

SEXUAL SELECTION, SOCIAL COMPETITION, AND EVOLUTION*

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INTRODUCTION: RENASCENCE OF AN OLD DARWINIAN THEME

Social behavior holds a special position among natural phenomena in relation to the Darwinian theory of organic evolution. When individuals of the same species live in close proximity they compete directly for essential resources. And intraspecific reproductive competition is the cornerstone of the theory of evolution by natural selection. Thus the drama of what G. E. Hutchinson (1965) referred to as the "evolutionary play" is heightened—or at least more obvious—among members of the same social group. If only by virtue of close physical proximity social organisms compete strongly for whatever they need to survive and reproduce. And the fact that social competitors meet face-to-face adds a theatrical dimension to the evolutionary play that is absent in "ordinary" selection among organisms.

Competition by social interaction (male combat and sexual display) was singled out by Darwin for lengthy treatment, first in his "extract" (1859) *On the Origin of Species*, and then in his book (1871) *The Descent of Man in relation to Sexual Selection*, but for an interesting reason quite different from that I have just given. Far from believing that selection would be unusually strong in such situations, Darwin considered "sexual" selection among socially competing males unusually *weak* or inefficient by comparison to selection in other contexts:

Sexual selection acts in a less rigorous manner than natural selection. The latter produces its effects by the life or death at all ages of the more or less successful individuals. Death, indeed, not rarely ensues from the conflicts of rival males. But generally the less successful male merely fails to obtain a female, or obtains a retarded and less vigorous female later in the season, or, if polygamous, obtains fewer females so that they leave fewer, less vigorous, or no offspring. (Darwin, 1871, p. 583)

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Darwin thus considered these purely social aspects of sexual competition not so much a matter of life and death as "merely" a matter of differential reproduction! This may strike modern evolutionary biologists as surprising, for it seems at first reading to turn things upside down: we have come to think of *natural* selection and "fitness" in terms of differential reproduction, whether by differential survival or mating success, and would thus consider sexual selection a subset of natural selection. However, for Darwin, successful "reproduction" meant mating success, and "fitness" meant differential survival in the face of environmental contingencies.

I agree with Mayr (1972, p. 88) that "something rather important was lost" in the process of redefining fitness and erasing Darwin's distinction between these two kinds of selection—just as something is lost by stretching the concept of sexual selection in order to make it suit new purposes which, however interesting in their own right, tend to obscure what Darwin was trying to say (e.g., Ehrman's 1972, p. 106, redefinition of sexual selection as "all mechanisms which cause deviations from panmixia," or Maynard Smith's, 1978, inclusion of all selection acting differently on the two sexes). When Darwin wrote about sexual selection he focused primarily on *social competition* for mates. Under this rubric he discussed two phenomena—male combat, and courtship—both of them social interactions. And he explicitly excluded characters involved in non-social competition for mates, as witnessed by his discussion of the clasping organs of male crustaceans:

The males of many oceanic crustaceans, when adult, have their legs and antennae modified in an extraordinary manner for the prehension of the female; hence we may suspect that it is because these animals are washed about by the waves of the open sea, that they require these organs in order to propagate their kind, and if so, their development has been the result of ordinary or natural selection. . . . So again, if the chief service rendered to the male by his prehensile organs is to prevent the escape of the female before the arrival of other males, or when assaulted by them, these organs will have been perfected through sexual selection. . . . (Darwin, 1871, p. 569).

Darwin restricted his discussion of sexual selection to social competition for *mates*. Why did he not extend it to include social competition for other resources, such as food, space, and nesting materials?

The answer resides in the structure of Darwin's argument regarding evolution by selection. It is as follows: given that populations tend to increase geometrically if unchecked, and yet do not in fact do so in nature, some individuals must regularly be eliminated. And since the individuals composing populations vary, it is expected that those variants most fit for survival in the struggle for existence in the environment will predominate. This process of differential survival Darwin called "natural selection." However, he observed a number of characters which seemed useless with respect to the "struggle for existence" in the environment, including especially the secondary sexual characters of males (particularly, in man), and showed with a massive collection of examples that such characters often come into play during mating competition—either in fighting or attracting females. Darwin placed these examples apart not because they constituted a special problem for his theory (he clearly appreciated the essential similarity of natural, artificial, and sexual selection), but because he wished to point out and explain certain peculiarities of characters selected under social competition for mates, for example, variability, extravagance of form, and effects on the breeding success of females, in addition to apparent uselessness with respect to the environment.

Several recent authors have fruitfully related Darwin's theory of sexual selection to more general analyses of social competition. Crook (1972) makes sexual selection a subset of what he calls "social selection," or selection involving direct competition via social interaction. He makes the important point that social dominance can relate to resources other than mates (although, p. 265, "rank in terms of mating and rank in terms of access to other commodities do not always correlate"; see also Rowell, 1966). Crook relates the concept primarily to the evolution of the social primates. He considers social selection "undoubtedly one of the main evolutionary processes responsible for the emergence of both individual and group behavioral characteristics" (Crook, 1972, p. 264).

Ghiselin (1974, p. 135) also finds that "the whole subject (of sexual selection) needs to be reconsidered from a more comprehensive point of view" and that "comparable phenomena have been overlooked," going on to list cooperation (parental care of young), and parental exploitation as being among the phenomena comparable to male-male and female-female competition for mates. Although Ghiselin says much of interest on these subjects, he loses the train of thought initiated by Darwin regarding social competition, and ends with individual selfishness the only common theme.

By far the most thorough recent treatise on the evolutionary significance of social competition is Wynne-Edwards's monumental work on *Animal Dispersion in relation to Social Behaviour* (1962). It is remarkable as a survey of all kinds of social interaction, as a synthesis showing similarities in pattern and consequences of social competition across the animal kingdom, and as the prime target in the war against group selectionism in evolutionary biology. Now that the latter battle of extremes has subsided, it may be safe to begin a salvaging operation on Wynne-Edwards's book.

Wynne-Edwards anticipated both Crook and Ghiselin in appreciating the extended domain of the theory of sexual selection. For example, in a discussion of social hierarchy he wrote:

The hierarchy is a purely internal phenomenon arising among the members of a society, but it can nevertheless enormously affect their individual expectations of life and reproduction. Its establishment places in their own hands, therefore, a powerful selective force, which can conveniently be described as social selection. It is similar in character to the one Darwin believed to apply in the more restricted field of sexual selection. (Wynne-Edwards, 1962, p. 139)

Throughout this book, Wynne-Edwards recognizes the fundamental similarity between social competition for mates and that for other resources essential to reproduction and in limited supply. And, with reference to the broader range of social interactions, he asks the classic questions of sexual selection theory, on the nature and significance of variability in the characters concerned, on the degree to which specialization is limited by selection in other contexts, on the significance of frequency dependence, and on the degree to which signal characters are "abstractions" or are reflections of superior fitness. It would probably prove rewarding to review Wynne-Edwards's entire meticulously documented analysis, showing how what he termed "density-limiting conventions" (selfish interactions in which the monopoly of one or a few group members limits the reproductive success of others) can arise from *intra*-group competition, rather than from *inter*-group selection for regulating population density as argued by Wynne-Edwards. Williams (1966) effectively countered Wynne-Edwards's group selection approach with one based on lower levels of selection. But many of the patterns and details revealed by Wynne-Edwards's scheme have not been adequately reexamined in the light of more recent theory. There has so far been no general synthesis of the type attempted by Wynne-Edwards, to explain the diverse phenomena of social life in lower-level (genic, individual) terms (however, see Dawkins, 1974; and Alexander, 1974; likewise, Wilson, 1975, while achieving important comparative syntheses in various subareas, did not attempt a cohesive

theoretical synthesis, which he regarded as "one of the great manageable problems of biology for the next twenty or thirty years"—Wilson, 1975, p. 5).

Meanwhile, the genetic theory of sociality (especially, altruism) (Hamilton, 1964) has flourished and begun to mature as a branch of population genetics, as have evolutionary theories of sex and sexual selection (e.g., Williams, 1975; Maynard Smith, 1978; and references therein). The connection between these "twin" topics, explicit in the writings of Crook (1972), Ghiselin (1974), and Wynne-Edwards (1962), may also underlie the fact that important theoretical contributions have so often been made in both areas by the same authors, (e.g., Alexander, 1974, and Alexander and Borgia, 1978; Charlesworth, 1978, and 1977; Charnov, 1977, and 1978; Hamilton, 1964, and 1967; Maynard Smith, 1972, and 1978; and Trivers, 1974, 1972 (works on social behavior and sex, respectively).

The purpose of this essay, then, is to further extend the direct comparison of sexual and social phenomena within a modern evolutionary framework. The common theme is selection under strong intraspecific (especially, social) competition, and its special consequences: marked intrapopulational differences in reproductive success, character divergence, and ritualized interaction; and, in certain circumstances, mutual dependence, convergence of interests, and social harmony.

THE VIRTUES OF GROUP LIFE

Social competition presumes a group, or at least the temporary proximity and interaction (or comparison) of rivals. O'Donald (1977) models some hypothetical examples of sexual selection—differential mating success—without groups (involving females with different thresholds for reacting to attractive characters), but they are outside the category being discussed here. As already mentioned, Darwin also excluded the differential courtship success of solitary males from consideration under "sexual" selection, even though the fine line was sometimes hard to maintain (as it is in the case of O'Donald's example). For the moment I want to follow Darwin's line of reasoning, and eliminate preconceptions arising from other ways of viewing selection (to include non-social competition). We begin with a group containing at least two rivals.

Any consideration of severely access-limiting rivalry requires some explanation of why the rivals stay together—why sociality persists, despite the obvious disadvantages of being near a competitor. Alexander (1974) summarizes the selective bases of group living as being of three general categories, which I have slightly modified here to include a broader range of relevant resources: (1) Defense. The presence of other alert aggressive individuals may lower suscepti-

bility to predation; (2) Resource location or procurement. The food, water, or mate seeking activities of others may provide cues as to the location of a resource; or simultaneous ("cooperative") pursuit (e.g., group hunting or mate calling) may facilitate its procurement; (3) Extreme resource localization. The concentration or rarity of a commodity (such as suitable food, mates, or breeding or sleeping places) may make it unprofitable to leave a site of known quality. Parental nests and territories might be included in this category. Group life is selected if its positive effects on reproductive success in one or more of these contexts outweigh the negative effects of proximity to competitors.

Once group living has evolved, the specializations associated with sociality, e.g., division of labor, loss of characters needed for solitary survival (as, for example, in the dependent young of species having solicitous parents), or the formation of alliances with particular group members, may make it additionally unprofitable to leave groups, or to move from one group to another. But these latter reasons for staying in groups are secondary effects, not primary bases, for the evolution of group living (see Emlen and Oring, 1977). Individuals of social species having these specialized characteristics are in a sense trapped into group life, and group living may become virtually "obligatory" for them. It is in such species that the special evolutionary consequences of social competition are most clearly manifest.

THE FUNCTIONS AND HONESTY OF COMPETITIVE RITUALS AND DISPLAYS

It was Darwin (1872) who first pointed out that social competition, like artificial selection, acts as a screening process by which the most successful breeders are chosen from among interacting members of a population. This screening process is mediated by direct interaction—sometimes by overt fighting, but more often by ritualized contests and elaborate displays.

Wynne-Edwards (1962) describes many examples of social interactions, such as territoriality, dominance, and threat, in which individuals compete by "conventional" means—via displays and ritualized aggression rather than overt fighting. Low-ranking individuals often have their reproduction severely curtailed (for recent reviews see Wilson, 1975, pp. 287–290; and West-Eberhard, 1975). If one accepts the conclusion (Williams, 1966) that group-beneficial traits usually become established primarily because of their individually beneficial qualities, then "conventional competition" is seen in a different light—as a means by which individuals may assess their competitive strength relative to others without actually doing battle, in order (as we shall discuss below) to adjust

their behavior according to their own individual advantage (see Maynard Smith, 1972). Or, more simply, in social competition individuals interact until some signal from their opponent indicates that it is no longer profitable for them to do so. The appropriate turning point is set (or "programmed") by natural selection. It corresponds to the point at which further ritual escalation has proven unprofitable to individuals in that situation in the past. This may be because the individual stands to gain more either by (1) Waiting: Winning is so hopeless and/or expensive that simply waiting is likely to pay more in terms of future reproduction (see West-Eberhard, 1979); (2) Deference to kin: The opponent is a relative, and the level of harm about to be inflicted is more costly in terms of inclusive fitness than the probability of gain by winning (see Hamilton, 1971; Maynard Smith, 1972); or (3) Performance of an alternative specialization: An alternative specialization is possible which, even though less profitable than winning, is more profitable than continued conflict.

Thus individuals confined to life in groups commonly "escape" severe competition by facultatively altering their behavior, as further discussed below. Indeed, ritualized fighting makes no sense without one of these three *conditional* alternatives—waiting, deference to kin, or performance of an alternative specialization. If there is no alternative to winning individuals should fight to the death.

Threats and displays are "abstract" in the sense that certain behaviors serve as signals or symbols of potential aggressiveness or fighting strength. But displays are evidently seldom truly arbitrary in form (Barlow, 1977, and references on p. 121 therein). The interpretation of their function as competitive testing interactions depends on the existence of a strong correlation between display signals and actual disposition or ability to fight, or, in the case of female choice of mates, male quality. Ethological studies of a number of birds and fishes demonstrate such a correlation, with certain display components being associated positively with subsequent tendency to attack (Hinde, 1970, pp. 370–377). Wilson (1975, pp. 178–181) gives numerous examples of "graded displays," characterized by increasing display intensity and increasing readiness to attack. This would sometimes be difficult to demonstrate, e.g., in socially specialized species in which actual combat is very rare. But presumably the evolution of deceit, such as feigned readiness to attack, would be countered by selection for detection of deceit, because of the high cost to losers of having an essential resource monopolized by another individual. This should tend to maintain a "truthful" correspondence between display signals and actual fighting ability.

Maynard Smith (1972, p. 23) argues that deception, or "poker faced" behavior will evolve because "it will not pay an animal to reveal the exact state of its motivation, any more than it pays a negotiator to reveal at what level he will settle . . . so long as there is a motivational balance in favour of continuing a conflict, display should be continued at full intensity." Interactions may sometimes begin with "typical intensity" displays of this kind. But I would expect true competitive differences to eventually be revealed, resulting in the resolution of conflict and the establishment of rank (a winner and a loser). This interpretation is supported by the examples cited by Maynard Smith (1972, p. 24): Rivals of the swordtail, *Xiphophorus helleri*, maintain a "typical intensity" S-posture threat display "until one attacks or the other flees" (after Cullen, 1966). And displays of rival female Siamese fighting fish, *Betta splendens*, end with the surrender of one fish after several minutes of interaction without escalated fighting, near the end of which "the eventual winner could be recognized from the fact that her gill covers were erected for a larger proportion of the time." Thus the poker face breaks down during the ultimate status-determining displays.

By the argument given here one expects that deceptive mutants will be temporarily successful. The evolution of checks on deception requires some time, so that over the long course of evolution there should be oscillations between deception and truthfulness in displays. Small deceptions should persist longest. Not only are they harder to detect (Otte, 1975), but they "matter" less (are less costly) to deceived individuals, and selection for their detection and elimination must be correspondingly weak. Deception in social displays must often be immediately punished by the escalation of the truly stronger individual. Some deceptions, e.g., mimicry of females by subordinate male sticklebacks who may thereby be able to sneak some eggs or fertilizations (Otte, 1975), may persist because it would be more costly to chase or attack offenders than the commodity is worth. Others, e.g., the imitation of infant cries by aid-seeking adult monkeys (Moynihan, 1970), may cost the deceived individual nothing at all, simply serving to stimulate behavior beneficial in terms of the respondent's inclusive fitness (if a relative). These last two examples of low-cost deception in contexts *other* than ritualized competition tend to support the idea that in a high-stakes social contest deception is selected against because of the high cost of being deceived.

An argument similar to that regarding the honesty of aggressive displays should apply to the "accuracy" of female choice: the cues used by courted females to choose mates should reflect some superiority, or signal some advantage (e.g., territory quality), for the

discriminating female. Otherwise, females should simply mate unceremoniously with the first male encountered, and get on with the business of producing a brood. Advantageous female choice is known to occur in nature. For example, in monogamous arctic skuas females prefer the male color form having the largest average territory size (O'Donald, 1977). This could give females an advantage if correlated, in turn, with greater male strength, which might be reflected in higher genetic quality of the brood, or (if males participate in defense or feeding of the young) in more effective brood care.

In polygamous organisms lacking parental care or chivalrous attentions by males some authors (Maynard Smith, 1978; Williams, 1975) have maintained that the choice would have to reflect genetic superiority of mates, since the only commodities at stake are gametes. Whether or not this can be adequate to explain the evolution of female choice is currently a subject of controversy. Fisher (1930) suggested that superior courtship *per se*, if heritable, is a sufficient basis for advantageous female choice, since it would tend to raise the courtship ability (and hence the reproductive success) of the female's sons even when not associated with superior fitness in other contexts. But such a "sensory trap" (or "self-reinforcing choice," Maynard Smith, 1978) could not originate as a purely arbitrary set of signals, or the females would pay no attention. Maynard Smith (1978) suggests that it could be derived from mating behavior elaborated as an isolating mechanism during speciation. Or it might build on an established indicator of superiority, producing an "exaggeration of the truth" rather than an outright lie. For example, if a red feather were a dependable indicator of superiority, two red feathers might be a more effective signal (see Tinbergen, 1953, and O'Donald, 1977).

Analogous signal enhancement occurs in aggressive displays, a dramatic example being "automimicry," e.g., of a stag's horns by its own ears, or of canine teeth by facial color patterns (see Guthrie and Petocz, 1970). Enhanced signals such as these spread until they characterize all competing individuals, even though they are deceptions. The success of such a trick may depend on using as a "model" a character (weapon or adornment) of very great importance as a stimulus to the deceived individual compared to its importance as a deception, so that strong selection for the desired response in the original (model) context would outweigh counterselection against the signal as a deception. Obviously, once such a character has reached fixation (become universal) it can no longer affect selection, which will then simply maintain the character (eliminate mutants lacking it). Thus, ironically, the cleverest deceptions are in the

long run the most ineffective, because they most quickly become common among competitors.

Before leaving the topic of the accuracy of female choice I should mention one possible alternative explanation for the apparent coyness of females, which would put the concept of female choice in quite a different perspective, and greatly diminish the importance of all of the hypotheses just discussed. This is that females may choose males with care simply because they are afraid of them! Socially competing, threatening, potentially hyperaggressive males must be fearsome creatures for conspecific females relatively ill-equipped to fight. Indeed, it is well known that the displays of courting males often consist of two elements—an aggressive component, presumably involved in the competition with other males which they are potentially disposed to attack; and an appeasement or "sexual" component, which is apparently important in "attracting" females (or, perhaps more accurately, in assuring them that they will not be attacked) (Hinde, 1970). Thus it is possible that the "coyness" of females sometimes represents waiting for a signal that a dominant male's approach will lead to copulation rather than attack, with reluctance to mate with nearby defeated males likewise mediated by fear of aggressive reprisals by a dominant male. In accord with this interpretation, various kinds of sensory tricks appear to be involved which induce females to approach or reduce their tendency to flee, e.g., by offering food (see Wilson, 1975, p. 227), or even by imitating characteristics of predators or rivals to stimulate approach to attack (see Hailman, 1977, for numerous examples; and also Wickler, 1969; and Tinbergen, 1964, on "persuasion").

The function of displays in determining relative strength or quality may be carried one step further in the case of organisms in which competition leads to a reproductive division of labor, with defeated individuals aiding dominant ones. For self-costing aid to be profitable in terms of inclusive fitness (see Hamilton, 1964) it is not enough simply to determine relative fighting ability. The winner must likewise have a relative reproductive capacity superior enough to make helping behavior profitable to the subordinate (see West-Eberhard, 1975). In such cases selection would have to define the difference in aggressiveness sufficient to signal a profitable switch to aid-giving behavior, and the cues used (e.g., relative aggressiveness) would have to correlate with reproductive capacity. There is evidence in social wasps that such a correlation exists, and the characteristics of dominance and subordination in certain social vertebrates also suggests that this model may sometimes apply (West-Eberhard, 1975). In the polybiine wasp *Metapolybia aztecoides* workers perform a display which apparently "tests" the relative dominance of competing

queens, and appear to "choose" the queens they will help by forcing subordinant-acting individuals to work (West-Eberhard, 1978). "Worker choice" behavior under social competition in this species is thus analogous to the process of female choice believed to operate under sexual selection.

It seems reasonable to conclude that social threats and displays can serve as testing interactions in which individuals judge the relative strength of rivals and then adjust their behavior to their own benefit. Other kinds of interactions may influence the choice of alternatives (e.g., see Bekoff, 1977). But this is expected to be a major function of displays in all kinds of social competition, whether for mates under "sexual" selection, or for other resources within social groups.

THE HANDICAP PRINCIPLE

A discussion of displays as indicators of quality would be incomplete without comment on the hypothesis (Zahavi, 1975, 1977) that handicaps might evolve as concrete demonstrations to females of the superiority of individual males, the idea being that males able to survive in spite of some burdensome visible character can thereby both prove and signal their superiority over males with lesser handicaps.

In one sense any display structure is a "handicap" in other contexts. Griffin (1976) comments that the great importance of social communication is demonstrated by the immense cost of producing and displaying cumbersome structures such as the enlarged claw of the male fiddler crab, which constitutes a third or more of the adult body weight and is rarely, if ever, used except for display (Crane, 1975). Indeed, if one accepts the premise that every character costs something to produce or maintain, the tradeoff of taking on a handicap because of some overriding benefit in another is commonplace in evolution. Given the general features of social displays as testing interactions, it seems but a small step for females to use large conspicuous handicaps as indicators of phenotypic strength if they can profit from it. If abstract cues can evolve, as just discussed, why not concrete ones?

Maynard Smith (1978, pp. 171-174) argues that no plausible genetic model of the handicap principle has been proposed, excluding from plausibility models in which the handicap is non-genetic. This seems to me an extreme stance, in view of the expected and observed commonness of "conditional strategies" in social competition (above; and see next section). The line of reasoning being developed here suggests that *proportional handicaps* could develop in conjunction with variable characters (such as size) contributing to, or indicative of, individual fitness. The development of the handicap could be genetically programmed so that it is directly proportional to strength or size,

e.g., the larger the individual the larger the handicap, with the proportion adjusted so that the cost of producing and bearing the handicap is less than the benefit (in terms of increased mating success) for possessing it. Such a handicap would be genuine in that a male would be better off in other contexts without it.

This model applies best to species in which a superior male phenotype benefits the female or her offspring, but it would also screen for additive genetic fitness. If the handicap-correlated character (e.g., size) to some degree reflects genetic constitution (quality of food-getting ability, digestive system, etc.), inferior genotypes would tend to be discriminated against. One attractive feature of this proportional-handicap model from a female's point of view is that it has a built-in mechanism for maintaining the honesty of the signal (handicap). Selection would always favor a handicap load graduated according to quality (as large as possible without passing the excessive cost ratio), and this would generate a standard relationship between handicap and male quality upon which the discriminating female could depend.

A handicap trait might originate, as do most signals in animal communication, in another context (Tinbergen, 1951)—any readily perceived weighty or cumbersome appendage might do (e.g., a giraffe's neck, or a toucan's beak; Zahavi has already suggested mammalian horns). It could become a signal if females began to mate preferentially with large-appendaged males, thereby tending to produce strong and attractive sons, or broods better protected by their fathers. Only then would the handicap principle begin to operate, with males selected which happened to produce super-sized appendages—larger than would be selected in the original context alone, but without undue cost. As long as handicap variants are distinguished by females, the handicap is advantageous if it satisfies the conditions

$$H_m \propto S_m, \quad \text{and} \quad B_h > C_h,$$

in which H_m is the size of the handicap carried by male m , S_m is some parameter (size, strength, adrenaline titer) affecting mate suitability, B_h is the benefit to the male carrying handicap H in terms of increased reproductive success via enhanced mating success, and C_h is the cost of producing and bearing the handicap. S_m represents *phenotypic* superiority, and can have both heritable and non-heritable components. As I shall discuss further below, sexual selection does not always require genetic differences among males, especially if they are involved in mate protection or care of young.

The idea that non-heritable differences in male fitness are involved in certain kinds of sexual selection is not new. Fisher (1930; 1958, pp. 153-154) gives

a detailed explication of an example from Darwin (1871) in which such differences are *required*. I will argue below that low heritability is likely to play a major role in social competition in general.

"RUNAWAY" PROCESSES IN SOCIAL EVOLUTION

The much-discussed idea that sexual selection can lead to "extravagant" characters, personified by the gigantic horns of Irish elk and the male peacock's tail, originated with Darwin (1871, p. 583). This idea has stimulated two lines of thought. One is that the resulting characters could become highly detrimental to survival, even (according to some) to the point of causing the extinction of the species in question. However, many authors (Darwin, 1871, Mayr, 1972, Selander, 1972—to cite but a small sample) have pointed out that selection in other contexts will tend to limit the development of such characters just as it does any other kind when detriment in another context is less than compensated by the benefits of further specialization.

The other aspect of "extravagance"—namely, that specialization *will* continue to increase until limited by counter-selection in another context (Darwin, 1871)—seems more interesting because it does seem to represent a special quality of sexual selection (and of social competition in general). Darwin reasoned that traits enabling an organism to confront ordinary environmental contingencies (for example, low temperatures) are expected to eventually reach a degree of refinement where further improvement would yield such greatly diminished returns that selection would not produce further marked change. In the case of sexual selection, however, a change improving competitive ability is always favored (unless checked by selection in another context). Each successive improvement sets a new standard which the next can profitably surpass. This is due to the fact that conspecific rivals are an environmental contingency that can itself evolve. In that respect social evolution is comparable to the coevolution of predator-prey, parasite-host interactions (and Darwin's interpretation of extravagance would likewise help explain extreme specialization of some parasites).

The accelerating quality of evolution under sexual selection was further analysed by Fisher (1930, p. 152), who noted that in the total absence of counter-selection, modification would proceed "with ever increasing speed"—at a rate "proportional to the development already attained, which will therefore increase with time exponentially, or in geometric progression." However, this would be true of any character in the total absence of checks. The fundamental distinction is, Darwin's regarding the absence of a diminishing-return environmental limit to increased specialization of traits under sexual selection.

This "complicating effect of life on its own complexity" (Haskins, 1951, p. 121) applies to selection under social competition in general, as was first pointed out to me by N. S. Thompson (pers. comm.). Obviously, the characters most subject to runaway selection are the primary determinants of the outcome of social competition—the competitive rituals and displays discussed above. Some examples of the piling on of social complexity through intragroup rivalry in insects, especially in the oviposition rituals of stingless bees (*Meliponinae*) and honeybees (*Apis*), are discussed elsewhere (West-Eberhard, 1979). The social primates are also characterized by complex activities affecting social competition (e.g., social grooming, play, threat, and the establishment of alliances) (see Jolly, 1972), and it is tempting to speculate that the explosive evolutionary increase in protohominid brain size, which had the appearance of a "runaway" process (see Mettler, 1962), was associated with the advantage of intelligence in the maneuvering and plasticity associated with social competition in primates.

VARIATION AND HERITABILITY UNDER SOCIAL SELECTION

There are many social rituals and displays which have nothing to do with social competition among rivals. Some, like the stereotyped movements preceding "nest relief" of one member of a breeding pair by another in birds, or exchanges of signals prior to copulation, function to regulate or coordinate cooperation between the sexes (Hinde, 1970). Some have evidently evolved or been exaggerated as isolating mechanisms during speciation (see Mayr, 1966). Others, such as the waggle dance of worker honeybees, stimulate or coordinate cooperative foraging. In some of these displays (e.g., isolating mechanisms) there must be strong selection against individual variation in the performance of critical signals. In others, like the bee dance, variation in intensity of performance communicates information enabling individuals and groups to more effectively confront the environment (in this case, find food).

Clearly, the behavior resulting in role determination, or in unequal resource distribution among group members must be variable (performed unequally by different individuals.) And, as already discussed, the variations are expected to reflect real, or deeper, individual differences, e.g., in physiology, strength, or size. Barlow (1977) discusses the evidence for variation in the performance of displays, and points out that it is more common than usually realized, since studies of ritualized behavior have emphasized stereotyped characteristics.

For selection (differential reproduction) to occur among the individuals performing these displays it is not necessary that the variations be genetic in origin. Of course, this is true of natural selection in general.

Selection acts on phenotypes, and causes "evolutionary" change in gene frequencies only insofar as phenotypic variation is genetically determined. This fact is often overlooked in discussions of genetic models of sexual selection, which tend to assume a direct correspondence between genotype and phenotype (see Lewontin, 1974).

Selection of non-heritable variation takes on a special importance in social life. First, the outcome of social competition is particularly affected by such factors as vigor and size, as witnessed by the commonness with which rivals adopt postures and display characters increasing their apparent size (Darwin, 1874; Hailman, 1977). And size and vigor are, in turn, particularly subject to non-heritable variation due, for example, to individual differences in nutrition or the performance of energy-costing activities. Furthermore, one expects alleles relevant to social success to be strongly selected and to go quickly to fixation, with occasional episodes of rapid evolution following favorable mutations (see Fisher, 1930), leaving non-heritable variation as the main basis of selection in the interim (see also Williams, 1975, p. 130). We thus have a seeming paradox: the possibility of very strong (social) selection with very little evolutionary (genetic) effect. Thus Darwin's intuition regarding the "weakness" of sexual selection, and its association with the "greater variability" of the characters involved, was quite apt, in spite of his confusion of various sources and kinds of variation in this context (see Selander, 1972).

Selection within groups will proceed whether there is genetic variation or not. When social individuals cannot profitably escape a group, even though critical resources are severely limited, social competition is inevitable (except when there is a marked convergence of interests, as I shall discuss below). Eventually, either because of initial differences in competitive ability, or differences arising or exaggerated during the contest, winners and losers (haves and have-nots) are distinguished. These categories may be relative or temporary, or, as in some social insects, dramatic lifetime differences in reproductive potential. The important point is that as long as there is resource limitation and obligatory group life, and no marked convergence of interests among group members, access-limiting competition and hence selection must occur. If individual differences affecting status are few, any that exist will become critical to determining the outcome of competition; and in resource monopolies (e.g., in some social insect colonies and mating leks) very small phenotypic differences may lead to very great differences in reproductive success. In this sense social competition "seeks" differences and exaggerates their significance.

So far we have only considered the effect of social competition on *social* characters. The expected effect of social life on *non-social* characters should be just the opposite (again, except under convergence of interests). Rather than decreasing heritable variability, social life should lead to an increase in the variability of inherited non-social characters, because socially important characters take precedence over non-social traits in determining procurement success, and certain non-social procurement weaknesses are "sheltered" in socially successful individuals. Consider, for example, a cooperatively hunting society, e.g., of wolves or of wasps, in which all group members contribute to a supply of food. An individual which is a relatively slow hunter but a relatively successful social competitor can appropriate more food, and reproduce more, than a socially inferior companion better equipped to hunt. In effect, social selection is intensified, and "ordinary" selection relaxed. Like the parents of altricial birds, the group protects the weak while fostering traits enhancing social dependency and competition (see Haskins, 1951). I therefore predict that species in which social competition replaces "scramble" competition for a particular resource may often prove both less efficient and more variable in the characters associated with solitary procurement of that resource than are their solitary relatives.

It may be significant in this regard that the social wasps (Vespidae) have long been regarded by taxonomists as morphologically unspecialized and uniform compared to related solitary taxa (Ducke, 1905, 1910; Richards, 1956, 1971). In many species of social wasps reproductive competition among group members involves *behavioral* rather than morphological specializations; and the greater structural specialization and diversity of solitary species must necessarily involve characters used in non-social resource procurement and brood care. It therefore seems possible that the hypothesized priority of social over non-social procurement traits is to some degree responsible for the lack of structural specialization, and uniformity, of the social wasps.

In summary, non-heritable variation is expected to play an important role in social selection, which should proceed whenever group life is highly advantageous, resources are limited, and there is no marked convergence of interests among group members (see below). Under social selection small phenotypic differences can lead to large differences in reproductive success. And selection on non-social characters may be relaxed, increasing the dependence of social individuals on life in groups.

DIVERGENCE AND PLASTICITY UNDER SOCIAL COMPETITION

In solitary species (or the non-social characters of social species) intraspecific reproductive competition

can lead to extreme specialization, for example, teeth especially adapted for meat-eating, grazing, or browsing. In "ordinary" competition of this sort, the better the teeth the better the nutrition and hence, presumably, the greater the number or success of progeny; reproductive success is some simple direct function of quality. Thus, a cow with slightly poor teeth is expected to feed (and hence reproduce) somewhat poorly, but not to be strikingly handicapped, or sterile. Continuous variation in dentition should produce continuous variation in reproductive success.

One of the special characteristics of social competition is that continuous variation in a character affecting social status, e.g., aggressiveness or size, can have a non-linear or "stepped" effect on reproductive success, so that populations are divided into discrete classes of relatively reproductive and relatively (or completely) non-reproductive individuals, with the socially strong limiting reproduction by the socially weak.

Individuals who lose out or resign under social competition usually do not simply retire from life or sit back and watch the winners take all. They frequently adopt alternative competitive patterns, sometimes involving specialized behavior and morphology, which enable them to salvage some reproductive output even though defeated (see Wilson, 1975, pp. 290-291; West-Eberhard, 1979). Documented examples include "satellite" males which sneak copulations on the periphery of dominant-male territories or while stronger rivals are distracted, e.g., in bullfrogs (Emlen, 1976; Howard, 1979), weevils (Eberhard, ms.), bees (Alcock *et al.*, 1977), and sage grouse (Wiley, 1978); helpers among birds and many social Hymenoptera (see West-Eberhard, 1979); and the facultative females produced by competition-dependent sex change in fish (Warner *et al.*, 1975). Dimorphic males are reported in many species known or likely to engage in male-male combat, but surprisingly few of them have been investigated to ascertain the developmental basis and functions of the dimorphism (see Gadgil, 1972, 1976, and Wynne-Edwards, 1962, for examples). Such structural divergence, and even behavioral alternatives, are often assumed to be genetically fixed. And the models proposed to explain them have often been genetic, e.g., depending on frequency-dependent selection (Gadgil, 1972; for a general summary see Dawkins, 1976); heterozygote superiority (Gadgil and Taylor, 1975); selection for "mixed strategies," with the proportions of alternatives genetically fixed (Maynard Smith and Parker, 1976; Bekoff, 1977); or balancing selection in other contexts (O'Donald, 1973). However, in all of the examples specified above, alternatives are temporary, age-dependent, or otherwise known to be condition-dependent. Indeed, it seems reasonable to hypothesize

that, except in special circumstances (see below), selection under strong local intraspecific competition should favor a *facultative* (rather than genetic) switch to some alternative (secondary) means of resource procurement.

The greater desirability of a conditional switch mechanism derives from two facts taken together: (1) "primary" specializations (e.g., fighting), which enable individuals to win in social competition and control essential resources, are potentially more profitable than "secondary" alternatives. Individuals would therefore do better to alter their behavior to a less profitable or more costly alternative (e.g., sneaking) only when the primary specialization yields sufficiently diminished returns to justify a switch; and (2) favorable switch conditions are competition-dependent, not simply frequency dependent. The intensity of competition experienced by an individual depends not only on the amount of resource and numbers of competitors present, but also on the individual's prowess in social competition relative to that of others. All of these factors can fluctuate widely and independently in nature. Therefore favorable switch conditions can be irregular, unpredictable, or of long periodicity, so that a "condition blind" genetic switch to a secondary (inferior) alternative often would be likely to prove less favored by long term selection than would rigid adherence to the primary specialization.

Mathematical models of selection for conditional alternatives have been proposed by Warner *et al.* (1975) and Maynard Smith and Parker (1976). In the evolution of genetically-fixed alternatives selection acts to set the ratio of morphs (alternatives) produced. In the case of facultative alternatives the strategy or morph ratio is situation-dependent, not evolved. But the situation-sensitive, genetically programmed switch point for adopting a secondary alternative should be adjusted by selection to correspond to the "equilibrium frequency" of frequency-dependent genetic models (e.g., of Gadgil, 1972; Maynard Smith, 1974; Hamilton, 1979) (see Warner *et al.*, 1975). At the facultative switch point a secondary alternative begins to be on an average more profitable than the primary specialization, and at that point the fitness values of the two alternatives are equal.

Alternatives occurring in genetically fixed ratios are most likely when an individual has no means of assessing the appropriateness of switching between alternatives, or when an adequate assessment would come too late in development to trigger a favorable change. For example, in various species of fig wasps, males are dimorphic, having an aggressive, wingless form which is confined to live and mate inside the fig where it emerges, and an unaggressive, winged form, which leaves its natal fig and mates in figs lacking wingless males (Hamilton, 1979). Wings are evidently dis-

advantageous to the fighting morph (either costly to produce, or a hindrance while inside the fig, perhaps interfering with effective fighting). One might wish to program a male fig wasp to first test rivals within its natal fig and leave only if defeated (in fact, in the genus *Idarnes* small wingless males visit hidden galls in search of females difficult for larger males to reach, rather than fighting, thus apparently pursuing a size-associated alternative within the fig—Hamilton, 1979). But insect wings develop prior to adulthood, so a wingless fighting morph cannot benefit from a switch mechanism causing it to leave. Hamilton's observations thus illustrate a pair of alternatives (winged and wingless) which cannot be facultatively determined following social interactions because of the nature of insect ontogeny, and therefore likely to be the result of a genetic switch mechanism.

Some competition-associated structural polymorphisms are nonetheless facultative—e.g., when the outcome of social competition can be predicted from variable characters set fairly early in development. The striking morphological differences between queens and workers in many social insects are usually (if not always) non-genetic, determined by differences in larval nutrition (see Wilson, 1971, for a summary). And the small- and large-horned males of some beetles are size-associated and evidently facultative (Eberhard, ms.). In these size- or nutrition-dependent polymorphisms some cue associated with larval size, rather than ritual testing, channels individual development into an appropriate specialization (reproductive or sterile helper; fighter or non-fighting disperser). The individual is programmed to predict its future social success from its immature size, and develop accordingly.

In all of the cases of facultative alternatives mentioned so far, the affected, alternative-adopting individual is also the situation-sensitive one. There is another conceivable class of facultative switch mechanisms in which alternatives are imposed, e.g., by a parent. For example, in the termites worker development is arrested prior to maturity, and is subject to control by substances ("pheromones") present in the colony. Termite workers do not differ genetically from reproductives, and Alexander (1974) hypothesizes that this and other worker-reproductive polymorphisms in social insects could be products of parental manipulation. This would involve two switch mechanisms: one, in the parents, determining the ratio of morphs produced; and another in the offspring, responsive to (and perhaps resisting) manipulation. In effect, manipulated offspring, like small-horned beetles, are individuals which have lost out in social competition at an early age.

The importance of facultative alternatives in social life cannot be overemphasized. As mentioned above,

if an individual has no alternative means of reproduction following social defeat, it should fight to the death. The rarity of this occurring among social animals is mentioned over and over in the ethological literature. Yet mortal combat does occur in nature—in cases which seem to confirm the association of ritual combat and facultative alternatives. Wilson (1975) gives several examples, and (p. 247) remarks upon how often such behavior becomes apparent "only when the observation time devoted to a species passes the thousand-hour mark." This accords with the expectation of occasional strong overt aggression even in species having highly ritualized combat, since, as already shown, signaled escalation should indicate a real willingness to fight. It is not surprising that tests of such willingness among rivals sometimes lead to serious injury, especially in predators equipped to kill (e.g., lions, Schaller, 1972; and hyenas, Kruuk, 1972). Hamilton (1979) gives some particularly illuminating examples from his studies of fig wasps. Wingless males of the genus *Idarnes* regularly engage in mortal combat within the fig where they are born, and from which they cannot escape—they have no alternative but to mate with the females in that fig. In another genus (*Blastophaga*) wingless males do not fight, and Hamilton gives sex-ratio and behavioral data indicating that competing males are likely to be relatives. These examples seem to support the rules of (1) honesty in rituals and displays, and (2) facultative alternatives following ritual defeat (and its corollary: mortal combat when no alternative is available). There should be a general tendency for a strong direct correlation between degree of ritualization and effectiveness of alternative strategies in nature. That is, the more productive the (secondary) alternative pursued by socially defeated individuals, the more ritualized the contest preceding its adoption (the lower the incidence of injury and death). This correlation may sometimes be confounded with that expected between relatedness and aggressive restraint (Hamilton, 1979).

In spite of its difficulty, the question of the evolutionary and developmental basis for individual differences in social role is among the most important to understanding social organization. Explaining the existence of altruism and mutual aid are really sub-questions in the larger endeavor to explain behavioral diversity within societies.

THE RULE OF MUTUALLY EXCLUSIVE SPECIALIZATIONS AND "DIVISIONS OF LABOR": THE EVOLUTION OF MUTUAL DEPENDENCE AND INTEGRATION

Under social competition some individuals prove better endowed than others for the "primary" specialization leading to social success; and those at the other

end of the scale are the ones likely to adopt an alternative specialization. Suppose that the primary specialization (e.g., actual or ritual fighting) is best performed by large individuals. Then the ideal alternative would be something (such as sneaking) particularly well performed by small individuals, and poorly suited to large ones. By adopting an "opposite" or antagonistic alternative an individual in effect alters the contest so that he or she can win.

Once two such mutually exclusive alternatives have evolved intermediates are at a disadvantage (e.g., relative to extremely large or small individuals), and disruptive selection should cause the two classes to further diverge—if not in the originally determining character (e.g., size), then in the development of associated specializations, leading to a bimodal distribution of types. (In the case of facultative polymorphisms, this would mean the evolution of an increasingly clear-cut switch mechanism during development.)

If mutually exclusive alternatives happen to involve different *essential* tasks, then divergence may lead to mutual dependence and obligatory association among competitors. Thus the "divisions of labor" so often cited as a product of cooperation and a source of group efficiency can be competitive in origin, a product of character divergence and task specialization among competing members of a population (see West-Eberhard, 1979).

Hertwig (1909, after Ghiselin, 1975, pp. 100–101) recognized the significance of opposite, or "interfering" specializations in the origin of the division of labor between the sexes. However, Ghiselin notes that Hertwig did not explain how selection might act to produce this difference, and finds it difficult to discern what was the original advantage to the difference in motility. Male-female gamete dimorphism ("anisogamy") could have originated as character divergence under strong competition according to the general pattern just outlined. Even in an "isogamous" population of like gametes, individual differences in endowment or energy-expenditure would lead to inequalities in size and motility among gametes. As Ghiselin (1974) points out, it would be developmentally advantageous to pair with a large cell, and so selection would first produce specialization in motility and seeking behavior (perhaps accompanied by a tendency to selectively unite with relatively large cells), with the smaller cells pairing most advantageously. The less successfully motile larger cells might then specialize in nutritive functions enhancing not only their capacity for development, but also their ability to attract and capture a motile cell as a mate. And intermediate-size cells, at a disadvantage in both roles, would be eliminated by disruptive selection leading to "sexually" differentiated gametes. This hypothesis is given in mathematical form by Parker *et al.*

(1972). Although the same argument applies whether the two kinds of gametes are produced by the same (hermaphrodite) or different (sexual) individuals, it is easy to see how separation of the sexes might follow due to the advantageousness of a gamete-producing individual being able to support the efforts of its gametes by specializing in one of their reproductive functions (either motility or nutrition). Thus the varied adaptations having to do with the "division of labor" between the sexes in courtship, parental care, and social life may have originated as character divergence according to the rule of opposite (mutually exclusive) specializations under strong competition.

The extreme, mutually exclusive specializations of the two sexes at these two levels—gametic and organismic—must contribute greatly to the maintenance of sexual reproduction, even when non-meiotic parthenogenesis would be genetically more profitable (see Williams, 1975; Maynard Smith, 1978). The original division of labor between somatic and germ cells would be increasingly exaggerated (and hence presumably less easily reversed) in sexual organisms. The somatic cells become highly specialized to different somatic functions, losing the capacity to give rise to the variety of cells required for the production of a multicellular organism; and the sex cells and their parent individuals become highly specialized to a reproductive process requiring meiosis, fertilization, and mutual stimulation (e.g., of egg by sperm) (see Williams, 1975, p. 104). It may therefore be very difficult to "escape" sex and the "cost of meiosis" (Williams, 1975) because of the difficulty of overcoming the limits of specialization sufficiently to give rise parthenogenetically to a new individual (Williams, 1975). Maynard Smith (1972, p. 123) once concluded that "long-term selection acts, not by eliminating parthenogenetic varieties when they arise, but by favouring genetic and developmental mechanisms which cannot readily mutate to give a parthenogenetic variety. It is not clear how this has been achieved." The rule of mutually exclusive specializations seems to hold an answer which has not been sufficiently appreciated in discussions of the maintenance of sexual reproduction. By contrast, this phenomenon has long been recognized as a source of social cohesion in insects (Haskins, 1951) and in man (Durkheim, 1893). I discuss its application to the evolution of insect sociality elsewhere (West-Eberhard, 1979).

Ghiselin (1974, p. 234) distinguishes between "competitive" divisions of labor (like that between artisans or firms) and "cooperative" divisions of labor (like those between members of a firm), thus raising the question of what unit of selection is relevant in producing a given division of labor. A division of labor could begin as a product of competition among individuals (or some lower level competing entities) and then be elaborated as a result of competition

among groups (higher level entities). How this could happen is clear from contemplating insect societies of different degrees of social integration. In "primitively" social species associated individuals compete directly, and adult specializations (e.g., to egg-laying, or foraging) are flexible. Individual reproductive success relative to conspecifics depends on both individual traits and (to a variable but lesser degree) the success of the group as a whole. However, in socially more "specialized" species, in which group life is obligatory and social role determined prior to adulthood, there is little or no intragroup competition or reproduction outside the group, and colony integration approaches that of a multicellular organism. Colonial associations can reach this degree of integration either via (1) increased genetic homogeneity (genetic convergence of interests), (2) increased efficiency of suppression and control of reproductive competitors (imposed convergence of interests), and/or (3) increased mutual dependence due to a common dependence on the presence of other group members, or mutually exclusive task specialization (mutualistic convergence of interests). These mechanisms are illustrated by the most highly integrated insect societies, which characteristically have only one, long-lived egg-layer (a high degree of genetic uniformity), highly developed pheromonal suppression of egg-laying by competitors (imposed convergence of interests), and highly specialized morphological castes (mutualistic convergence of interests due to task specialization) (see Wilson, 1971, for examples).

Thus the evolution of higher levels of social integration can be an "emergent" result of selection on competing individuals. As stated in more general terms by Alexander and Borgia (1977, pp. 469-470), "To the extent that natural selection has produced coalitions of genetic units or individuals, whose numbers and cooperative interactions toward common interests enable them to deny success to subunits with conflicting interests or abilities to reproduce differentially, the coalitions themselves may be properly described as the units of selection."

In summary, intraspecific competition can lead to intraspecific character divergence. And when different classes of individuals develop opposite, or mutually exclusive specializations to essential tasks they may become mutually dependent and cooperative. By this means virtually irreversible cohesion and harmony can arise from extreme competition, in the evolution of both sex and sociality.

CONCLUSION AND PROPHECY

The books cited in the introduction, by Darwin, Wynne-Edwards, and Ghiselin, are all "inspired" works. They were all written with a sense of major synthesis, a feeling that some important pieces had finally fallen into place for the first time. Darwin's genius and care—and perhaps luck—were such that

he managed to avoid fatal errors, of the kind that cause a critic to abandon the main argument and (albeit sometimes unfairly) throw out the whole thing, lesser insights and inspirations included.

I believe that in all three cases the excitement was justified—that it came from being on the (same) right track until, in the cases of Wynne-Edwards and Ghiselin, getting seriously derailed, especially by failure to fully appreciate the significance of intra-group conflicts of interest.

All of these authors saw that major insights can result from attempting to generalize about the significance of social competition in a wide range of circumstances. Dawkins (1976, p. 90) evidently sensed the same thing when he wrote that we may come to look back on the invention of game theoretic analyses of social conflict as "one of the most important advances in evolutionary theory since Darwin" because it shows "how a collection of independent selfish entities can come to resemble a single organized whole."

As Wilson (1975) has foreseen, a major synthesis regarding social behavior and natural selection is in the making. I believe, and the intuitions of earlier authors confirm, that it will develop along the lines crudely sketched in this essay. The main theme is competition within groups, and its special consequences: competitive rituals and displays, "runaway" specialization in traits contributing to social success, intraspecific character divergence (the evolution of alternative strategies), mutually exclusive specializations, divisions of labor, mutual dependence, and social integration.

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