

SYMPOSIUM PARTICIPANTS



From left: R. L. Smith, T. G. Forrest, J. Sivinski, H. J. Brockmann, J. E. Lloyd, R. Thornhill, T. J. Walker, and W. H. Cade. Photograph by Dr. F. W. Mead.

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COMPETITIVE, CHARMING MALES AND  
CHOOSY FEMALES: WAS DARWIN CORRECT?<sup>1</sup>

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“. . . it has been said by several critics that when I found that many details of structure in man could not be explained through natural selection, I invented sexual selection; I gave, however, a tolerably clear sketch of this principle in the first edition of the 'Origin of Species,' and I there stated that it was applicable to man. This subject of sexual selection has been treated at full length in the present work, simply because an opportunity was here first afforded me . . . *My conviction of the power of sexual selection remains unshaken* . . . When

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<sup>1</sup>This and subsequent superscript numbers refer to notes in an appendix, p. 19.

naturalists have become familiar with the idea of sexual selection, it will, as I believe, be much more largely accepted; and it has already been fully and favorably received by several capable judges" (C. Darwin, 1874, Preface to Second Edition of *The Descent of Man and Selection in Relation to Sex*) (emphasis added).

Darwin's theory of sexual selection was outlined briefly in *On the Origin of Species* in 1859. In *The Descent of Man and Selection in Relation to Sex* (1871) Darwin expanded and documented his theory. He provided support and arguments for sexual selection as the evolutionary force behind many sexual characteristics of animals, including many sexual and racial differences in humans. Darwin pointed out the distinction between characteristics promoting survival and those promoting reproduction. He viewed the characteristics promoting reproduction as often contrary to survival but maintained by sexual selection because the benefit of the traits in reproduction could exceed their cost in survival to the individual. Darwin felt that the elaborate and often bizarre plumages of birds, the horn-like projections of deer and some insects, and many other traits could best be explained in terms of benefit to an individual's reproduction exceeding costs to an individual's survival. The reproductive benefits associated with most secondary sexual features, Darwin reasoned, were related to winning in the competition among males for females and in coaxing females to mate.<sup>2</sup>

Darwin's theory of sexual selection was severely criticized by the capable theoretician A. R. Wallace (1889). Wallace believed that the more elaborate colors and morphologies of many male animals relative to females of the same species evolved by natural selection rather than sexual selection. He felt sexual differences function in mimicry, warning or protection, and species and mate recognition. Huxley (1938, 1963) was an important later critic of sexual selection. He felt that the term sexual selection should be replaced (1938) and that sexual selection is less important than natural selection in bringing about evolutionary change because selection operates primarily by means of differential survival of individuals to maturity (1963: xviii-xix). Mayr (1972) expressed the view that sexual selection has been a very useful principle for analysis and prediction of sexual differences in animals. Otte (1979) recently wrote that a distinct separation of sexual selection from natural selection is without merit.<sup>3</sup> Why was Darwin so convinced of "the power" and ultimate wide acceptance of his theory of sexual selection? Sexual selection has some features that are not components of natural selection (West-Eberhard 1979a). It is important to distinguish 2 features to understand the potency of sexual selection relative to natural selection. The first feature is the absence of a definite limit to reproductive returns for individuals associated with a trait evolving by sexual selection. The second feature is related to the first and is that male-male and male-female interactions represent coevolutionary races. Darwin was aware of these features and this provided the basis of his unyielding position on sexual selection despite criticism.

These 2 features are fundamental to a broader category of selection called *social selection*, a very useful category to distinguish.<sup>4</sup> West-Eberhard (1979a) has provided an analysis of the unique features of social selection in terms of social behavior in general. In this paper I will discuss some of West-Eberhard's (1979a) points as they relate to traits evolved by Dar-

winian sexual selection, i.e. traits selected because they allowed individuals better access to superior mates. Such access may involve winning in male-male competition and/or being chosen by females. The discussion focuses on sexually-selected insectan features. The topics often associated with sexual competition that related to this discussion are: 1) distinct differences in reproductive success of individuals within populations, 2) divergence of characters under selection, 3) the reduction of genetic variation underlying sexual traits, 4) the weak relationship between the fitness of parents and offspring, and 5) the relationship between sexual selection and nongenetic differences between individuals.

#### ALTERNATIVE SPECIALIZATIONS AND DIFFERENCES IN INDIVIDUAL REPRODUCTIVE SUCCESS

Darwin (1871) documented that sexual selection is a potent means by which successfully reproducing individuals are determined through direct competition. As evidence he cited the observable fights and ritualized aggression and displays found in many animals. Unsuccessful individuals often have their chances for reproduction significantly reduced or eliminated completely (see Darwin 1871, Wynne-Edwards 1962, Alexander 1974, Wilson 1975, West-Eberhard 1975, 1979a, papers in Blum and Blum 1979). It is assumed that ritualized interaction during aggression and display evolved because further escalation was unprofitable in terms of reproduction and most social animals have alternatives to winning an individual sexual or aggressive interaction. Social interactions clearly function as a means by which individuals assess the capabilities of other individuals relative to their own and "decide" on alternative ploys for reproduction (Parker 1974, West-Eberhard 1979a). An animal can wait for a situation that more likely will result in winning a social encounter, i.e., in dominating a competitor or being chosen as a mate by a female(s). Also, the loser of a particular social interaction can adopt an alternative specialization or strategy other than waiting (Parker 1974, Alcock 1979a, Ligon and Ligon 1978, Ligon in press, West-Eberhard 1979a, 1979b). In the absence of alternatives an animal should fight to the death, because death and losing in social contests without alternatives are equal genetically. An alternative specialization is an alternative route to reproduction that is expected to be less successful than winning, but more profitable than continuing conflict and direct competition at a particular time.<sup>5</sup>

For a long time we have known that males in some insect species show considerable morphological variation in body size and size of structures like horns and mandibles presumed to be associated with fighting (Darwin 1871). Recently, studies have shown considerable variation in male behavior within insect species and in some cases the behavioral variation has been related to morphological variation. Detailed studies of variation in male mating behavior have been conducted on a dungfly, *Scatophaga stercoraria* L. (Parker 1970, 1979 and references therein, Borgia 1979), some wasps and bees (Alcock et al. 1977, Alcock 1979a and references therein, Evans and O'Neill 1978, Hamilton 1979), grasshoppers (Otte 1972 and references therein), crickets (Cade 1979 and references therein), fireflies (Lloyd 1979a and references therein), other beetles (Eberhard 1979 and references therein, also

see Otte and Stayman 1979, Hamilton 1979), and scorpionflies (Thornhill 1979a, 1979b, in press a).

Studies of the resource-based mating system of *Panorpa* scorpionflies allow understanding of the costs and benefits of alternative strategies employed by winners and losers in sexual competition. Male *Panorpa* have 3 distinct behaviors leading to copulation. First, a male may disperse a long distance pheromone while standing adjacent to a dead arthropod he had found in the habitat. A female attracted to the pheromone feeds on the dead arthropod during copulation. Second, a male may disperse pheromone from the vicinity of a hard salivary mass that he secretes on the substrate and upon which an attracted female will feed during copulation. In each of these 2 cases, males vigorously display to attracted females and aggressively defend dead insects and salivary masses from other males that attempt to take them. The third behavior employed by males is rape (Thornhill 1979a, in press a, in press b).

Males of most species of *Panorpa* that I have studied have well-developed salivary glands and may secrete salivary masses to feed females during copulation. Males of all of these species sometimes feed females dead insects during copulation. Nocturnal and crepuscular mating is typical of *Panorpa*, which makes field observations difficult. However, I have observed rape in nature in 7 species of *Panorpa*. Males of most of the species I have studied exhibit rape in the laboratory.

A rape attempt involves a male without a nuptial offering (i.e., dead insect or salivary mass) rushing toward a passing female and lashing out his mobile abdomen at her. On the end of the abdomen is a large, muscular genital bulb with a terminal pair of genital claspers. If the male successfully grasps a leg or wing of the female with his genital claspers, he slowly attempts to re-position the female. He then secures the anterior edge of the female's right forewing in the notal organ, a clamp-like structure formed from parts of the dorsum of the male's third and fourth abdominal segments. Females flee from males without nuptial offerings. If grasped by such a male's genital claspers, females fight vigorously to escape. When the female's wings are secured, the male attempts to grasp the genitalia of the female with his genital claspers. The female attempts to keep her abdominal tip away from the male's probing claspers. The male retains hold of the female's wing with the notal organ during copulation, which may last a few hours in some species. The insemination success by rapists is lower (11% of attempts) than that of males with dead arthropods as nuptial offerings (100%).

The behavior of females toward males with and without a nuptial offering is quite different. Females flee from males that approach them without a nuptial offering; however, females approach males with nuptial offerings. Also, females struggle to escape from the grasp of rapists, but females do not resist coupling by the notal organ of males with nuptial offerings.

The fertilization rate of ejaculates of *Panorpa* rapists is unknown. Female *Panorpa* have been observed to mate twice in a day and up to 5 times in a week. Data on ejaculate competition between males are unavailable for *Panorpa*. However, an important generalization in insect reproductive behavior, supported by a large amount of comparative data, is that the last male to mate with a female in a multiple-mating species fertilizes most of

the eggs that the female lays until she mates again (Parker 1970). If this is the case in *Panorpa*, a successful rapist may obtain a fertilization rate similar to a male that feeds a female a nuptial offering.

*Panorpa* males can apparently distinguish size of dead insects because male aggression is most intense around large dead insects. Once in possession of a dead insect, males initiate pheromone emission to attract a female. The female feeds on the dead insect during copulation. Males aggressively excluded from dead insects by other males tend to adopt the behavior of using salivary secretions as nuptial offerings; when salivary secretion is no longer possible because of previous use of salivary masses in nuptial feeding, males attempt rape.

*Panorpa* male behavior is directed by female preference of males. The copulatory success of males possessing large dead insects is greater than that of males guarding small dead insects. Also, males using dead insects as nuptial gifts attract more females for copulation than males using salivary masses, and males using salivary masses have a greater copulatory success than rapists.

Although successful rape (i.e. including insemination) may be infrequent, it is an appropriate behavior for a male to adopt when he is aggressively excluded from possession of a dead insect and his salivary secreting abilities are exhausted. The fitness potentially gained by a *Panorpa* rapist is understood when the behavior of these insects is coupled with their ecological setting. A 5-year study of the 9 species of *Panorpa* in southeastern Michigan reveals that the species overlap almost completely in their feeding ecology and that dead insects are a limiting resource for these insects. *Panorpa* compete primarily in an interference manner through intense intra- and interspecific aggression around food. Competition for food influences the fitness of competing *Panorpa*, since increased competition results in increased movement and reduced adult longevity in these insects under natural conditions (Thornhill in press c). A selective history involving competition for food accounts for the evolution of the risky *Panorpa* behavior of feeding on dead insects in the webs of spiders. About 25% of *Panorpa* foraging is in spider webs, and web-building spiders cause 65% of adult *Panorpa* mortality. The predation of *Panorpa* by web-building spiders is significantly male-biased despite adult *Panorpa* sex ratios near unity. This bias is apparently due to risky male behavior associated with obtaining a dead insect or feeding in order to produce salivary masses for copulation (Thornhill 1975, 1978a). A *Panorpa* rapist need not incur these risks and thus rape results in increased survival for the rapist.

If rapists avoid risks associated with obtaining food for copulation, why do not all males use rape as their primary behavior? The answer must be related to the greater fitness gained by males that feed females nuptial offerings of dead insects or salivary masses. Male bittacid scorpionflies that feed females large insects during copulation gain reproductive success because their mates lay more eggs and females prefer mates with large insects (Thornhill 1976a, 1976b). That female fecundity may be related to quantity or quality of nuptial offering in *Panorpa* is suggested by female preference for males possessing large dead insects. In addition, male *Panorpa* using nuptial feeding behavior may reduce the amount of subsequent feeding and movement by their mates and thus reduce chances of mortality from web-

building spiders during the time females are laying eggs they have fertilized. Since food is limited, and feeding is necessary for a female to experience high fecundity, rape is detrimental to females because during rape a female is removed from activities associated with obtaining food. Also, the struggling to escape from rapists by females suggests rape may reduce the likelihood that a female can later obtain a resource-providing male. That is, raped females may be detected and discriminated against to some extent by males with nuptial offerings.

Yet another alternative specialization has been observed in studies of Hymenoptera and Orthoptera. In some species apparently subordinate males adopt "satellite" behavior.<sup>6</sup> Cade (1979) investigated the costs and benefits associated with this form of alternative specialization in field crickets. He found noncalling (satellite) (? = subordinate) and calling males in the same population of field crickets. Noncalling males position around a calling male and intercept females attracted by the call. The calling males get more matings than noncalling males, but silence in the later males results in less exposure to parasitic flies that track cricket hosts acoustically.

Other examples of variable male mating behavior include pseudofemale behavior in fireflies (Lloyd 1979a) and scorpionflies (Thornhill 1979b) and fighting males and nonfighting males in some species of Hymenoptera and beetles. The fighting vs. nonfighting alternatives are often associated with specialized morphological variation in wingedness and horn and mandibular structure, and in some cases the costs and benefits of the alternatives are partially understood (Alcock et al. 1977, Alcock 1979a, Hamilton 1979). The advantage of male size in fighting has been documented by Alcock et al. (1977) for *Centris* bees in which variation in male size is related to variation in copulatory success. I will return to the evolution of alternative specializations after a discussion of other features of sexual selection.

The outcomes of competition for mates and of indirect reproductive competition are quite different in terms of their influence on traits with continuous variation (West-Eberhard 1979a). Sexual selection (and social selection in general) acting on behavioral and/or morphological variation may often have a "stepped" effect on the reproductive success of individuals in a population. When this occurs, the population will be divided into 2 or more distinct reproductive categories, depending upon the extent of sexual selection. Under intense sexual selection as seen in highly polygynous animals (e.g. lekking birds, mammals, and some insects; see Alexander 1975), 2 categories of individuals may emerge from the competition: highly successful and non-reproductive. Under most circumstances, however, there are categories of reproductive individuals between these 2 extremes. However, the "stepped" effect on the reproductive success of individuals in a population remains apparent and often there may be considerable difference in reproductive success between individuals found on different "steps." The losers in initial competition for high reproductive success are predicted to adopt alternative specializations in order to gain some reproduction. As discussed in a later section, the "stepped" effect on reproductive success has important consequences for understanding heritable variation in relation to alternative specializations and female choice.

## THE EVOLUTION OF ELABORATENESS

Darwin created sexual selection theory in part to explain certain elaborate morphologies and displays. Indeed, sexual selection has often been treated as different from natural selection because the former is often felt to lead to elaborateness in male traits (Darwin 1871, Fisher 1930, Otte 1979, West-Eberhard 1979a). Under sexual selection, elaborateness may evolve because 1) of the lack of a definite upper limit to reproductive return to individuals from traits important in sexual competition, 2) male-female and male-male interactions coevolve and a trait typically can be countered by a more adaptive modification, and 3) female choice can lead to "runaway" evolution (Fisher 1930) of traits (West-Eberhard 1979a).

UPPER LIMITS TO SELECTION AND COEVOLUTION: Darwin (1874) used a comparison of limits to evolution under sexual and natural selection as an important way for distinguishing these 2 forms of differential reproduction (West-Eberhard 1979a).<sup>7</sup> This difference between natural and sexual selection that Darwin envisioned is fundamental to understanding the relative potency of these 2 forms of selection (West-Eberhard 1979a). Darwin felt natural selection could change a trait to a point at which further change would result in only negligible reproductive returns for an individual. At each step in the evolution of a trait under natural selection, individuals received less and less reproductive success from the modification until the "upper limit" is reached and the returns are so small that further evolution stops. There is no definite upper limit to change in a trait evolving in the context of sexual selection. The reproductive returns for a better trait associated with sexual competition, regardless of how minor the change, need not decline. The only factor limiting the degree to which sexual selection can elaborate a trait are constraints associated with selection in the context of natural selection as recognized by Darwin.<sup>8</sup>

The absence of a decreasing reproductive return from a better trait in sexual competition is clearly illustrated by the coevolutionary aspect of the battle within the sexes (West-Eberhard 1979a). In general, any new ability in relation to sexual competition that arises can effectively be countered by an ability that confers more reproductive return. An individual's sexual environment evolves back, unlike an individual's nonsocial environment. A tactic favored by sexual selection will spread until a better tactic arises and so on.

The often bizarre morphological and behavioral features of many male insects are indicative of the lack of a definite upper limit to adaptive return associated with improvement for coping with a competitive and coevolving sexual environment. Female-mimicking male scorpionflies (Thornhill 1979b), abdominal clamps in male scorpionflies for holding females during rape (Thornhill in press a), penis structure in male damselflies for removing sperm deposited by competing males in the spermatheca of females (Waage 1979), male mating swarms and aggregations in a variety of insects (Alexander 1975, Thornhill in press d), the injection of confusing flashes into the flash patterns of other males by fireflies (Lloyd 1979a, 1979b), cuckoldry avoidance tactics in waterbugs (Smith 1976, 1979) reflect the coevolutionary selective circumstances described. See Lloyd (1979b) for a fascinating discussion of male sexual tactics in fireflies and many other insects.

FEMALE CHOICE: According to much of sexual selection theory, choosy

females are an important aspect of the sexual environment leading to nonrandom differential reproduction of conspecific males. Darwin argued that female tastes for male beauty caused in many cases the elaboration of male morphologies and behaviors and "that the power to charm the female has sometimes been more important than the power to conquer other males in battle." Darwin assumed that females prefer certain males as mates because of their morphological and/or behavioral features and that this preference alone would lead to elaborateness. He did not attempt to explain how such female preferences might have originated and he said little about selective maintenance of these male traits other than that females preferred them. The lack of any apparent connection between male ornamentation and male fitness caused problems for the acceptance of the female choice aspect of Darwin's theory. Wallace (1889) felt that female choice was unimportant for this reason and because of the lack of evidence that females choose certain conspecific males over others as mates.<sup>9</sup>

Fisher (1930) provided only theory for Wallace's objections. Fisher explained how elaborate male traits could arise and then be maintained by female choice via his so-called "runaway process." He assumed inheritance of male traits. The first step in Fisher's scheme involves females finding a male trait that confers enhanced survival on a female's offspring. Any female with a preference for the male trait would gain reproductively because she would produce fit sons. This would lead to the spread in the population of the male trait as well as female preference for the trait. When females with the preference became common, the second step or runaway process could come into play. Any female with the preference that mates with a male with the trait will produce attractive sons, i.e. sons preferred by females. The advantage to females which choose males with the trait during the runaway process would involve only the benefit gained because females in the population have the same preference. Thus, any female with the preference will produce more grandsons and so on as long as the female preference remains the same through time. The elaboration of the trait will continue because of its advantage due to female preference even after it has exceeded the point in elaboration at which its advantage in ordinary natural selection no longer exists. Natural selection may oppose further elaboration, but the further development will continue as long as the advantage due to female preference is offset by the disadvantage in natural selection. Elaboration will stop at the point where further elaboration would cause greater detriment to survival than the benefit gained through sexual selection.<sup>10</sup> Darwin realized that sexual selection, unlike natural selection, has no definite upper limit and that sexual selection can act counter to the action of natural selection, but at some point natural selection will prevent further elaboration.

Fisher argued that females gain reproductive success only by producing attractive sons during most of the evolution of attractive male features; only initially was female preference envisioned to result in the production of sons more fit to cope with environmental contingencies. Zahavi (1975), Trivers (1976), Hailman (1977), Borgia (1979), and Thornhill (manuscript) argue that females prefer certain male traits throughout their evolution because the traits result in the production of offspring capable of surviving; the traits themselves convey information to females that the male



has abilities that are important for offspring survival and ultimately reproduction. I will return to these ideas later. Regardless of the theory one uses to explain the evolution of male secondary sexual traits, all the theories involve very rapid evolutionary change.

**PROBLEMS WITH FEMALE CHOICE THEORY:** The role of female choice in the evolution of male traits remains controversial. There are 3 problems as follows: 1) there is little evidence that females actually prefer certain conspecific males over others in nature; 2) many traits presumably preferred by females do not seem to be obviously related to the choosy female's own fitness or that of her offspring; and 3) genetic variation in male traits is necessary to provide the adaptive basis for female choice, but little genetic variation should be associated with traits under strong and continuous female preference.

Wallace (1889) first criticized female choice theory because of few supporting observations for females actually discriminating males. Huxley (1938) made a similar criticism. Poulton (1890) supported Darwin's view of the role of female choice and claimed that the lack of evidence stemmed from the lack of attempts to observe animals in nature. Mayr (1972) expressed the view that the important role of female choice was beyond question. His opinion was primarily based on observations "that females are very fickle indeed and usually remain for a long time unimpressed by the displays of large numbers of suitors before finally accepting one of them" (p. 92). However, coyness may merely mean that females are discriminating about the general ecological circumstances for reproduction other than the characteristics of or resources controlled by a potential mate (see Williams 1966). Also, West-Eberhard (1979a) has suggested that females might sometimes behave in a coy manner simply because they are "afraid" of males which often are larger and more aggressive. Clearly, coyness in itself is not evidence for female choice.

The paucity of evidence for female preference in nature remains to date an important problem in understanding the role of female choice in the evolution of male traits. Most evidence for female choice is very indirect and based on the distribution of females around males of different ages or sizes or males that possess different amounts of some resource such as a territory (see studies discussed in Wilson 1975, Davies 1978, Halliday 1978, Alcock 1979b, and Downhower and Brown in press). Also, female choice is often inferred when females mate with some males and not others.<sup>11</sup>

Laboratory studies of female choice have revealed, in general, the same kind of indirect evidence for female choice as field studies. For example, Maynard-Smith (1956) found that female *Drosophila subobscura* mate more with outbred than with inbred males. He inferred preference on the basis of a difference in courtship behavior between the 2 types of males, but other differences between the males unrelated to female choice could account for the results.

One could argue that all the above examples involve female choice, because females have the option of staying with a male that will serve as a mate or leaving and looking for another more suitable mate (see Maynard-Smith 1978: 169). I feel that the argument alone is unsatisfactory. Females under some circumstances may be forced to remain with certain males because, as is typical in many species, males are larger, more aggressive and/or

more armored than females. The question of whether females choose males can only be answered by direct field observation of females interacting with males.

Few field studies have been directed at observing female behavior in relation to criteria females use in mate choice.<sup>12</sup> I have demonstrated that females of the scorpionfly, *Hylobittacus apicalis*, prefer mates with large nuptial prey over males with small or no prey in nature (1976a, 1977, 1979a, in press e). The hangingfly system is perhaps unique in that individual females can be watched and followed after they interact with males and the fitnesses of discriminating and nondiscriminating females assessed in nature.

To me it is clear that direct evidence for Darwinian female choice is very meager. In actuality, male choice has been demonstrated in about as many cases as female choice. Manning (1975) provides good evidence for male preference for larger, more fecund females in *Asellus* isopods, and the detailed work of Shuster (1979) on *Thermosphaeroma* isopods demonstrates male preference for larger females and for females in an advanced stage of reproduction. 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 and Brown in press, and Lloyd 1979b); however, it has yet to be determined that females typically are discriminate of mates.

The second problem associated with our understanding of the role of female choice is that many traits presumed to be preferred by females (e.g., elaborate male morphological features) do not seem to be correlated with the choosy female's fitness or that of her offspring (see Maynard-Smith 1978, Borgia 1979, and Thornhill unpublished for detailed discussions). In many species males have a resource in their possession that females apparently assess. This resource may be a territory, nest site, food item, etc. Females choosing males on the basis of resources that the female herself will use or that will be provided to offspring present no problem for female choice theory because of the immediate reproductive benefit that can be envisioned for a discriminating female. However, there have been few demonstrations that females choosing certain resource-holding males over others actually increase their own reproductive success, a critical demonstration if one wishes to argue that female choice is adaptive (see Maynard-Smith 1966, Thornhill 1976a, 1979a). Adaptive female choice is apparent in the scorpionfly *Hylobittacus apicalis*. Females assess males on the basis of the nuptial prey which is presented to females by the male just prior to copulation. Most females prefer males with large nuptial prey and such females lay more eggs than females that do not exhibit discrimination of mates. Discriminating females in this system may accrue other advantages—e.g. increased survivorship because they do not expose themselves to predators—but increased fecundity is the most apparent and relevant. Number of eggs laid by a female is an important parameter of fitness in *H. apicalis* because females drop eggs randomly among the leaf litter (thus oviposition site selection is not related importantly to variation in female reproductive success), egg size does not vary, and there is no parental care of young (Thornhill 1976a, in press e).<sup>13</sup>

On the other hand, there are many species in which males do not display a resource to females during courtship, which may consist only of complex

dances, flights and ritual chases often involving specialized male morphology. In other species the only differences between males are in phenotypic traits like size or age. It is species in which males show no parental care and no protection or nurturing of the female that female choice theory is most problematical, because the only benefit females are likely to receive is male genes. How could the courtship antics of male insects and birds be related to superior genes that would enhance offspring fitness?

Fisher's (1930) theory argues that the male traits preferred by females only initially enhanced offspring survivorship. Indeed, when the runaway process in Fisher's scheme comes into play, the further elaboration of the trait by female choice is viewed as contrary to male offspring survival. There are good examples of morphological traits of males that females are suspected of using in mate choice that are actually contrary to survival.<sup>14</sup>

Zahavi (1975) proposed a theory he called the "handicap principle" as an alternative to Fisher's "runaway" selection model. Zahavi argues that females should select males on the basis of traits that are true phenotypic indicators of a male's genetic traits related to survival. He reasoned that elaborate male characters represent a survival handicap to the male possessing them. A female preferring a male with such a handicap would be assured of getting a father for her offspring with superior survival genes, because the male had survived despite his handicap.<sup>15</sup>

Trivers (1976), Hailman (1977), and Thornhill (1979a, manuscript) argue that female preference may be directed at discriminating certain male traits that indicate male abilities of value for survivorship of both sexes of offspring. Such traits might be under autosomal genetic control so that both sexes of offspring would benefit (Trivers 1976, Thornhill 1979a). For example, a female Hawaiian drosophilid that preferred a male with colorful wings might be actually choosing a male with superior genes for obtaining essential or rare nutrients as indicated to the female by the nature or extent of wing pigment. Females preferring males with colorful wings would produce sons and daughters with the ability to find and process the essential or rare nutrient. A similar example might involve the antlers of male deer, the size of which could indicate a male's ability to obtain and process calcium. This line of thinking can be extended to include behaviors as well as morphological features of males (Thornhill manuscript). These theories are different from Fisher's notion because they explain benefit to the discriminating female in terms of more than merely having attractive sons. However, these theories, like Fisher's theory, when applied to explain male traits in species without male parental care or male-provided nourishment or protection to the female, depend on genetic differences between males that are discriminated by females on the basis of phenotypic differences between males.

The third problem associated with female choice results from population genetics theory. The argument is that females which discriminate mates on the basis of genetic differences between males (as expressed in the phenotype) will deplete additive genetic variance for fitness if only a small portion of males mate. That is, female choice should lead to a low parent-offspring correlation for fitness in the trait preferred. Phenotypic variation related to fitness will not, according to this argument, reflect underlying genetic fitness variation (Williams 1975, Maynard-Smith 1978, Halliday 1978,

Harpending 1979). Many animals (Wilson 1975) including most insects (Thornhill 1979a) are highly polygynous (only a few males may inseminate most females); therefore, this criticism of female choice is widely applicable.

However, Maynard-Smith (1978) points out that despite this problem females still appear to exercise choice in lekking bird species in which very few males obtain most of the matings. For example, in lekking sage grouse 7% of the males copulate with 85% or more of the females visiting the male aggregation and central males do most of the copulating (Wiley 1973). Inter-male contests determine the position of males in the lek. The female gets nothing from the central male but genes, as there is no male parental care. It appears that females prefer these central males as mates as they pass up copulations with peripheral males while moving toward the lek's center. Maynard-Smith further states that the preference of central males only makes sense if there is some inheritance of fitness associated with the traits that enable a male to obtain the central position. He suggests that, although small, there is enough genetic variation associated with male traits contributed by harmful mutations and the establishment of newly introduced favorable mutations to make female choice adaptive in lekking birds. Variance in male copulatory success in some lekking insects may be as high as in sage grouse (see Alexander 1975, Thornhill in press d). Borgia (1979) provides a fascinating discussion of some alternative ways in which necessary genetic variation can be maintained in lekking birds as well as other highly polygynous animals.

On the other hand, female choice on the basis of "good genes" is not necessary to account for lek structure or the relative mating success of males in the lek as first explained to me by John Sivinski. If the central area of the lek is safer in terms of reduced predation, female choice on the basis of male genetic quality is not required for an understanding of the female preference for the central male. This interpretation of female choice in lekking birds is consistent with the predation-pressure hypothesis for the evolution of lek behavior provided by Lack (1968) for birds and by Spieth (1974) for Hawaiian drosophilids (see Thornhill 1978b, in press a).

#### GENETIC VARIATION AND THE INHERITANCE OF FITNESS

There is another very important point that counters the problem for female choice theory created by the likelihood of little genetic variation underlying male traits discriminated by females and thus virtually little or no variation upon which further selection can act. The argument is simple and has been overlooked until recently (see Alexander 1977, West-Eberhard 1979a). Sexual selection will not necessarily stop when genetic variation underlying male traits is absent. Evolution (changes in gene frequency) due to selection will cease without genetic variation, but selection can continue. The nonrandom differential reproduction associated with any form of selection results from phenotype differences. These differences may be totally heritable, totally nonheritable, or some mixture of these 2 extremes. Selection will act on any differences whether genetic or nongenetic. Nonheritable variation should be especially important as a basis of sexual selection (and social selection in general, see West-Eberhard 1979a). Traits such as male size, age, and general vigor are felt to be important in both male-male competition for females and female choice. Variation in these traits may be to

a large extent related primarily to differences in nutrition obtained directly by individuals and/or provided by parents.

For the reasons discussed earlier, sexual selection is a potent form of non-random differential reproduction and thus a gene associated with success in sexual competition should spread very rapidly to fixation. Selection for better alternative genes following their introduction into the population will also be rapid. Thus over most of evolutionary time genetic variation may be irrelevant to the strength of sexual selection operating at any 1 time. The most successful male Hawaiian drosophilid in the lek and the central male sage grouse may be identical with other conspecifics in the lek in regard to genes associated with achieving the dominant position which allows great reproductive success. Tremendous reproductive success in these situations may be due to phenotypic traits like size that are entirely nonheritable. Females are expected to still exercise choice because: 1) the traits of the preferred male (e.g. size) have related generally to offspring fitness over evolutionary time, 2) any mutants deleteriously influencing offspring that occur and are expressed in the phenotype of males would be detected and avoided by such a preference, and 3) any mutants advantageously influencing offspring that occur and are expressed in the phenotype of males would be detected and chosen by such a preference (also see Alexander 1977).

The arguments involving strong sexual selection using up genetic variation but then remaining potent as a form of nonrandom differential reproduction on the basis of nonheritable phenotypic differences can be applied to traits under social competition in general (West-Eberhard 1979a). This interpretation is consistent with population genetics fact and theory: characters directly related to fitness have the lowest heritability in many species (Mukai et al. 1972; Falconer 1960; see Harpending 1979 for recent discussion). However, this interpretation may seem in conflict with our knowledge of genetic variation in natural populations, because most species that have been studied are genetically variable at a large number of loci (see Antonovics 1976). This includes "living fossils" like the horseshoe crab (*Limulus polyphemus*); also included is the rare and highly polygynous orangutan, one of the most genetically variable primates known (see Antonovics 1976 and references therein).

West-Eberhard (1979a) offers an hypothesis that could account for this apparent inconsistency of sexual selection acting primarily on nonheritable variation and high levels of genetic variation in natural populations. The genetic variation observed may be the result of a reduction in the intensity of natural selection in the presence of strong sexual selection. If traits important in mating competition (and social competition in general) are more important than nonsocial traits in determining an individual's relative reproductive success then slight inabilities in nonsocial traits may be sheltered from selection in sexually successful individuals [e.g. the male that obtains the most matings in a mating aggregation of lovebugs (Thornhill in press d) or in certain Hawaiian *Drosophila*] In lovebugs the position of the male in the aggregation determines a male's access to females and is decided by the outcome of aggressive interactions (Thornhill in press d). The most successful male may be less fit than another male at feeding in the adult stage or at some other nonsexual task, but because of his sexual prowess

he wins the mating competition and thereby perpetuates not only his prowess but also his inadequacies which are sheltered from selection.

I now return to a discussion of alternative specializations often employed by individuals under sexual selection which, although resulting in less genetic success than winning, are attempts to obtain some reproductive success despite defeat by males or discrimination by females. The typical view is that alternative behavioral and morphological specializations are due to different genotypes (Gadgil 1972; Gadgil and Taylor 1975; Maynard Smith and Parker 1976; Alcock 1979b; Parker 1979; Cade 1979; Borgia 1979). The above discussion of sexual selection suggests an appropriate interpretation other than that of genetic differences between winners and losers in the sexual competition. The intraspecific variation in male insect behavior and morphology observed, including the examples of alternative specializations discussed earlier, could be facultative rather than genetically fixed, and responses to *phenotypic* differences between males (West-Eberhard 1979a; also see Alcock 1979a). Maynard Smith and Parker (1976) point out that certain variable behaviors may not be based on genetic differences.

It is unclear whether alternative specializations occur in genetically fixed ratios or are facultative in the sense of being situation or condition dependent. The best evidence for the former situation involves the ratio of wingless (fighting) and winged (dispersing) males in various species of fig wasps (Hamilton 1979). West-Eberhard (1979a) suggests that genetically fixed ratios of alternatives are most likely to evolve when an individual has no ability to obtain information on the appropriateness of switching between alternatives during its lifetime, or when the information would be available too late in an individual's development to allow initiation of an adaptive change. West-Eberhard (1979a) feels that the fig wasps studied by Hamilton fit these conditions.

Further, West-Eberhard (1979a) points out that the circumstances favoring a facultative (situation or condition dependent) switch, when possible, will be more desirable than a genetic switch because: 1) a "big-winner" alternative will typically exist, which will be far more profitable than any other alternative. Individuals should therefore switch to an alternative other than the most reproductive one when costs to reproduction (e.g. injury due to male-male interaction) exceed benefits associated with the most reproductive alternative; and 2) conditions favorable for switching to an alternative are dependent not only on the amount of resource available and the number of competitors present, but also on an individual's ability to conquer males and attract females relative to these abilities in other males. Thus, circumstances for a switch to an alternative will often be unpredictable.

The point at which a facultative switch becomes advantageous corresponds to that point where the benefit and cost ratios for the alternatives adopted by an individual are equal. This point may be reached during development of an immature individual or in the adult stage. Larval size may be a cue for a facultative switch to an alternative specialization. For example, this may explain small- and large-horned male beetles of the same species. One can imagine a genetic program in such cases selected to evaluate and predict future reproductive success from larval size and triggering appropriate development. If success is unpredictable from larval circumstances but only from adult experience appropriate genetic programs might direct adoption

of appropriate alternative strategies only after adulthood. In *Panorpa* scorpionflies discussed earlier winners are males that control large nuptial offerings. These males have won the male-male competition and will be preferred by females as mates because of their offering. The other males appear to be losers in the sense that they will obtain fewer matings. Access to females will depend on the quality of their nuptial offering and/or their ability at rape. The evidence suggests that the alternative behaviors that may be employed by *Panorpa* males are not dependent on genetic differences. The males appear to be facultative in their adoption of alternatives dependent on conditions experienced as adults such as the nature and extent of male-male competition and the availability of nuptial offerings (Thornhill 1979a, in press a).

I began this paper with the question: why was Darwin so convinced of the power and ultimate wide acceptance of his theory of sexual selection? Darwin was very knowledgeable about the diversity of living things and was impressed by male characteristics that did not seem to clearly relate to coping with environmental contingencies. He envisioned, therefore, a different process—sexual selection—to explain the traits that seemed neutral or negative to survival. He felt that both forms of sexual selection—male-male competition and female choice—would be stronger on males than on females and that 1 or both forms could explain even the most elaborate male features. The role of male-male competition for females as a potent form of selection has never been seriously disputed. Darwin was aware of its occurrence in many animals and, indeed, it can be observed at will in most species. However, the role of mate choice as a process leading to nonrandom differential reproduction of males is controversial and our understanding of this process is just beginning. Darwin's conviction about the power of sexual selection was soundly based in his understanding of the lack of a definite upper limit to reproductive return from traits changing under sexual selection leading to an accelerated coevolutionary race between and within sexes, a feature sexual selection does not share with natural selection. Therefore, it is useful to distinguish sexual selection from natural selection, but the former is similar in potency and operation to the broader category of social selection which defines all processes of nonrandom differential reproduction due to the social environment.

#### APPENDIX

<sup>1</sup>This paper is based on aspects of a paper by M. J. West-Eberhard (1979a) that I feel presents important ideas for entomologists investigating the sexual and social behavior of insects.

<sup>2</sup>The importance of the Process of non-random differential reproduction, so-called natural selection, as a mechanism for evolutionary change was first clearly stated by Darwin (1859) and Wallace (1889). Both of these theoreticians had similar ideas about the role of natural selection in the evolutionary process; however, Darwin's synthesis was much more complete and was published earlier. Darwin and Wallace had very different views about the role of sexual selection in evolution. Darwin defined the basic components of his theory of sexual selection in 1859 in *The Origin of Species*. The following passages were used by Darwin in 1859 to contrast natural and sexual selection and to distinguish the 2 forms of sexual selection, male combat and female choice:

"Sexual selection . . . depends, not on a struggle for existence, but on a struggle between the males for possession of the females; the result is not death to the unsuccessful competitor, but few or no offspring . . . Generally, the most vigorous males, those which are best fitted for their places in nature, will leave the most progeny. But in many cases, victory will depend not on vigour, but on having special weapons confined to the male sex . . . Amongst birds, the contest is often of a more peaceful character . . . there is the severest rivalry between the males of many species to attract by singing the females . . . and successive males display their gorgeous plumage and perform strange antics before the females, which stand by as spectators, at last choose the most attractive partner . . . It may appear childish to attribute any effect to such apparently weak means [female choice] . . . but if man can in a short time give elegant carriage and beauty to his bantams, according to *his* standard of beauty, I can see no good reason to doubt that female birds, by selecting, during thousands of generations, the most melodious or beautiful males, according to *their* standard of beauty, might produce a marked effect . . . I believe that when the males and females of any animal have the same general habits of life, but differ in structure, colour, or ornament, such differences have been mainly caused by sexual selection; that is, individual males have had, in successive generations, some slight advantage over other males, in their weapons, . . . or charms; and have transmitted these advantages to their male offspring". (p. 88-90) (emphasis added).

The main points made by Darwin in 1859 and later in 1871 are: 1) natural selection is the form of differential reproduction that leads to characters associated with survival; 2) sexual selection is the form of differential reproduction that leads to traits associated with competition for mates and may lead to an elaborateness useless with respect to survival (or contrary to survival, see Otte 1979); 3) differential reproductive success of males under sexual selection occurs because of male-male competition for females and female choice, 4) all sexual differences cannot be attributed to sexual selection alone. Ghiselin (1969), Otte (1979), and Bajema (in press) provide discussion of other points conveyed by Darwin (1871, 1874) in his original formulation of sexual selection theory.

<sup>3</sup>For the most part it appears that Darwin had firmly in mind a distinction between natural and sexual selection (see Otte 1979, West-Eberhard 1979a, Bajema in press). He was aware of their similarity in regard to causing evolutionary change by differential perpetuation and their difference in regard to the types of traits resulting from each of the 2 types of selection.

Some controversy has surrounded attempts to distinguish natural and sexual selection and the utility of such a distinction. Wallace (1889) felt that male-male competition is best considered as a form of natural selection, and he felt female choice of conspecific males was generally unimportant (except in humans; see Bajema, in press). Wallace (1889) wrote

"The term "sexual selection" must, therefore, be restricted to the direct results of male struggle and combat. This is really a form of natural selection, and is a matter of direct observation; while its results are as clearly deducible as those of any of the other modes in which selection acts. And if this restriction of the term is needful in the case of the higher animals it is much more so with the lower. In butterflies the weeding out by natural selection takes place to an enormous extent in the egg, larva, and pupa states; and perhaps not more than one in a hundred of the eggs laid produces a perfect insect which lives to breed.



Here, then, the impotence of female selection, if it exists, must be complete; for, unless the most brilliantly coloured males are those which produce the best protected eggs, larvae, and pupae, and unless the particular eggs, larvae, and pupae, which are able to survive, are those which produce the most brilliantly coloured butterflies, any choice the female might make must be completely swamped. If, on the other hand, there *is* this correlation between colour development and perfect adaptation to conditions in all stages, then this development will necessarily proceed by the agency of natural selection and the general laws which determine the production of colour and of ornamental appendages" (p. 296).

In 1927 the distinguished entomologist O. W. Richards said in his classic paper on sexual selection in insects:

"The line between Natural and Sexual Selection is not, of course, sharply marked, but some definition of their respective actions is necessary. . . . A character that has been acquired or preserved by the action of Sexual Selection must either be displayed to the other sex in courtship or used to drive away rivals" (p. 299-300).

Although Huxley (1938) doubted the role of female choice and the widespread existence of male traits contrary to survival evolved by sexual selection, he expressed a view similar to Darwin's on the distinction between natural and sexual selection. He wrote in 1963:

". . . we must differentiate between two quite distinct modes of natural selection, leading to different types of evolutionary trend which we may call survival (= natural) selection and reproductive (= sexual) selection . . . survival selection is much the more important" . . . (p. xviii).

Mayr (1972) feels that a distinction between natural and sexual selection makes sense only if one adopts the meaning of fitness used by Darwin. Fitness to Darwin meant well adapted for individual survival in the face of non-biotic environmental contingencies. An individual's ability to acquire mates through competition with other individuals was viewed by Darwin as that individual's performance under sexual selection.

Williams (1966) was one of the first to clearly place all types of selection in the broad framework of *general* nonrandom differential reproduction and thus provided a logical means of eliminating the separation between sexual and natural selection. He pointed out that all adaptations must ultimately enhance reproductive success and genetic perpetuation whether the traits are associated with individual survival or direct reproduction. (Also see Wilson 1975, Dawkins 1976, Alexander and Borgia 1979). Sexual selection is simply a form of natural selection that acts in the context of direct reproduction. All forms of selection involve nonrandom differential reproduction, but natural and sexual selection describe the process as brought about by Darwin's "hostile forces" and the sexual environment, respectively.

<sup>4</sup>West-Eberhard (1979a) has placed the topic of individual selection in a broader and more realistic framework using the concept of social selection. Social selection was outlined by Wynne-Edwards (1962) in his detailed analysis of social behavior and later discussed by Crook (1972) in work on primate social behavior (West-Eberhard, 1979a). Referring to social hierarchies, Wynne-Edwards wrote:

"Its (the hierarchy) establishment places in their own hands . . . a

powerful selective force, which can conveniently be described as *social selection*. It is similar to the one Darwin believed to apply in the more restricted field of sexual selection" . . . (p. 139).

Crook (1972) expressed the view that sexual selection is a category of social selection which is in turn a subset of natural selection. He argued that reproductive competition between individuals determines which individuals leave the most genes in successive generations and that this competition may be direct or indirect. The outcome of direct reproductive competition is determined by social interaction aimed at gaining access to essential commodities (e.g. food and mates), while winners and losers in indirect reproductive competition are not determined by interaction with other individuals. Therefore, 2 categories of natural selection can be distinguished on the basis of the nature of the reproductive competition involved: environmental (= ordinary, West-Eberhard 1979a; = natural, Darwin), and social. Social selection is defined by Crook (1972) as:

" . . . that process leading to the evolutionary enhancement of morphological, allaesthetic and behavioral characteristics that function within a social system to provide biological advantages to the individual in relation to survival prior to reproduction, the formation of zygotes and the birth and rearing to maturity of young or the progeny of close kin" (p. 269).

This definition encompasses 3 types of social selection (Crook 1972): 1) competition for resources (food, territories, oviposition sites, etc.) that are essential for individual reproductive attempts and for parental investment in offspring after a successful attempt; 2) differential reproduction in establishing and maintaining a social organization effective in nourishing and protecting offspring of the individuals involved and their close kin (selection in contexts of nepotism and non-nepotistic reciprocity), and 3) competition for access to superior mates exemplified typically through male-male interactions and female choice. Darwinian sexual selection is equal to the third type of social selection.

<sup>5</sup>Outside the social Hymenoptera there is little evidence for waiting being employed as a strategy in insects. West-Eberhard (1975, 1979b) has provided evidence that sub-dominant females employ waiting in certain social wasps. The waiting strategy is commonly used by males of polygynous vertebrates and is called bimaturism (e.g. Wilson 1975). Delayed maturity in males relative to females allows males to attain larger size before initiating competitive interactions for females and status.

Recent work on "helpers at the nest" in birds reveals that help in rearing the offspring of parents provided by younger birds allows the helpers the best opportunity at future individual reproduction. Helping behavior results in territory acquisition and future helpers for the helping individual. Helping behavior is an alternative specialization that the birds adopt in circumstances when an attempt at direct reproduction is less profitable (Ligon and Ligon 1978, Stalleup and Woolfenden 1978, Ligon in press). Similar "helpers at the nest" occur in some social wasps (West-Eberhard 1978, 1979b).

<sup>6</sup>In vertebrates alternative specializations associated with male mating strategies occur in fish, frogs and toads, birds, and mammals (see Cade 1979, Thornhill 1979a, 1979b, in press a). In these cases, dominated males employ mating tactics very different from those used by dominant males. A frequent circumstance involves dominant males possessing a territory that allows them access to females, and subordinate males, often called "satellites",

position themselves around the territory holder and intercept females attracted to the territories of dominant males. Satellite males sometimes have specialized morphology for "stealing" females attracted to dominant males. Pseudofemale morphology and/or behavior is sometimes seen under these circumstances. In 1 fish (the Gila topminnow, Constantz 1975), satellite males have long, flexible "penises", allowing them to copulate with females that are moving rapidly toward territorial males.

<sup>7</sup>Darwin (1874) wrote:

"In regard to structures acquired through ordinary or natural selection there is in most cases, as long as the conditions of life remain the same, a limit to the amount of advantageous modification in relation to certain special purposes; but in regard to structures adapted to make one male victorious over another, either in fighting or in charming the female, there is no definite limit to the amount of advantageous modification; so that as long as the proper variations arise the work of sexual selection will go on" . . . (p. 256).

<sup>8</sup>On the topic of the interaction of natural and sexual selection, Darwin wrote:

"Obscure tints have often been developed through natural selection for the sake of protection, and the acquirement through sexual selection of conspicuous colors appear to have sometime been checked from the danger thus incurred . . . natural selection will determine that . . . [secondary sexual] characters shall not be acquired by the victorious males, if they would be highly injurious, either by expending too much of their vital powers or by exposing them to any great danger. The development, however, of certain structures . . . has been carried to a wonderful extreme; and in some cases to an extreme which, as far as the general conditions of life are concerned, must be slightly injurious to the male. From this fact we learn that the advantages which favored males derive from conquering other males in battle or courtship, and thus leaving a numerous progeny, are in the long run greater than those derived from rather more perfect adaptation to their conditions of life." (1874, p. 256-7).

<sup>9</sup>Wallace (1889) wrote:

"Natural selection . . . acts perpetually and on an enormous scale in weeding out the "unfit" at every stage of existence, and preserving only those which are in all respects the very best. Each year, only a small percentage of young birds survive to take the place of the old birds which die; and the survivors will be those which are best able to maintain existence from the egg onwards, an important factor being that their parents should be well able to feed and protect them, while they themselves must in turn be equally able to feed and protect their own offspring. Now this extremely rigid action of natural selection must render any attempt to select mere ornament utterly nugatory, unless the most ornamented always coincide with "the fittest" in every other respect; while, if they do so coincide, then any selection of ornament is altogether superfluous. If the most brightly coloured and fullest plumaged males are *not* the most healthy and vigorous, have *not* the best instincts for the proper construction and concealment of the nest, and for the care and protection of the young, they are certainly not the fittest and will not survive, or be the parents of survivors . . . and as the direct evidence for

any such female selection is almost *nil*, while the objections to it are certainly weighty, there can be no longer any reason for upholding a theory which was provisionally useful in calling attention to a most curious and suggestive body of facts, but which is now no longer tenable" (p. 295).

<sup>10</sup>Fisher's model can be illustrated by a hypothetical example. One may consider the evolution of elaborate male morphology displayed in courtship in many insects, e.g., lekking Hawaiian drosophilids. Originally, a male with slightly larger than average wings may have been better at flying and escaping predators. Females preferring such males would perpetuate this advantage through their male offspring. The frequency of males with larger wings and of females with the preference would increase in frequency due to this initial preference connected with increased female fitness. As females with the preference for males with larger wings increased in frequency, females would also benefit merely because of having preferred sons. As long as the preference remained, it would increase wing size over evolutionary time, even though beyond a certain size, larger wings might interfere with the flight of a female's sons. The elaboration of wings would continue until the advantage in mating success of males with large wings was offset by the disadvantage of large wings in flight. When the net advantage in favor of a further increase in wing size no longer exists, the runaway process would stop. O'Donald (1962) developed Fisher's argument mathematically.

<sup>11</sup>The successful males may show differences in courtship behavior in comparison to unsuccessful males, but this does not mean females choose males on the basis of these differences. The fact that certain males obtain more copulations than others may be entirely unrelated to female choice, and only determined by male location in relation to female movements. A male's location may be determined entirely by male-male interaction or by chance. For example, in certain dragonflies the males that mate the most are those defending territories at the time when females arrive (Campanella and Wolf 1974).

<sup>12</sup>Females of some lekking birds may select mates on the basis of age and/or size (e.g., Wiley 1975). Howard's (1978) work on bullfrogs indicates female preference for males with suitable territories. Cronin and Sherman's (1977) and O'Donald's (1972, 1973, 1974) work indicates female choice in nonlekking birds in nature. Borgia (1979) provides good evidence for female choice in dung flies (*Scatophaga*). A few laboratory studies have been designed to observe female behavior in relation to apparently natural criteria of mate choice with interesting results (see Collias and Victoria 1978, Thornhill 1979a, in press a).

<sup>13</sup>Adaptive female choice involving male territory size may occur in the arctic skua (a bird) (O'Donald 1977). However, the lack of correlation between the number of young produced by females and indirect measurements of territory quality (e.g. male harem size) often found in the well-studied redwing black bird do not support an interpretation of adaptive female choice (see Weatherhead and Robertson 1979).

<sup>14</sup>In the great-tailed grackle, the elaborate display morphology of males apparently interferes with flight and thus contributes to the likelihood of male mortality (Selander 1972). In the fishes *Notobranchius guentheri* (Haas 1976), the three-spined stickleback (Semler 1971), and the guppy (Haskins et al. 1961), nuptial coloration, apparently preferred by females, makes males more subject to predation. Why should females prefer a mate whose son will suffer a higher likelihood of mortality? Why do not females prefer less elaborate or colorful males? Why does not natural selection favor males with less elaborate plumage and nuptial color? Fisher's theory of runaway evolution by female preference can supply an answer to these

questions: male characters evolve to elaborateness simply because they are attractive to females. However, another way to look at the matter of female preference of males with specialized behaviors and morphologies that appear contrary to male survival is that the traits may not be contrary to the survivorship of offspring (Trivers 1972, 1976; Zahavi 1975; Hailman 1977; Thornhill 1979a, manuscript).

<sup>15</sup>Again consider Hawaiian drosophilid males. Females preferring males with elaborate structures would be choosing handicapped males because these structures would interfere with other activities and increase the likelihood of predation; however, the structures would be indicators of survivorship ability despite the handicap incurred and the offspring could benefit. Males not possessing the elaborate trait might be more fit than males with it, but there is no way a female can be sure of this. The handicap possessed by a male conveys to females his true genetic quality related to survivorship.

Zahavi's theory has received considerable attention from theorists. Both verbal and mathematical genetic models have been used to analyze the conditions under which the theory might apply (Davis and O'Donald 1976; Dawkins 1976; Maynard Smith 1976, 1978; Zahavi 1977; Bell 1978; Halliday 1978; Borgia 1979; West-Eberhard 1979a). In general, these analyses indicate that the original theory will only operate under very restricted circumstances (e.g., when genes coding for the handicap are non-additive and genes for survival are additive or when the handicapping trait is non-genetic) (see Bell 1978, Halliday 1978, Maynard Smith 1978, Zahavi 1977). The major problem with the theory is that females with a preference for handicapped males will produce offspring with the handicap. According to Maynard Smith (1978), only if Fisher's runaway selection process was also operating could Zahavi's form of sexual selection be effective. Maynard Smith (1978) maintains that the theoretical conditions under which the handicap principle can be shown to operate are not plausible, but in some modified form the theory may be important. He ends the discussion of the handicap principle by saying ". . . I see little point in further discussion until it has been shown to work in at least one plausible genetic model" (p. 174). Alcock (1979b) and West-Eberhard (1979a) have pointed out that the handicap principle as originally proposed is probably valid at some level because extravagant features presumably preferred by females are handicaps in other contexts as males would be better off in terms of survival without them. Before Zahavi's theory is laid to rest, I feel it is worthwhile to test it using real animals rather than computer simulated genetic models or verbal arguments. I have attempted such a test with the scorpionfly *H. apicalis* (Thornhill in press a).

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## ALTERNATIVE MALE REPRODUCTIVE BEHAVIORS

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Male-male competition and female mating preferences are often believed to result in some males reproducing more successfully than others. The high variance in individual male reproductive success is 1 aspect of the general process of sexual selection. Although formalized by Darwin (1871) over a century ago, the past decade has witnessed an important revival of interest in sexual selection (Otte 1979). In 1 area of research, theoretical and empirical studies have shown that the males of a species may pursue very different mating behaviors. For example, some males defend territories and signal visually or acoustically for mates. Other (satellite) males also occur and sometimes intercept females enroute to the territory holder. This and other forms of intraspecific variation occur in diverse types of animals, including species from several orders of insects. Sometimes alternative male sexual behaviors pose an interesting problem for applying natural selection. If 1 behavior is more successful at acquiring mates, the alternative forms of behavior should be eliminated or kept at a low frequency in the population. My aim here is to review and discuss the evolutionary basis for the occurrence of alternative male reproductive behaviors, and give specific examples that illustrate the need for a consistent terminology for the different types of variation. I will also use the theory and categories of alternative male reproductive behavior to analyze variations in the reproductive behavior of male field crickets.

### TYPES OF MALE VARIATION

Alcock (1979) (see also Alexander 1975) outlined the general categories

