aggregations or in isolated pairs. Courtship can be simple or complex and copulation rapid or prolonged. Males may seek females while females either hide or signal their whereabouts, or these sex roles may be reversed. All of these patterns may vary independently and do so even among related species. What causes this enormous diversity in the circumstances and conditions of sexual competition?

Factors that influence the evolution of mating arrangements have been studied under several major headings, which are really interrelated topics basic to the study of sexual conflict: parental investment theory, mating systems (especially in relation to ecology), sex allocation theory, and sex ratio theory (especially considerations of the operational sex ratio). In our discussions we have deliberately excluded a detailed examination of these topics, which would require whole Dahlems within a Dahlem. However, we have seen that these factors are complexly interrelated in setting the rules of sexual selection and that it may prove fruitful in the future to consider their relationships in a formal theory. We record the following thoughts in the hope that they may help point the way toward the development of improved concepts.

Environmental conditions (such as the distribution, availability, and defensibility of limiting resources) can determine the relative investment of the two sexes in their offspring and thus influence the degree of sexual selection and sexual dimorphism. The influence of environmental conditions on the mating system is discussed elsewhere (e.g., Emlen and Oring 1977; Thornhill and Alcock 1983). A mating system is sometimes taken as a good indicator of whether male-male competition or female choice will predominate in a species.

This is, however, clearly inadequate. Among lek species, for example, males may be chosen without interference in some species (e.g., in sage grouse), whereas in other species male-male interruption may predominate (e.g., in buff-breasted sandpipers). We thus need a better set of predictors for sexual selection patterns (see Bradbury and Davies, this volume).

Game theory is one avenue of approach. Maynard Smith (1977) has used game theory to investigate the relationship between parental investments and the freedom of each sex to compete for mates. He has shown that in the many cases where more than half the offspring can be raised successfully by one parent alone, the other one should leave to search for a new mate if there is a reasonable chance to find one. However, he was unable to decide which of the two alternative evolutionary stable strategies (ESSs) the system would evolve — the "stickleback" (female leaves) or the "duck" (male leaves) ESS. Such questions may sometimes be resolved by considering a sequence of related games. Whichever parent leaves the offspring, both then face a "mobility game" (see Hammerstein and Parker, this volume) whose logic suggests that males rather than females are likely to search for mates (the "roaming male" ESS). Perhaps the mobility game, coupled in some way with the parental investment game, may provide a more general answer as to why it is more likely that females have to care for offspring. More complex arrays of alternatives might be analyzed by dividing sexual options into a series of games, e.g., the parental investment game, the mobility games, and the persistence game (Hammerstein and Parker, this volume). As with the determination of mating systems, each of these games has an outcome in part dictated by ecological and phylogenetic contexts. The difference is that factors such as mobility and persistence may be more important in deciding the relative roles of female choice and male-male competition than more structural decisions such as whether to form a harem by resource defense or by female defense (see Bradbury and Davies, this volume). The first game must be the parental investment game: who gets left with the baby? Certainly the outcome of this game will constrain the latitude of one sex to exercise its sexual options. This is not sufficient, however. The mobility game is then involved: where males are more mobile most species show some emphasis on male-male competition; in contrast, female mobility appears to be a necessary, but not always sufficient, condition for wide female choice as on leks. This is suggested by the parallel evolution of some insect swarms and vertebrate leks where the parental investment game left the female with the baby and the mobility game left males localized in groups to await females, but, the two taxa appear to show different levels of female choice. The persistence game might then be involved as a final factor: which sex has the time the energy to court or resist courtship longest? Thus, although not always independent, these games considered to relation to ecological factors affecting their outcomes may predict patterns of sexual selection better than does the classical approach of investigating the influence of ecology on the evolution of mating systems.

MALES VERSUS FEMALES: WHO WINS?

Sexual conflict has so far been analyzed by studying game theoretic models. The game theory approach lacks any explicit treatment of the underlying genetics. However, it has the virtue of allowing a greater variety of strategies and thus more phenotypic complexity than might be possible with the standard framework of population genetics. Put simply, in constructing theory to explain and predict patterns of sexual behavior we are often forced to choose between complexity on the one hand and genetic rigor on the other.

There are many kinds of conflict between the sexes, from the primordial conflict over anisogamy to those just discussed involving investment in searching for mates, mate choice, and parental care. Who wins depends on a number of factors, according to the type of conflict concerned. In anisogamy the very existence of males in multicellular organisms implies that, in an evolutionary sense, males have "won" this primordial conflict. In this section we first present a conceptual framework for viewing conflict between the sexes regarding the costly activities and decisions associated with mating. We then discuss the mechanisms by which males and females manipulate each other in their own interests.

A conceptual framework for the study of male-female sexual conflict

Conflict over which sex will be mobile (or incur the costs of mate search), like conflict of interest over parental investment, can commonly have more than one stable solution for a given set of conditions. In such cases perhaps the most important consideration concerning which outcome is likeliest is the starting condition (i.e., evolutionary history). If we can deduce the plausible starting conditions, the equilibrium attained can usually be predicted. For example, suppose that in a parental investment game the two ESSs were male guard/ female desert and female guard/male desert. We might expect to find males sometimes guarding offspring in fish, where males and females are usually equally equipped to do so, whereas female guard/male desert might be more common in mammals in which only females lactate.

A second way to deduce the probable outcome — and one that may be particularly useful if no a priori assumptions can be made about starting conditions — concerns the payoff-relevant asymmetries present in the game. If, for instance, it were much more costly for male fish to guard eggs than female fish, then even though the opportunity to guard may be similar for both sexes we would perhaps predict a greater "zone of attraction"* for the female guard/male desert ESS. If the zone of attraction for one of the ESSs is sufficiently small, then drift alone may be enough to ensure that we would

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* range of initial conditions that will lead eventually to the establishment of a particular ESS.

eventually attain the alternative ESS and stay there.

Games between the sexes will always be asymmetric in the sense that one player is irreversibly labeled male and one player is labeled female. However, there will usually also be a payoff-relevant asymmetries, which will be important in establishing the outcome on the "zone of attraction" for alternative ESSs.

The solution to some sexual conflict games can be a single ESS (e.g., some of the mating decision conflicts by Hammerstein and Parker, this volume). Which sex generally wins can then be deduced from a knowledge of the payoff-relevant asymmetries. For the sexual war of attrition, these would be the cost to a male of time spent in attempting rape versus the cost to the female of equivalent time spent avoiding rape and the relative value of winning the contest for each player. For the sexual arms race the costs would be morphological. However, in both of these games, we would expect to see examples in a given population where one sex appears to "win," and other examples where the other sex appears to "win," although one outcome may be overwhelmingly predominant.

In some cases it seems likely that the formal models proposed by Hammerstein and Parker (this volume) are inadequate since they may properly be dealt with as repeated games. For example, a female may be able to eject or resorb an unwanted ejaculate after mating (see *MATE CHOICE AFTER MATING* below). Sometimes males show no inclination to persist in courting a female that is uninterested in them. Such phenomena could be attributable to the persistence game or sexual arms race. However, such solutions could imply a repeated game, in which the female has the strategic possibility of rejecting unwanted sperm. A set of models of repeated games in sexual conflict might be useful, especially in parental investment models. Even when the female has the last, controlling move regarding mate choice, the entire sequence of preceding games has significance for sexual selection as a series of circumstances in which males compete with each other to be the beneficiaries of the final decision.

The mobility game is relevant to the question of how sexual selection is achieved — whether via male-male interaction or female choice. There is a general correlation between male-male competition and mobile males on one hand and fixed males and female choice on the other. With regard to leks, the outcome of the mobility game may be *preset* by ecological conditions (e.g., those leading to very large, overlapping ranges in females: the correlation between female range size and male aggregation for mating is quite good). Unfortunately, the correlation between male aggregation and "strong" female choice is less strong.

It would be of interest in this context to know if female choice occurs in the "mating swarms" of insects, which in some respects resemble leks. "Explosiveness" of mating may be one factor affecting the likelihood of female choice, (Emlen and Oring 1977; Linsenmair, personal communication). Factors affecting relative persistence of the sexes may also play a role, and this also may

be related to seasonal synchrony (explosiveness) of breeding. In short, the weight is thrown from male-male interaction to female choice given ecological generation of high female mobility and a) sufficient breeding time to accomplish choice and/or b) factors favoring female persistence in mating activity over male persistence.

Manipulation of mate choice

Whatever the (often complex) causes of limited access to mates, the common occurrence of asymmetry in this regard leads to two sets of manipulations, one performed by the sexually limited competing sex (usually the males) and the other by the limiting sex (usually the females). In this section we will restrict discussion to manipulations of the opposite sex regarding mate choice and exclude other possible kinds of male-female manipulations (e.g., of parental investment or the sex ratio). As will be clear from the examples discussed below, "manipulation," or the exercise of control over the responses of another, need not imply conflict, force, or coercion although these negative descriptions may sometimes apply.

Males employ a very large array of behavioral and morphological features which can influence or restrict choice of mates. Well-studied examples seem to fall into two categories:

1) mechanisms involving force including rape, persistent pursuit or "harrassment," intromittent genitalia, and infanticide (further discussed below); and
2) material enticements including nuptial gifts, nutritive spermatophores, participation in parental care, protection against predators, and prevention of harrassment by other males.

In addition, ethological studies and theoretical considerations suggest that a third kind of manipulation is likely, namely deception (sensu Otte 1975) or mimicry (Lloyd 1980). Examples include inflation of the body or plumage erection simulating large size, the bubbles added to balloon-fly nuptial gifts enlarging their appearance, imitation of non-sexual signals, and stimulation of behavioral or hormonal responses evolved in nonsexual contexts, but increasing the likelihood of mating or gamete acceptance (see "Post-mating mate choice" below).

On the other hand, individual females may increase the opportunities of effectiveness of choice via:

1) increased mobility (searching, comparison);
2) inciting congregation and/or contests among males (e.g., via female aggregation or female attraction to male aggregation and interaction);
3) multiple mating in species which manipulate sperm (e.g., in which there is sperm precedence or sperm destruction by females).

There is a striking lack of information on the activities and abilities of females compared to those of males as regards these activites, despite their great potential importance in sexual conflict. The following points may help to focus research in this area.

Inciting contests among males may enable comparison of strength and vigor of potential mates at little cost to the female, thus superimposing the "truth" of male contest on potentially deceptive or male coercive courtship. However, inciting male-male contests may sometimes "backfire" on females, if fighting males are selected for increased size (as they often are in fighting species). This could lead to trapping females into parental care expenditures in producing large male offspring which constitute larger investments than are desirable under natural selection so that selection on *females* might limit the exaggeration of the male trait (large size). Partridge and Endler (this volume) discuss other aspects of the costs of sexually selected traits under natural selection in different life history stages.

As already discussed, part of the cost of female choice (when males offer resources) may be the loss of access to males who are busy garnering resources at the time the female is making a choice. Or choice may require that she spend more time searching for these males. In effect, the operational sex ratio (and freedom of "choice") for such a female is lowered by her choosiness regarding the males.

Multiple mating does not, of course, necessarily lead to increased female choice, since special mechanisms (such as sperm manipulation) must be involved and multiple mating may have many different explanations (such as avoidance of harrassment, formation of protective or parental care alliances with multiple males, inability of females to resist copulation, etc.). Studies of the pied flycatcher (*Ficedula hypoleuca*) exemplify the kinds of research that can illuminate conflict between the sexes. Males of this species may be residential at the nest or may go off for further matings. Females mated monogamously have a higher fitness than do females mated with a polygynous male because of the greater parental investment of monogamous males. However, polygynous mating occurs even when there are some unmated males in the population. The polygynous males may deceive females into mating against their own interests (see Alatalo et al 1981); alternatively, the second females may accept their status due to the costs of searching for unmated males (Slagsvold 1986).

MATE CHOICE AND INTRASEXUAL COMPETITION AFTER MATING

Most familiar forms of mate choice occur before mating, but there is also potential for choice after mating. The choice could be of male gametes, of offspring, or (in plants) of endosperms. In animals, gametic choice would amount to delayed mate choice since gametic genes are not expressed. Such

forms of choice can be quite cryptic. For example, Thornhill (Thornhill and Alcock 1983) studied female scorpion flies that mated randomly but used sperm differentially by laying eggs only after mating with large males who offered large nuptial gifts. Post-mating mate choice is considered at length by Eberhard (1985), who shows that females manipulate sperm following copulation in four different ways: prevention of complete intromission; restriction of sperm transfer within the female reproductive tract; sperm inactivation, removal, and storage; and by remating. There is also evidence that these processes are influenced by male phenotype and/or behavior prior to or during courtship in some species.

In plants, gametic choice is potentially different because the male gametophytic stage does express its own haploid genotype. Such choice is well-known for gametophytic self-incompatibility mechanisms but needs to be investigated for finer kinds of discrimination. Differential success of pollen genotypes is well known (Jones 1928), but distinguishing female choice from simple pollen competition will be difficult.

Selection of offspring should also be investigated. Strictly speaking this is not sexual selection, but it shares some properties with sexual selection, and it can result in favoring one father over others in broods of mixed paternity. There is one crucial difference from true mate choice in that the mothers might choose good offspring on the basis of non-additive genetic effects (Queller, this volume).

Intrasexual competition likewise does not necessarily end with the fertilization of the egg, as long ago appreciated by Haldane (1932) in discussing "certation," or pollen-tube competition, in plants. Infanticide can represent either male-male competition (e.g., in langurs, lions, etc.) or female-female competition (e.g., prairie dogs). Observations of langur monkeys (*Presbytis entellus*) (Sommer and Mohnot 1985 and references therein) illustrate how infanticide can be the result of male-male competition for mates. Some langur populations breed in harems. There are few harem leader positions within the population, resulting in severe male-male competition for harems and short tenureships for each harem-possessing male. Under these conditions a male can increase his reproductive success by killing those infants sired by his predecessor which still hold their mothers in the state of lactational amenorrhea, thereby bringing those females quickly into estrus again. Field data strongly support the hypothesis of Hrdy that male infanticide in langurs is thus an adaptive reprodutive strategy evolved under sexual selection on males.

In a model considering female reproductive characteristics and the fequency distribution of male tenure lengths within the population, it can be shown that a mixed ESS may be established, stabilizing a rather fixed proportion or infanticidal or non-infanticidal "take-overs" of harems. Langur females seldom (if ever) succeed in their efforts to defend their infants against infanticide. Thus, in this case males appear to be the winners in a dramatic example of postfertilization conflict.

SPECIAL PROPERTIES OF SEXUAL CONFLICT IN PLANTS

In plants, sexual selection may act on gametes (gametophytes) or embryos, but most frequently it acts on sex allocation to male versus female function as pointed out by Queller (this volume). In quite the same way, hermaphroditic animals are under sexual selection for the allocation of resources to male versus female function. In monogamously mating hermaphrodites this may lead to minimal development of the testes and maximal egg production, while under a promiscuous mating system the majority of the resources may be allocated to the male function. Similarly, in sequential hermaphrodites, sexual selection may determine the time or body size at which sex change occurs as well as the direction of the change (i.e., from male to female or vice versa).

Although we recognize that sex allocation in hermaphrodites as well as in animals with separate sexes is strongly influenced by sexual selection, we chose not to discuss this issue further since it has been reviewed recently (Charnov 1982) and is too vast a subject to be included in our discussion. Nor did we cover the large subject of how sex allocation and sexual selection influence the evolution of plant breeding systems (Charlesworth and Charlesworth 1979).

Table 1 compares some important differences between higher animals and plants. Sedentary animals would share some features of both groups.

TABLE 1 Differences between plants and higher animals relating to the nature of mate choice in plants

Plants	Higher animals	Consequences
Fixed	mobile	pre-mating choice difficult in plants
Usually hermaphrodite	dioecious	sexual differentiation rarer, weaker in plants; recognition of male and female traits more difficult (even if dioecious, higher similarity between male and female)
Developmental canalization* weak	strong canalization	
High fecundity	lower fecundity	post-mating choice of genetic quality theoretically easier (on pollen tubes or on zygotes)
Common genes expressed in n and $2n$ phase	fewer such genes expressed	

* Cellular differentiation is much stronger and more definitive in animals (as revealed by regeneration from tissue culture possible in plants and still impossible in most higher animals).

Pre-mating choice in plants would be difficult to achieve. However, females (or a female function of a hermaphrodite) can choose their mates by flowering time (demonstrated only in cases of hybridization or incest avoidance), floral morphology (e.g., distyly demonstrated in cases of incest avoidance), gamete

choice (e.g., gametophytic self-incompatibility demonstrated in cases of incest avoidance), and zygote choice (e.g., self-incompatibility in Cacao-demonstrated in cases of incest avoidance).

In *Thymus vulgari* (Gouyon et al., in preparation), hermaphrodites have bigger flowers than the female. If one measures seeds, pollen, and flowers one finds that in the hermaphrodite, pollen number and flower size are positively correlated, while both are negatively correlated with seed number. In females, flower size is negatively correlated with seed number. Growth hormones of the flower, however, are produced in the anthers. These are more or less completely aborted in the female. These observations could possibly be interpreted as the result of developmental constraints. However, regarding sexual conflict, it is of interest that the flower growth is controlled by a male organ.

It seems likely that males (or male functions) in plants may compete for pollinator attraction and overproduce flowers (see Queller, this volume). It also seems likely that pollen competitively enters the style. But no *effect* of this selection is yet known. A runaway process might be possible affecting the efficiency of pollen in the style (females favoring a certain type of pollen and therefore their own sons as better males), but in hermaphrodites this could be in conflict with mechanisms preventing inbreeding.

In conclusion, although possible mechanisms of sexual selection are known in plants, sexual selection has rarely been demonstrated to act. All suggestive examples involve self-incompatibility mechanisms or prevention of interspecific crosses. Is this because ideas regarding sexual selection have only recently been applied to plants? Or does it indicate a true difference in the biology of these organisms when compared to animals? Similarly, one might ask why plant-like (sessile) animals such as sponges and corals lack some of the outstanding sexual features of plants, such as agents of sperm transport ("pollinators").

SUGGESTIONS FOR FUTURE STUDY

During our discussions it became clear that certain kinds of information are simply not available that are essential for the analysis of conflict within and between the sexes. There is a shortage not so much of hypotheses but of certain kinds of critical information that could contribute to both the formulation and testing of theory. Some of these gaps in our knowledge or organisms were mentioned repeatedly in this and other working groups. We therefore propose a list of areas where new information is urgently needed and seems possible to obtain.

1) Observational and experimental evidence that mate choice occurs, of both the characters chosen and the "protocols" or procedures (behaviors) used to effect choice, including the timespan and number of comparisons made during choice. We have very few data on how females behave when choosing among

males. How many males does a female sample before she mates? Does she actively reject some males in favor of others? Frog choruses and vertebrate leks would seem excellent systems to study this in detail.

2) What are the precise effects of male displays on female behavior? In some peacocks and pheasants the ocelli on the tail and tail coverts are argued to have a hypnotic effect on females. Following Dawkins and Krebs' (1978) ideas on "communication or manipulation," it seems possible that the elaboration of plumage and displays are an end result of male-male competition for better and better manipulation of females. Some males may therefore be inducing copulation through sensory-psychological effects in much the same way that other males use physical force for the same ends. Recent reviews (Eberhard 1985; West-Eberhard, 1984) provide evidence that sexual signals manipulate particular widespread behavioral or physiological responses of females in ways likely to affect male mating success. This provides an alternative to the common view that differential female responsiveness ("female choice") originates under selection on females to choose their mates (whether in a mate-quality or species-recognition context).

3) Measurements are needed of the costs of female choice. For example, if predation pressure is high at the breeding site it may be costly for a female to sample several males before she chooses. Other possible costs are time and energy spent in sampling. It is important to document costs because they influence the outcome of certain theoretical models for the evolution of female preference. It is important here to distinguish between costs of choice and costs of mate-seeking.

4) In cases where males defend a resource, are females choosing the male or the resource? Some experiments suggest that females are influenced by the male character even when resource differences are important influences on female reproductive success (Andersson 1982). Other experiments have shown that it is the resource rather than male display which influences female choice (Slagsvold 1986).

5) Evidence of gamete and zygote competition, choice in plants and higher animals, and post-copulatory female choice (manipulation of male gametes). In plants, do larger pollen grains have an advantage? What is the function of differences in pollen structure? Do female structures have features encouraging or otherwise influencing pollen competition? Since the haploid genome actually affects the phenotypic characteristics of pollen (see Haldane, 1966), there is an opportunity in plants (not know to be present in animals) for female choice of male genotype. Is there any evidence that female plants take advantage of this opportunity?

6) Information on role of both sexes in influencing mating decisions. Many studies focus on either male behavior or female behavior but not both. There may be differences not only in the relative importance of male-male competition versus female choice both between species (e.g., explosive breeders with a

low probability of female choice versus prolonged breeders with a higher probability) but also within the same species due to demographic factors. We need comparative studies of:

a) different populations of the same species under different ecological or demographic conditions;

b) different species of the same taxonomic group living in different habitats to determine factors which influence the importance of male-male competition versus female choice (see example).

7) Comparative study of related species designed to show whether or not there is an evolutionary progression toward refined sensory discrimination of male traits by females in a sexual context. Female choice (differential sexual responsiveness) of females due to stimulation by males of response repertoires evolved in a nonsexual context is a neglected and possibly very widespread means of sexual coercion. Comparative study may allow discrimination between responses evolved under selection for female choice, and those "preadapted" for it: if, in a group of closely related species, most show a female response in a nonsexual context, whereas in only one or a few species it is stimulated by males during courtship in addition (leading to differential mating success), this would provide positive evidence for the occurrence of preexisting preference.

8) There is much scope for future development of models of sexual conflict. On the one hand there is much potential for increasing the strategic complexity of some of the existing models (e.g., sequential game analyses of parental investment and conflict over mating decisions). On the other hand simple ESS models should be examined for their robustness with regard to explicit genetic interpretation. In particular we should like to establish whether certain sexual conflict games are less robust than the classical ESS models in this respect. There would certainly be difficulties in attempting to model the central problem in Fisherian runaway processes with its assortative mating and correlation of signal and response, without explicit genetics.

CONCLUSION

Given the very great diversity of patterns of sexual selection, which we have noted over and over again in our comments, the testing of the plausibility of particular theories may depend not on the kind of single-stroke tests possible in physics and chemistry and certain experimental areas of biology but on the accumulation of information like that just listed for a large number of species. This has been pointed out by Hamilton in discussing the parasite model of female choice, and it is a general feature of many questions in evolutionary biology, including the general question of the importance of Darwinian natural and sexual selection in nature.

In the case of alternative hypotheses for the basis of female choice, the "alternative" hypotheses may not be truly competing generalizations but may prove complementary: all may be needed to explain the diversity of courtship signals observed. The relative importance of these hypotheses depends on the regularity with which their requirements and predictions are fulfilled within species in nature.

One role of sexual selection hypotheses, in addition to promoting broadly applicable generalizations, is to draw attention to features of behavior and morphology whose functions and even existence have gone unnoticed in the past. Some of these features may contribute yet unimagined "alternative hypotheses and critical tests" of sexual selection theory. Should those fail, we can always return to the way we were:

The Way We Were

A sweet and friendly porcupine,
Snuffled up; his eyes met mine,
I pickled him in bright red wine,
And labelled each and every spine.

A thousand more I then did nail,
and measured all from head to tail,
and plotted on a log/log scale,
. . . but everything to no avail.

An orgy of regression failed—
So algebra I then assailed,
With all the fun that this entailed
I modelled . . . and results prevailed.

My future now was quite secure,
And to the field I go no more,
Papers, papers by the score
Full of sums and such a bore.
                                    –G.A. Parker

REFERENCES

Alatolo, R.V.; Carlson, A.; Lundberg, A.; and Ulfstrand, S. 1981. The conflict between male polygamy and female monogamy: the case of the pied flycatcher, *Ficedula hypoleuca*. Am. Natural. 117: 738–753.
Andersson, M. 1982. Female choice selects for extreme tail length in a widowbird. Nature 229 (5886): 818–820.

Charlesworth, B., and Charlesworth, D. 1979. Population genetics of partial male-sterility and the evolution of monoecy and dioecy. Heredity 41: 137–154.

Charnov, E.L. 1982. The Theory of Sex Allocation. Monographs in Pop. Biol. 18. Princeton: Princeton Univ. Press.

Dawkins, R., and Krebs, J.R. 1978. Animal signals: information or manipulation? In: Behavioral Ecology: An Evolutionary Approach, eds. J.R. Krebs and N.B. Davies, pp. 282–309. Sunderland, MA: Sinauer.

Eberhard, W.G. 1985. Sexual Selection and Animal Genitalia. Cambridge, MA: Harvard Univ. Press.

Emlen, S.T., and Oring, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197: 215–223.

Haldane, J.B.S. 1966. The Causes of Evolution. Ithaca, NY: Cornell Univ. Press.

Jones, D.F. 1928. Selective Fertilization. Chicago: Univ. of Chicago Press.

Lloyd, J.E. 1979. Sexual selection in luminescent beetles. In: Sexual Selection and Reproductive Competition in Insects, eds. M.S. Blum and N.A. Blum, pp. 293–342. London: Academic Press.

Lloyd, J.E. 1980. Male *Photuris* fireflies mimic sexual signals of their females' prey. Science 210: 669–671.

Maynard Smith, J. 1977. Parental investment: a prospective analysis. Anim. Behav. 25: 1–9.

Otte, D. 1975. On the role of intraspecific deception. Am. Natural. 109: 239–242.

Parker, G.A. 1985. Phenotype limited evolutionary stable strategies. In: Current Problems in Sociobiology, ed. Kings College Sociobiology group, pp. 173–201. Cambridge: Cambridge Univ. Press.

Slagsvold, T. 1986. Nest site settlement by the pied flycatcher: does the female choose her mate for the quality of his house or himself? Ornis Scand. 17: 210–220.

Sommer, V, and Mohnot, S.M. 1985. New observations on infanticides among hanuman langurs (*Presbytis entellus*) near Jodhpur (Rajasthan/India). Behav. Ecol. Sociobiol. 16: 245–248.

Thornhill, R., and Alcock, J. 1983. The Evolution of Insect Mating Systems. Cambridge, MA: Harvard Univ. Press.

West-Eberhard, M.J. 1984. Sexual selection, competitive, communication and species-specific signals in insects. In: Insect Communication, ed. T. Lewis, pp. 283–324. New York: Academic Press.