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ABSTRACT

Rapid divergence and speciation can occur between populations with or without ecological differences under selection for success in intraspecific social competition—competition in which an individual must win in contests or comparisons with conspecific rivals in order to gain access to some resource, including (under sexual selection) mates. Sexual selection theory is extended to encompass social competition for resources other than mates. Characters used in social competition can undergo particularly rapid and divergent evolution owing to (1) their great importance in determining access to critical resources, (2) the absence of a limit to change (except by selection in other contexts), (3) the generation-to-generation relentlessness of selection on these traits, (4) the potential for mutually accelerating evolution of preference and attractiveness in contests involving "choice," and (5) the very large number of factors that can initiate trends, including mutation and drift leading to use of different physiological or behavioral characteristics as signals, the role of novelty per se in the evolution of combat and display, ecological or habitat differences influencing the form of combat and of signals, and (in species capable of learning) imitation of idiosyncratic characteristics of successful individuals. Many species-specific signals heretofore attributed to selection for species recognition ("isolating mechanisms") are probably instead products of social selection. This may help explain the rarity of reproductive character displacement and other phenomena predicted by the species recognition hypothesis. Examples from a wide variety of organisms illustrate patterns predicted by social selection theory, including (1) exaggeration and rapid divergence of traits (e.g., weapons, pheromones, plumage, flowers, and song) used in social competition, (2) a correlation between type of social system (intensity of social selection) and distinctiveness and exaggeration of social traits, (3) sexually monomorphic extreme development of socially selected traits when both sexes compete socially, (4) occurrence of distinctive signals in allopatric populations lacking sympatric congeners, and (5) more rapid divergence (less phylogenetic conservatism) of socially competitive compared to non-competitive signals. Rapid divergence under social selection may accelerate speciation due to effects on pre-mating interactions, as well as on critical social determinants of survival and reproductive success which would put hybrids at a disadvantage. Maintenance of parapatric boundaries (extensive contact with little or no geographic overlap) between socially selected species may sometimes be due to competitive exclusion in sympatry between populations whose primary divergence has been social rather than ecological. Patterns of variation in socially selected characters demonstrate the wisdom of Darwin's distinction between natural and sexual selection, and the applicability of sexual selection theory to social competition in general.

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INTRODUCTION

EXPLAINING THE diversity of life is among the most ancient and persistent puzzles of philosophy and biology, and the one that inspired Darwin's *The Origin of Species*. A scientific understanding of organic diversity means understanding the multiplication of forms during the long history of life on earth. And this requires understanding the process by which new species originate—the process of "speciation."

Present-day discussions of speciation emphasize the importance of ecology in the origin of species. According to the most widely accepted theory of speciation (Mayr, 1963; see Lewontin, 1974), allopatric or geographically isolated populations initially diverge largely under selection for adaptation to the different environments in which they are found. Then if ecological divergence is sufficiently great, hybrids are at a disadvantage where the populations come into contact. Pre-mating "isolating mechanisms"—species-specific signals and courtship behavior that prevent mating between individuals of incompatible, or differently adapted, lineages—evolve either as an incidental by-product of the genetic divergence and reorganization of isolated populations (see Mayr, 1963, p. 551), or by selection against hybrids in zones of sympatry (e.g., see Fisher, 1930; Dobzhansky, 1940). Thus isolating mechanisms have been seen largely as, ultimately, products of ecological divergence. Ecological divergence plays a key role in all current theories of speciation. Theories differ over whether divergence occurs in geographic isolation, at different positions along a cline (Endler, 1977), or in different subdivisions (habitats) of the same locality (Bush, 1975). But they agree in describing the critical divergence as ecological: "The geographic variation of species is the inevitable consequence of the geographic variation of the environment" (Mayr, 1963, p. 311; see also Endler, 1977, p. 7, and his citations of Huxley, Dobzhansky, and Grant).

An outstanding exception to the rule of describing virtually all divergence in ecological terms is provided by Darwin's writings on speciation. Darwin (1859, 1871) showed how non-ecological selection, or "sexual selection"—competition for mates involving male combat or female choice—could be an important cause of the divergence characterizing new varieties and species. He argued extensively and explicitly that variation distinguishing subspecies and "allied" (closely related, recently diverged) species very commonly involves variation in sexually selected characters. Indeed, he devoted a book (Darwin, 1871) to showing that racial (subspecific) divergence in man has occurred primarily under sexual selection, and in order to substantiate this he cited massive evidence that the same was true in a wide variety of other organisms, including crustaceans, insects, fish, birds, reptiles, and mammals.

For various reasons (discussed by Ghiselin, 1974; O'Donald, 1977, 1980; Otte, 1979; Mayr, 1982a, p. 595 ff.), this prominent aspect of Darwin's theory of speciation was subsequently ignored. The Forgotten Era of sexual selection theory began in the 1930s when mathematical geneticists redefined fitness as a change in gene frequency, and thus emphasized the similarities of, rather than the differences between, natural and sexual selection (see Mayr, 1972); and when Huxley (1938) suggested that the term sexual selection be eliminated and the phenomena viewed as similar by Darwin be given diverse other explanations, including some based on "general" (that is, species) benefit (Huxley, 1938, p. 431). It ended in the 1970s (see especially Campbell, 1972) with the resurgence of interest in the evolutionary consequences of intraspecific competition (Williams, 1966). Ironically, the Forgotten Era of sexual selection theory coincided with the Golden Era of neoDarwinian speciation theory (highlighted by the contributions of Dobzhansky, 1937; Mayr, 1942, 1963; Simpson, 1944; Stebbins, 1950; and others), with the result that sexual selection theory, although occasionally mentioned (e.g., Mayr, 1963, pp. 199–201), played no important role in the formation of modern ideas about speciation. This is patricularly ironic since the principles most emphasized, and most solidly established, by this era of thought about speciation included the importance of geographic isolation in promoting divergence (Mayr, 1963), and the importance of courtship and pre-mating signal divergence in effecting reproductive isolation (Alexander, 1962). Sexually selected characters provide particularly dramatic evidence of both phenomena: as Darwin (1871) showed, divergence of sexually selected traits "useless" in the struggle for existence explains much of the geographic variation associated with race formation and the origin of species. And the signals and morphology involved in courtship are among the principal kinds of traits he so extensively cited.

Recent advances in evolutionary theory and the study of behavior have led to a renewed awareness that sexual selection is real and important in the lives of animals (e.g., see Campbell, 1972; Blum and Blum, 1979; Lloyd, 1979–81; Mayr, 1982a). Many authors (e.g., Hoenigsberg, de Navas, and Chejne, 1964; Spieth, 1974; Ringo, 1977; Carson, 1978; Alexander and Borgia, 1979; Lloyd, 1979; Thornhill, 1980; Lande, 1981, 1982; Thornhill and Alcock, in press) have mentioned the likelihood that sexual selection affects or accelerates speciation, or has led to unusual species diversity in particular groups. Nevertheless, there has been no new attempt at a general synthesis broadly relating sexual selection theory to speciation theory, and exploring the degree to which its predictions regarding divergence are upheld in nature (but see Thornhill and Alcock, in press). Probably many biologists would echo the questions raised by a recent critique (Templeton, 1979) of a sexual-selection explanation of speciation in Hawaiian *Drosophila:* Why would intrasexual selection favor intraspecific *variants* in courtship display? How can deviations from the norm be selected if accurate species recognition is at a premium. Is the special role of sexual selection in speciation confined to its effects on the evolution of species recognition and mate preference? And if not, why are the interspecific variants observed apparently "arbitrary" with respect to the environment? "Why, for instance, in one isolated population of bellbirds should the males develop three long bare wattles, . . . in another population a single wattle studded with small feathers, in another a beard consisting of a mass of stringy wattles on the throat, and in another a bare throat of colored skin?" (Snow, 1976, p. 88). And why the seemingly erratic and complex variation in horns of beetles with similar life histories and habitats (Howden, pers. commun.; see Howden, 1979)?

This paper begins to answer such questions by outlining the special features of sexual selection (and social competition in general) expected to accelerate divergence between isolated populations. It then discusses evidence that striking "non-ecological" divergence has occurred in a variety of organisms that compete socially for mates and other resources, and discusses the relevance of this to current ideas about speciation and the evolution of species-specific signals.

SOCIAL COMPETITION AND DIVERGENCE: THEORY

When Darwin (1871) distinguished between natural selection and sexual selection he referred to the difference between characters involved in the "struggle for existence" in the environment, and those concerned with competition among conspecific individuals for mates. He illustrated this distinction by comparing the natural-selection and sexual-selection functions of male prehensile organs. If, as in the case of some oceanic crustaceans, males have such organs in order to maintain a grasp on a female while being washed about by the waves of the sea, then their development has been the result of "ordinary or natural selection." But "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, that is, by the advantage acquired by certain individuals over their rivals" (Darwin, 1871, p. 569). Sexually selected characters, then, are molded to confront or surpass conspecific rivals rather than to deal with other aspects of the environment.

The special characteristics of sexual selection discussed by Darwin apply as well to social competition for resources other than mates. For this reason several authors (Wynne-Edwards, 1962; Crook, 1972; West-Eberhard, 1979) have attempted to generalize regarding selection under "social competition"—competition in which an individual must win in interactions or comparisons with conspecific rivals in order to gain access to some resource. The contested resources may include food, hibernation space, nesting material, mates, or a place to spend the night. Seen in this broader perspective, *sexual selection* refers to the subset of social competition in which the resource at stake is mates. And *social selection* is differential reproductive success (ultimately, differential gene replication) due to differential success in social competition, whatever the resource at stake.

In solitary species, or in the solitary stages of a life cycle, success depends primarily on the adequacy of characteristics enabling an individual to deal with environmental contingencies — success under what Darwin called natural selection. The expected result is evolutionary progress in non-social behavior and morphology — traits associated with feeding, hunting, defense against parasites and predators, and battling the elements. In certain circumstances, however (e.g., under ecological circumstances favoring aggregation or group life — see Alexander, 1974; Emlen and Oring, 1977), conspecific competitors may stand between the individual and one or more essential resource. Then social interactions can act as a screening process determining access to vital commodities. This can involve (1) a race (see Ghiselin, 1974; Parker, 1978; Lloyd, 1979); (2) the testing of a series of competitors in different places, as by a female Indigobird (Payne and Payne, 1977) or hammer-headed bat (Bradbury, 1977) visiting a number of displaying males in succession; or (3) a contest within a group. Whatever the forms of social competition, the morphology and behavior involved in battles, threats, and attractive or stimulatory display are expected to often show (1) rapid and extended evolution leading to exaggerated forms, and (2) a diversity of forms in different populations (Darwin, 1871). That is, there should be evidence of rapid divergence of socially selected traits when related populations (e.g., subspecies and species) are compared. The accelerating and diversifying causes of rapid divergence are discussed separately below.

Causes of Rapid and Prolonged Evolution under Social Selection

Strength of Social Selection

In species and life stages in which group living is obligatory or highly advantageous, one or a few socially dominant individuals may monopolize essential resources, severely limiting the survival or reproductive success of others, in some extreme cases even permanently sterilizing them (West-Eberhard, 1981). In such high-stakes social competition, social characters are critical determinants of survival and reproductive success: an individual superior in other respects may have its reproduction severely curtailed if unable to win in social contests. When this is true, social characters — the weapons used in fighting, and the signals used in ritualized combat and competitive display — should evolve rapidly, for they are under especially strong selection (slight variations in these characters are associated with great variance in reproductive success — see Warner, Robertson, and Leigh, 1975, for a well-analyzed example).

Unending Nature of Change

Another factor contributing to the exaggeration of social traits is the absence of a ceiling or limit to change, except by selection in other contexts. This property of sexual selection was noted by Darwin (1871), and it applies to the evolution of all socially competitive traits as well as to certain interspecific interactions (e.g., coevolved interactions of hosts and parasites, or predators and prey). As long as the interacting elements (e.g., competitive behavior or morphology of conspecifics) are mutually capable of evolutionary change or improvement, such change will continue in what has been called an unending evolutionary race. New traits keep leading to further competitive innovations until exaggerated characters are finally checked by some disadvantageous consequence (e.g., antlers grow so large as to hinder movement excessively, or the cost of their production outweighs their advantage). By contrast, change in ordinary or ecological characters — those responding to unchanging aspects of the physical environment, or organic aspects either not evolving or evolving very slowly in response to the adaptations in question—can approach a ceiling of perfection (optimum). Divergence in such characters in closely related species is therefore expected to be more limited than divergence in social traits.

Constancy of Social Selection

The generation-to-generation constancy of social competition makes social evolution an unusually relentless coevolutionary race. A particular parasite or predator may attack only a limited percentage of the individuals of a host or prey species, and may be able to switch to an alternative species if a primary host or food organism becomes rare or evolves an effective defense. But under intraspecific social competition every reproducing individual of every generation is involved in the same increasingly specialized unending contest, as long as the framework conducive to such competition (e.g., life in groups) persists. This constancy in the action of social selection should augment the amount of evolutionary change accumulated over time, even in species under weak social selection (species in which there is little variance in reproductive success associated with winning and losing—see Wade and Arnold, 1980; or species in which there is only low or transitory heritable variation in competitive ability).

Accelerating Effect of Novelty

The very nature of the functions—attraction, and combat—served by socially selected characters may sometimes put a premium on novelty per se (Darwin, 1871; Moynihan, 1975), and this may considerably increase the rate of evolution of weapons and display. In the evolution of weapons, a small change in behavior or morphology could prove decisive, owing in part to the lack of a countermeasure in opponents; and the very distinctiveness and conspicuousness of a novel signal might be advantageous in display (Armstrong, 1965, p. 251, 305). Hinde (1970) has discussed the role of novelty in the evolution of display and described its possible physiological basis. Perhaps the best demonstration of the advantage of sheer novelty under sexual selection is the rare-male phenomenon in *Drosophila* (see Ehrman, 1972, and references therein). The fact that flooding experimental mating chambers with odors and other cues produced by rare-type males eliminates the females' preference for them indicates that rareness per se is indeed selected (cf. an alternative interpretation involving female polymorphism for constant preferences—O'Donald, 1977). Although this frequency-dependent advantage would decline with the evolution of countermeasures (in the case of weapons) or with its increasing commonness (in the case of displays), its effect on the initial spread of innovations might be an important factor accelerating the overall rate at which the coevolutionary race proceeds, as well as in changing the focus of selection and, hence, the direction of evolution.

The Potential for Runaway Change

The only major insight regarding the special nature of social competition not mentioned by Darwin himself was contributed by Fisher (1930). Fisher pointed out that selection under female choice differs from that involving real or ritualized male combat in that there is the potential for a "runaway" process—rapid evolutionary exaggeration of competitive signals not constrained to reflect true superiority of their bearers (other than in the ability to signal per se). This would occur because any true indicator of superiority that is used by females in mate selection soon becomes an advantage in itself, due to the increased attractiveness of its bearers. Males showing the most developed expression of such traits are more successful at obtaining mates, and females mating with them gain an advantage through the greater attractiveness and mating success of their sons. [In male-male combat, on the other hand, selection on contestants to call the bluff of dishonest signallers should eventually limit the evolution of signals not indicating a true underlying ability or willingness to fight (see Zahavi, 1977; West-Eberhard, 1979). The latter paper errs in not making this distinction.] Fisher reasoned that runaway selection could lead to striking genetically correlated increases in the discriminatory powers of females and the exaggeration of signal characters of males, which would change "geometrically" in proportion to the development already achieved, until limited by (natural) selection in some other context (cf. O'Donald, 1980).

There is a potential for mutually accelerating selection for attractiveness and choice whenever one class of individuals is in a position to choose the winners among those competing. For example, in some social insects (e.g., honeybees and certain social wasps and ants) workers systematically persecute or kill all but one of several queens, or choose which of several to join in founding a new colony (Michener, 1974; West-Eberhard, 1978). Thus, there could be mutually reinforcing selection on the characters used to discriminate winner from loser queens, as well as on the workers' ability to distinguish them. Extremely attractive (to workers) queens would produce attractive daughter queens and thus yield a larger indirect genetic payoff to workers investing in their colonies (social traits of workers can be regarded as selected indirectly in relation to their effects on the reproductive success of genetically related queens). In this case a genetic correlation of genes for attractiveness and preference could develop not as a result of assortative mating, as in the case of sexual selection (see Lande, 1981), but as a result of the close genetic relatedness of colony members (West-Eberhard, 1973, 1978): male and female sexual offspring of attractive queens attended by discriminating workers are likely to carry genes for both attractiveness and choice. Such selection might affect characters like the "piping" and pheromone signals of honeybee queens (Michener, 1974) and the ritualized (and probably also pheromonal) dominance behavior of certain wasps (West-Eberhard, 1978, 1979, in press; Forsyth, 1980). The characters chosen as signals could initially be traits indicating reproductive superiority (robustness or egg-laying capacity), and then become elaborated under selection for signal effectiveness per se. Worker choice of queens might be importantly limited by the great significance of testing for the phenotypic quality of queens: there may be a great deal of variation in quality (especially, egg-laying capacity) among potential queens at the time of worker choice. Thus worker choice, like mate choice in species with large post-mating male investment in reproduction, should give relatively great weight to true indicators of *phenotypically* superior individuals, which would retard the evolution of signals (e.g., products of runaway selection) not truly indicative of quality. Worker choice might also sometimes be limited by the advantage to workers of favoring the queens most closely related to them—a not inconceivable possibility in light of recent research on social insects (Greenberg, 1979; the references in West-Eberhard, in press). This tendency, however, would also increase the genetic correlation of preference and attractiveness.

Parents are also frequently in a position to exercise favoritism, or parental choice, in treatment of their offspring; and offspring compete strenuously for parental attention, sometimes employing highly specialized and exaggerated signals, like the huge (and sometimes elaborately marked) gaping mouths of nestling birds (see Welty, 1962; Skutch, 1976), or the "hunger signals" of larval hornets (Ishay and Brown, 1975). Such characters could originate as releasers or guides of parental feeding behavior (Skutch, 1976), or even indicators of true superiority, then become elaborated under mutually reinforcing selection; since offspring of successful signallers would in turn be parentally favored, there would be a premium on the ability of parents to distinguish and favor them. Again, a genetic correlation of characters enhancing attractiveness and preference would develop due to genetic relatedness of interactants. And such a process would be checked eventually by natural selection against bearers of extreme characters, and by the advantage of parental genes contributing to the detection of phenotypically superior offspring (those most likely to be superior propagators of genes like the parent's).

The importance, in nature, of runaway selection like that visualized by Fisher (1930; see also Lande, 1981, 1982) is currently controversial (see Thornhill and Alcock, in press; Bradbury and Gibson, in press). Runaway selection can occur in only a limited subset of the characters under social selection, namely, some (but not all, see below) characters subject to choice. It can be arrested or slowed by two kinds of disadvantage: that to the survival ability of individuals producing and bearing an extreme trait; and that to individuals choosing superior signallers if the most desirable (genotypically or phenotypically, if the male aids the female) mates in the population cannot be identified by this means. That is, if male superiority in some other context is greater than that accruing to producers of a particularly extreme signal, then female attention to additional indicators of quality may reduce the consistency of a preference for the extreme signal. Recent studies indicate that this latter limit to runaway selection may be more important than heretofore appreciated. Theoretical consideration of the possible importance of resistance to parasites and disease as a basis for mate choice (Hamilton and Zuk, 1982) shows how true indicators of genetic quality in traits other than signalling ability can be important, even in polygynous species in which the male contributes nothing to the female other than genetic material. And experiments on female choice in frogs (Ryan, 1980) and crickets (Forrest, 1982) indicate use of a cue (call frequency) closely associated with a complexly determined phenotypic trait (size) that could serve as an index of general (genetic) superiority without being easily subject to runaway change. [Perhaps selection favors use of such generalized indicators of male superiority between what Fisher predicted would be relatively short-lived episodes of (eventually disadvantageous) runaway evolution.] Furthermore, female choice may sometimes prove to be indirect, as when females show a mating preference for the males who win in contests with other males (see Payne, in press), with females sometimes even inciting competition among males (see Thornhill and Alcock, in press). Under indirect female choice (called "passive selection" by Lloyd, 1979) males may produce spectacular male-male competitive signals, and females would exercise preference, but a runaway process would not occur, for the male characters (and the female preference) would be subject to the checks on bluff thought to characterize the evolution of male-male combat (see Borgia, 1979; West-Eberhard, 1979). Thornhill and Alcock (in press) provide examples demonstrating the importance of caution in attributing even greatly exaggerated sexually selected characters to Fisherian runaway selection.

Diversifying Factors

All of the factors discussed so far would contribute to rapid or continuing evolution of socially selected traits once a particular trend had started. But what determines the *direction* of evolution of social traits, and hence their diversity? Why should one expect not only exaggeration but also *variety* in the kinds of beetle horns and in the plumage and competitive displays of birds?

Unending Nature of Change

The lack of an optimum solution, or limit to change, under social selection means not only long-continued change, but also that a large variety of directions are possible. In the evolution of combat and display, a great diversity of novelties can serve as the basis for a whole new line of development (can be a strategic breakthrough). This applies not only to progress in the evolution of weapons, countermeasures, and enhanced display, but also to improvements in the sensing, or monitoring, ability of choosing and (in combat) contesting individuals. Sensory innovations are another source of new directions in the evolution of social behavior and communication. A great variety of characteristics constitute potential signals, given the ability to recognize them. As ethologists have long realized, social signals are often derived from movements or changes in color, posture, or odor, indicating motivational state or intention (see Hinde, 1970). And a large variety of cues—size, color, activity level, and numerous, more specific attributes—can serve to indicate the quality of competitors. For example, Hamilton and Zuk (1982) list detectable signs of infection and corresponding male displays that may be used by females to judge the level of resistence achieved by prospective mates; and courting and fighting males frequently perform complex and difficult feats which might be used to evaluate their quality (see Thornhill and Alcock, in press; and discussion below). A theoretically unlimited number of such characteristics may become signals under social selection, which would always favor improved ability to recognize them and respond appropriately.

The Role of Mutation and Drift

As in any evolutionary sequence, which among a large number of potential cues actually evolve as signals must depend in part upon random processes (mutation and drift) determining, respectively, (1) the initial ability to react to a trait as a signal, and (2) the commonness of particular potential signals in the sampled (interacting) population. Both processes would be expected to vary from one population to another.

The coevolutionary nature of change in weapons and displays may confer a special importance on the role of drift, or sampling of traits, in local populations. The success of a particular tactic depends on what others (or the majority of others) are doing. This may help explain why it is reasonable to conclude that random drift or founder effects are frequently important initiators of divergence and speciation in sexually selected groups such as Hawaiian *Drosophila* (Carson, 1978; see also Kirkpatrick, 1982). A dramatic illustration of the effect of local population composition on competitive tactics is provided by the highly sexually selected labrid fish, *Thalassoma bifasciatum,* which (facultatively) changes color and sometimes sex at different sizes, depending on the competitive situation on individual coral reefs (Warner, Robertson, and Leigh, 1975).

Ecological Factors

While I have argued above that divergence in social traits can proceed even without ecological differences between isolated populations, this is not to say that such evolution is independent of ecology. Indeed, environmental differences, when they exist, make the divergence of social traits even more likely. Smith (1977, pp. 348-52, 364-88) has reviewed some of the environmental factors that could initiate divergence in the characteristics of social communication (see also Gorman, 1968; Morton, 1975; Lloyd, 1979, 1983; Brenowitz, 1982; and references in Payne, in press). They include amount and location of sunlight available for visual displays; availability of leaves (or other substrates) suitable as sounding boards for particular kinds of acoustical displays; amount of background noise (e.g., visual and/or sonic) interfering with particular kinds of signals; density of vegetation obstructing particular signals; intensity of predation, which may limit the exaggeration of certain signals or the circumstances in which they are performed; and patterns of resource distribution, which may influence individual spacing and intensity of display. Spieth (1981) has described environmental factors possibly affecting the mode and morphology of male-male combat in *Drosophila.* The location of combat must often affect its form. For example, different species of male beetles fight in tunnels, at the entrances to cavities, or while clinging to grass stems, and have correspondingly different fighting behavior and morphology (see Eberhard, 1977a, b, 1979, 1980, 1981).

Different ecological circumstances may lead to the evolution of different patterns of distribution and parental care (Emlen and Oring, 1977), in turn affecting the nature of social signals (Alexander, 1975). And several authors have pointed out that the signal repertoire of a species is itself an aspect of its environment that can affect the further evolution of social signals. For example, social signals may evolve to increase contrast with signals used in different contexts (Hinde, 1970), or to achieve deceptive effects (mimicry) (West-Eberhard, 1975, p. 10; Lloyd, 1979). In dendrobatid frogs, species differences in the territorial aggressiveness and parental behavior of females are related to species differences in the role of distance signalling and appeasement in the courtship behavior of males (Wells, 1980). See Hinde and Tinbergen (1958) for a general discussion of social context as a source of signal diversity.

Learning

In animals capable of learning, evolutionary divergence of social signals may be influenced by initially fortuitous associations of individual differences and social success. Payne (1982, in press) suggests that locally distinctive birdcalls, or "dialects," sometimes originate via "song matching" when younger males imitate the distinctive call of a particular dominant or older, established male and thereby gain a competitive advantage. And Lloyd (1980) has suggested that comparable phenomena may occur in insects. Similarly, Darwin (1871) argued plausibly that the (inherited) physical differences among the races of man evolved under social selection in isolated populations having long histories of different learned "tastes" or culturally determined preferences affecting status and mating success. Learning could accelerate (genetic) divergence whenever a distinctive phenotype happens to be consistently associated (whether genetically or otherwise, e.g., hormonally or traditionally) with superior status. Then any genes contributing to the production of the successful phenotype would be favored.

In summary, extreme and rapid divergence of the signals and weapons used in social competition can occur with or without ecological differences between isolated populations. This is expected because of (1) the great importance of these characters in determining access to resources critical to survival and reproduction, (2) the potential for unending evolutionary change in socially competitive traits, (3) the generation-to-generation relentlessness of selection on these traits, (4) the effect of novelty in accelerating the initial spread of traits, and (5) the potential for mutually accelerating, genetically correlated evolution of preference and attractiveness in contests involving choice. A large number of factors can initiate divergent evolutionary trends, since a very large and theoretically unlimited array of physiological or behavioral characteristics may be used advantageously as signals, and ecological or habitat differences as well as mutation and (to an unusual degree) drift can produce local variants in those used. In species capable of learning, idiosyncratic traits of successful individuals may be advantageously imitated by others, and this may additionally influence the direction of evolution. Whatever the source of a new signal or weapon, it would be subject to strong selection for elaboration and improvement, the course of which would further vary under the influence of all of these accelerating and diversifying factors.

Alternative Hypotheses: Social Selection and Species Recognition

It has long been realized that sexually dimorphic characters like those used by Darwin (1871) to illustrate sexual selection can function in contexts other than competition for mates (see Wallace, 1878; Huxley, 1938; Mayr, 1963; Selander, 1972; Baker and Parker, 1979). They may function in identification of sex, species, and intention; in physiological synchrony or location of mates ("epigamic" displays); as adaptations to different ecological niches; or in defense against predators.

"Epigamic" courtship displays of males are believed to promote cooperation between the sexes by facilitating the location or stimulation of females. Such displays would likewise be subject to sexual selection, however, since superior performances by some males would lead to increased mating success in competition with others. As concluded by Mayr (1972, p. 97), ". . . sexual selection is presumably superimposed in all cases in which a male may gain a reproductive advantage owing to an extreme development of an epigamic character" (see also O'Donald, 1977). I therefore consider elaboration of so-called epigamic courtship displays an aspect of sexual selection in species where the female interacts with more than one male prior to copulation. In general, if there is direct evidence that a particular character is exposed or wielded in intraspecific competitive display or combat in a way illuminating its precise form or variability, and there is no comparable evidence for its use in other contexts (e.g., to frighten a predator), I consider this positive evidence that it has likely evolved primarily under social selection. (Such traits may of course have additional, secondary, functions.)

Species recognition has been the most influential alternative hypothesis explaining the diversity and species specificity of social signals. The species-recognition hypothesis holds that species-specific signals and morphology originate or persist in a particular form because they function as *isolating mecha-*

nisms (Dobzhansky, 1937; see also Fisher, 1930)—barriers to wasteful interaction or pair formation between members of differently adapted populations. Some authors (e.g., Mayr, 1963; see also discussion in Blair, 1960) have emphasized that isolating mechanisms can originate in isolated populations as incidental byproducts of genetic divergence under selection in other contexts. This latter view is compatible with the ideas presented here regarding the role of social selection in producing species-specific signals independent of or prior to a species-recognition function. It provides no explanation, however, for complex, coordinated divergence in the production and reception of species-specific signals, other than as an "incidental byproduct" or pleiotropic effect of general divergence (Mayr, 1963, pp. 551, 311). Perhaps for this reason, the species-recognition hypothesis seemed for a time the only sufficiently explicit explanation for such elaborate diversity, leading some authors to conclude that the "only obvious contexts of evolutionary change" in communication systems are "(1) perfection of intraspecific compatibility" (increased efficiency of interaction), "and (2) perfection of interspecific incompatibility (reproductive isolation)" (Alexander and Otte, 1967, p. 6). It is now clear, as I shall explain below, that "what had previously been regarded as species isolating mechanisms are to a large degree evolved instead in the context of sexual selection and competition within the species" (Alexander and Borgia, 1979, p. 437; see also Alexander, 1975). But during the Forgotten Era of sexual selection theory it would have been difficult to devise a hypothesis more perfectly suited than species recognition to displace sexual selection theory, and to distract biologists from its rediscovery. Many of the predictions of the two hypotheses are the same (see Payne, in press), or at least not contradictory. Both hypotheses predict species specificity of social signals. And several other phenomena cited in support of the species-recognition hypothesis (Alexander, 1962) can be explained as well by sexual selection theory. For example: (1) Some closely related species hybridize readily when distinguishing courtship or calling interactions are bypassed in the laboratory (e.g., by forcing non-conspecifics together). This could represent elimination of the species-recognition step in rapprochement; or in sexually selected species it could represent elimination of the step where the female would exercise (intraspecific) choice, with males from alien populations producing such inappropriate signals that they are normally discriminated against. (2) When related species overlap geographically they often have distinctive signals. This could evolve either as a mechanism of species recognition preventing wasteful interaction and hybridization; or it could represent divergence under sexual selection in reproductively isolated populations, either before or after sympatry. (3) Allopatrically (geographically) or allochronically (temporally) isolated populations sometimes lack signal distinctiveness. The species-recognition hypothesis can explain this as absence of selection for species recognition in the absence of overlap; or it could be due to absence or weakness of social selection, if the signals in question do not importantly affect access to critical resources. (4) Stereotypy (lack of individual variability of performance, at least of certain elements) could function to promote certain identification of conspecifics; or it could be the result of strong social selection having driven the character to fixation throughout the population (for a discussion of the selective basis of stereotypy in competitive signals see Zahavi, 1980).

Understanding the interaction of species recognition and social selection (intraspecific competition) in the evolution of species-specific communication is a crucial question raised by the revival of sexual selection theory. Fisher (1930) pointed out that species recognition signals would be subject to elaboration under sexual selection (female choice); and signals that originate under social selection must sometimes be used in, and may be channeled or maintained by, selection for species recognition (e.g., in sympatric vs. isolated populations; and see section on *Anolis*, below). The following discussion emphasizes examples (e.g., of non-sexual social selection and male-male competition) where it is possible to separate the two functions in order to establish social selection as an important cause of divergence. It must ultimately be considered, however, to be just one of several interacting causes.

There are several purely theoretical reasons for expecting social selection to be more often important than species recognition as a cause of divergence in socially competitive traits. Species in which social competition is important are subject to social selection in every generation and in every population, whether sympatric or allopatric with related species, with or without hybridization, and whether in the presence or absence of confusingly signalling neighbors. Furthermore, every reproducing individual is involved, not just those who happen to interact with inappropriate mates or respond to their signals in a zone of overlap, and at a time and site (habitat) when both are disposed to produce or react to signals. The species-recognition hypothesis is much more restrictive: it requires sympatry (or a history of sympatry) and disadvantageous hybridization or courtship interaction between populations that are genetically distinct but do not yet possess mechanisms for avoiding such interactions. It implies that distinctiveness evolves following and because of costly interaction between diverged populations. It is likely, however, that selection for species recognition would often favor discrimination of distinctive traits evolved in other contexts whenever such traits are available; in such cases species recognition could not be considered responsible for their divergence. By this reasoning, divergence under social selection may greatly reduce the number of situations in which divergence occurs as a result of selection for species recognition per se, since it can rapidly pre-adapt populations for species recognition by producing distinctive signals prior to contact and without special selection in the species-recognition context. On the other hand, signal divergence in the species-recognition context (if it occurs), would not restrict the scope of action of social selection (except to require maintenance of signal distinctiveness), and may even extend it by establishing characters subject to runaway change under female choice (Fisher, 1930). In sum, the effects of social selection are expected to predominate over, and often preclude, the effects of species recognition in the evolution of species-distinctive social signals.

It is therefore not surprising that the predictions of the species-recognition hypothesis are seldom borne out in socially selected groups, except when they coincide with those of the social selection hypothesis (above). For example, the species-recognition hypothesis predicts reproductive character displacement, or accentuated divergence of social signals, in areas of overlap with closely related species. This has seldom been demonstrated, even in the groups (e.g., singing Orthoptera and anurans, birds, and lizards) where it has most diligently been sought (see Walker, 1974; Blair, 1974; Payne, in press; Crews and Williams, 1977; and Ferguson, 1971, 1977, respectively). The failure to find reproductive character displacement common in these groups may be in part due to the difficulty of documenting its occurrence (Walker, 1974; Waage, 1979), and to the fact that courtship signals in these groups are known to be subject to sexual selection and are therefore likely to diverge *independent* of (and preclude) selection for species recognition (see Walker, 1974; Blair, 1974; and Williams and Rand, 1977 for examples). Reproductive character displacement may turn out to be most common in species under relatively weak social selection, since their signals are less likely to diverge in isolation prior to contact.

The species-recognition hypothesis also predicts that signal distinctiveness should be reduced on islands and in isolated (allopatric) populations. The plumage dullness (and increased sexual monomorphism) of male birds on remote, congener-free islands has long been considered decisive evidence for the importance of the species-isolation function in maintaining bright plumage in mainland populations having sympatric relatives (Sibley, 1957; Mayr, 1963, 1972). It may have, instead or in addition, a sexual-selection explanation (see Ghiselin, 1974; Selander, 1972). Recent studies of island waterfowl (Waller, 1980) indicate that pair bonds are maintained longer in island than in mainland (migrant) forms, a situation that would reduce sexual selection on males relative to females. And males of some species dedicate more time to brood care (Waller, 1980), a factor that might favor dull or cryptic plumage in males independent of selection (or relaxed selection) in the species-recognition context. Furthermore, loss of display distinctiveness in island populations is not a general phenomenon (see Ghiselin, 1974, p. 183 ff.). Gorman (1968) found the displays of isolated island *Anolis* species to be as distinctive and stereotyped as those of species having many sympatric congeners (e.g., those of Greater Antillean islands — see Ruibal, 1967), and cited similar diversity of displays in lizards (*Tropidurus*) isolated on different Galapagos Islands (Carpenter, 1966). The displays in question — agonistic and courtship movements — and their striking associated morphology (dewlaps and body coloration) are well known to function in intraspecific social competition (see below), which would account for their divergence in both sympatric and isolated populations. Other examples are given in a discussion of "superspecies," below.

Pre-mating isolating mechanisms are thought to evolve because of the advantage of early species recognition, prior to copulation, zygote formation, and other costly investment in disadvangaged (hybrid) offspring (Mayr, 1963; Alexander and Otte, 1967). Extending this argument, one would expect species recognition to occur early in courtship, and to involve brief interaction. Long, complex interactions, while predicted by the sexual selection hypothesis if females examine males using complex, repeated, or subtle comparisons, should usually be selected against in the species-recognition context. If species recognition occurs early in a courtship sequence, diverting mismatched pairs from further interaction, complexity and diversity in subsequent behavior cannot be regarded as being evolved or maintained under selection for species recognition. For example, in some *Drosophila* species, species recognition occurs prior to courtship, and involves different characters (Manning, 1966). And in Western grebes (*Aechmophorus occidentalis*) there is strong positive assortative mating between two color phases having virtually identical complex courtship displays, with recognition occurring as a result of phase-specific simple advertising displays given early during intersexual interactions and (unlike the courtship displays) showing greater phase specificity (or learned "response displacement") in areas where both phases are present (Neuchterlein, 1981a,b). In a review of song playback experiments involving various bird taxa, Emlen (1972; see also Neuchterlein, 1981b) concluded that in most species only a small fraction of available song features are essential for species recognition.

Failure to document the major predictions of the species-recognition hypothesis has given rise to several remedial hypotheses: the signal redundancy hypothesis (see Rand and Williams, 1970 on *Anolis*; discussed critically in relation to birds by Krebs and Kroodsma, 1980), which explains continued divergence as redundancy presumably improving the efficiency and certainty of species recognition; the lost neighbor hypothesis (the failed invasion hypothesis of Williams and Rand, 1977), which explains signal distinctiveness in allopatric isolates in terms of (hypothetical) former overlap with now extinct or allopatric populations of related species (Schodde, 1976; Fine, Winn, and Olle, 1977, p. 497); and the semi-assortative mating (or sub-species recognition) hypothesis (Crews and Williams, 1977), which envisions geographic variation in signals as having evolved to reduce possibly disadvantageous mating between forms adapted to somewhat different local ecologies. These hypotheses have the effect of salvaging the species-recognition idea when its more conventional interpretations are not supported by the available data. When cited without evidence to explain divergence of characters known to be under social selection, they should be regarded as explanations of last resort, since social selection can explain such divergence without special assumptions.

DIVERGENCE UNDER SOCIAL SELECTION: PREDICTIONS

Social selection theory makes the following predictions which distinguish it from the species-recognition hypothesis (see also Payne, in press; and Thornhill and Alcock, in press):

(1) Character exaggeration, and geographic variation suggesting relatively rapid divergence, should often occur in all kinds of

traits used in social competition—not only those used prior to or during courtship, but also weapons, threat signals used in male-male contests over mates, and other signals (e.g., of juveniles or females within groups) specialized to function in competition for resources other than mates.

(2) There should often be a correlation between social (or mating) system, and distinctiveness and exaggeration of social traits (modified after Payne, in press): the stronger the social selection in a particular social situation (the greater the variance in reproductive success due to social competition), the more complex and exaggerated the weapons or signals used, and the more rapid and greater the expected divergence between isolated populations. There should thus often be a positive association between degree of exaggeration of a social trait and its degree of geographic variability and species specificity.

(3) When social competition involves both sexes, the socially selected traits (weapons or signals) should be similarly or monomorphically extreme and species specific (or geographically variable) in both sexes. When only one sex is involved (or the sexes are involved unequally) sexual dimorphism in the socially selected characters should occur.

(4) Distinctive signals should often evolve even in allopatric isolated populations (in the absence of sympatric closely related species or others producing similar signals).

DIVERGENCE UNDER SOCIAL SELECTION: EXAMPLES

Predictions (1) and (2), above, were made with regard to sexual selection by Darwin (1871), who listed many illustrative examples of both invertebrates and vertebrates, especially insects, birds, and mammals. The following examples, while far from an exhaustive review, indicate that these predictions hold in a wide variety of organisms, and illustrate ways in which they can be tested. For information on divergence I have referred to taxonomic monographs and comparative behavior studies. If socially selected characters are used as "key" characters for the identification and description of species or subspecies this indicates that they have been among the fastest visible or measureable characters to diverge. Although many important behavioral and physiological characters are not taken into account by taxonomists, this at least gives a rough indication of the degree of divergence of social characters relative to non-social aspects of morphology. Non-social traits may, of course, also undergo rapid evolution under strong selection. Conversely, if a particular social character happens to be only weakly socially selected (e.g., it is rarely expressed in nature, or has little effect on survival or reproductive success), it would not follow the predictions suggested here.

I have relied mainly on descriptions of behavior as evidence for the competitive social function of the characters discussed below. They are considered basically competitive in nature if they fit Hinde's (1970) definition of "agonistic" behavior: "behavior directed towards another individual which could lead to physical injury to the latter and [or] often results in settling status, precedence, or access to some object or space between the two." Agonistic interactions sometimes lead to cooperation and group-beneficial social integration (see West-Eberhard, 1979, 1981), but there are good reasons for regarding their evolved nature as fundamentally competitive (see Williams, 1966).

Sexually Selected Displays

Among the most famous likely products of the sexual-selection subcategory of social selection are the spectacular plumes and markings of certain polygynous birds, which use their extravagant morphology in elaborate intraspecific male-male (threat) and male-female (nuptial) displays. Examples (with references describing displays) include those of grouse (Wing, 1946; Wiley, 1978); birds of paradise (Gilliard, 1969); manakins (Snow, 1976); cotingas and bellbirds (Armstrong, 1965; Snow, 1976); ducks (Armstrong, 1965); and pheasants (Armstrong, 1965). That these traits diverge relatively rapidly is reflected in the characters used to distinguish species and subspecies in these groups (see, respectively, Robbins, Bruun, and Zim, 1966; Gilliard, 1969; Davis, 1972, and Meyer de Schauensee and Phelps, 1978;

and Delacour, 1970). Although the females of related species are often very similar, males (the more strongly sexually selected sex) are easily distinguished by their plumage, indicating that it evolves more rapidly than that of females (the less strongly sexually selected sex). Furthermore, when behavior not involving plumage (e.g., bower construction or song) predominates in the competitive displays of males, plumage is relatively conservative and the competitive morphology or behavior is taxonomically and geographically distinctive (Sibley, 1957; Gilliard, 1969; Krebs and Kroodsma, 1980).

The species-specificity of bird plumage and song have often been considered products of selection for pre-mating isolating mechanisms, or species identification (e.g., see Marler, 1960; Mayr, 1963; and Smith, 1977). This hypothesis has been most explicitly tested and related to sexual selection as an alternative explanation in the case of vocalizations. There is evidence that bird song functions in both contexts: song repertoire affects the mating success of individual males (Yasukawa, Blank, and Patterson, 1980; Krebs and Kroodsma, 1980, pp. 147–8; Payne, in press); and females are preferentially attracted by songs of their own species and even local "dialects" (Baker, Spitler-Nabors, and Bradley, 1981; Payne, in press). Both theory and observations, however, support sexual selection as the more consistent cause of divergence (Payne, in prep.), without denying that species recognition could be an important (perhaps often secondary) effect. The fact that song affects male mating success, by means of effects on both male-male interactions and female choice (Payne, in press), means that it is subject to all of the divergence-accelerating factors discussed above; and there is no evidence for character displacement in song (Payne, in press). Payne (in press) has also tested the prediction that mating system and intensity of sexual selection (variance in male mating success) should correlate positively with the exaggeration of sexually selected traits, and finds that in general it does: sexual dimorphism in size and male ornamentation is greater in the lekking species in several families of birds, though not in all (lek-forming species were shown to have greater variance in male mating success than non-lek-forming species).

The major cheliped of male fiddler crabs (*Uca* species) is likewise a weapon used primarily in highly ritualized male-male displays (Crane, 1975). Crane (1975, p. 457) has called the giant claw of the male ". . . one of the most highly and variously specialized organs known to zoology, and certainly unsurpassed in the number of adaptations for ritualized combat." Cheliped displays are sometimes directed at females. But "regardless of the additional uses in the acoustics of courtship, the entire complex armature of both merus and claw forms a vast system reserved for intermale behavior"—both occasional real combat, and ritualized tapping displays. "Antler-bearing mammals, including even moose and Irish elk, show in contrast minor specializations. In fiddler crabs the claw alone, at its maximum relative weight, reached almost half the total weight of the crab" (Crane, 1975, p. 456). In fiddler crabs, morphology and behavior concerned with ecological adaptation and maintenance are "as a whole conservative" (p. 526), showing little variation within and among the 62 species recognized by Crane. In contrast, characters concerned with reproduction—the male gonopods (genitalia) and the major cheliped—show striking variation, with the claw being the most consistently used for distinguishing species and subspecies. Among the species-specific details of claw morphology are small knobs known to be used in male-male interactions (tapping displays). Since these aspects of morphology are unlikely to ever be perceived by females it is doubtful that they function in species recognition.

The dewlap of male (and in some species, female) *Anolis* lizards is a reptilian equivalent of the plumage and song of birds. It is a large, usually brightly colored, and variously patterned flap of skin that is extended during courtship and aggressive displays (see Gorman, 1968; Rand and Williams, 1970; Trivers, 1976). Field and laboratory observations (Greenberg and Noble, 1944; Ruibal, 1967; Gorman, 1968; Trivers, 1976) leave no doubt that dewlaps function in competitive social (territorial and courtship) displays and, hence, that they are subject to social selection.

As in the case of other socially selected traits, dewlaps and other lateral head and body markings are key taxonomic characters at the species level (Lazell and Williams, 1962; Williams, 1963; Gorman, 1968); and they show marked geographic divergence (Schwartz, 1968; Webster and Burns, 1973), often even in the absence of sympatric congeners (e.g., in the "solitary" island populations of *Anolis conspersus* and *A. lineatopus*—Williams and Rand, 1977; in island subspecies of *A. distichus* and *A. marmoratus*—Crews and Williams, 1977; and in island populations of the *A. roquet* group—Gorman, 1968). That is, dewlaps and other display characters probably do diverge independent of selection for reproductive isolation. This conclusion is reinforced by the fact that there is so far no unequivocal example of reproductive character displacement in *Anolis*. In one carefully studied case (the *brevirostris* species complex in Haiti), clinal variation in dewlap coloration within one species was in a direction that would maximize contrast with the closely related species contacted at opposite ends of the cline (Webster and Burns, 1973). This has been cited as the only good example of character displacement in reptiles (Ferguson, 1977). The geographic variation observed, however, could as well be a product of social selection.

Whereas there is thus good reason to believe that social selection is an important cause of display divergence in *Anolis*, there is also evidence that dewlap displays function in species recognition and reproductive isolation: experiments demonstrate an effect of dewlap color on mate selection (Ferguson, 1977), and studies of multi-species sympatric associations show that each species has a distinctive dewlap color (Rand and Williams, 1970; Williams and Rand, 1977), with the species that are most similar in size and general appearance differing most strikingly in dewlap color. In some populations, however, the displays seem to have diverged far beyond the degree necessary to effect species recognition: in a community containing eight species, Rand and Williams (1970) estimated the redundant information content of displays to be sufficient to separate up to 502 species!

I suggest the following interpretation of these facts: divergence under social selection is the primary source of intraspecific and interspecific variation in dewlaps and displays, and is a continuing source of distinctiveness whether species contact occurs or not. This must sometimes contribute to speciation by producing local differences in pre-mating signals, preadapting diverging populations for reproductive isolation. Such differences would be reinforced in the species-recognition context if, at species boundaries, there were selection against hybridization. In that case selection for species recognition may limit or direct the variants possible under social selection. But social selection would continue to increase the complexity of displays in sympatric populations. This could explain the apparent excess of diversity in display characters compared to that believed necessary for species recognition.

The genus *Anolis* thus serves to illustrate interaction of social selection and species recognition during speciation. It may prove a key genus in elucidating the roles of social competition, ecology (references in Jenssen, 1977, p. 204), and species recognition in the origin of species. Other well-studied and taxonomically useful ethological isolating mechanisms, such as cricket calls (Alexander, 1962), firefly flashes (Lloyd, 1966), frog calls (Blair, 1962), and bird songs (Lanyon, 1969), have undoubtedly diverged importantly under sexual selection (see, respectively, Ehrman, 1972, and Alexander, 1975; Lloyd, 1979; Ryan, in press; Payne, in press), and should therefore also serve to illuminate this interaction of factors. For a concise summary of an already well-analyzed example, see Thornhill and Alcock (in press) on *Drosophila*. Silberglied (in press) provides evidence that male intrasexual display is responsible for the diversity of brilliant male coloration in butterflies.

Competitive Displays of Plants

There is a clear (but not perfect) analogy between the evolution of competitive displays in animals, and that of comparable displays in plants—the colors and fragrances of flowers and fruits (see Stiles, 1982) of animal-pollinated and animal-dispersed species. When pollination is a limiting resource for plants, and nectar and pollen for pollinators, there is strong selection on the attractive displays of the plants as well as on the powers of discrimination and exploitation efficiency of pollinators. This has led to adaptations in animal-pollinated flowers that have been compared in flamboyancy and extravagance to the sexual displays of animals (Rothschild, 1975). The analogy with sexual selection for displays in animals is strongest in species such as some orchids that have one or a few specialized pollinators (Dodson, 1975; Dressler, 1981). And in such plants a spectacular diversity and specialization of pollinator attractants and pollination devices have sometimes evolved (see Darwin, 1862, on orchids; Meeuse and Schneider, 1979, on water lilies). Flower structure is of great importance in the taxonomy of most groups (Ordnuff, 1978; Dressler, 1981), especially at the species level. This indicates that, as in the case of socially selected characters in animals, the competitive displays of plants diverge relatively rapidly. The intervention of a second species (the pollinator) in the case of plants means that a runaway process of the kind visualized by Fisher is impossible. But the other factors discussed above as favoring rapid signal divergence and speciation would apply, and pollinators introduce an additional important source of signal diversity: interspecific competition for pollination. The resource at stake (the effective services of pollinators) is often shared, and strongly contested, in geographically diverse mixtures of flowering species. Pollen of heterospecific competitors can seriously interfere with fertility and may lead to local divergence (character displacement in floral characteristics) (see review in Waser, in press); and the presence of highly attractive species can lead to local convergences (floral mimicry) (Heinrich and Raven, 1972). Both tendencies would contribute to the species and subspecies distinctiveness of animal-pollinated flowers. In addition, geographic variation in the relative abundance of different pollinators can lead to changes in flowering times associated with changes in pollinator (for possible examples see Frankie, 1975, p. 205). Such changes must sometimes also lead to changes in flower morphology and odor (Grant and Grant, 1965). The idea that competition for pollination contributes importantly to floral diversity is supported by the observation (Anderson, 1979) that remarkable conservatism in the pollinator-attracting features of flowers in the neotropical Malpighiaceae is associated with lack of nectar production and, hence, a limited clientele of potential pollinators (restricted avenues of local divergence). This interpretation would seem to be contradicted by the "endless" floral diversity of orchids (Darwin, 1862, p. 284), which likewise have extremely specialized pollinators. The correct resolution, however, may be that suggested by Darwin (1862), who believed the floral diversity of orchids to be driven by a low pollen:seed ratio, which, he argued, places a special premium on efficient pollen transfer. The population pollen:seed ratio, like the operational sex ratio in animals (see Emlen and Oring, 1977), must be an important determinant of the strength of social selection on competitive displays and, hence, mating (pollination) systems. In other words, *intra*specific competition for efficient pollination may be unusually strong in the orchids; and this would increase the accuracy of the analogy with sexual selection and the applicability of generalizations regarding rapid evolution under intraspecific social selection. If Darwin's suggestion is correct, one would expect floral conservatism (low floral diversity) to be associated not only with low pollinator diversity but also sometimes with high pollen:seed ratios. As in animals, signal (floral characteristics) divergence in plants can affect reproductive isolation and speciation when animal pollinators are involved (see Grant, 1971, on "ethological isolating mechanisms" in plants).

Sexually Selected Weapons

The elaborate thoracic and head horns of male beetles offer a well-documented example of pattern in the evolution of weapons generally confined to one sex (the males). Beetle horns are used in male combat in all of a taxonomically wide variety of species in which the behavior of living males has been studied (Eberhard, 1977a–1981, and cited references). In each case the peculiar and sometimes outlandish shape of the horns proved appropriate for some distinctive method of fighting, such as prying, holding, flipping, ramming, pinching, twisting, or lifting conspecific male opponents of a particular (species characteristic) size or shape and behavior. There is no evidence for use of beetle horns in displays to females (Eberhard, 1979). And females do not fight. A recent, detailed taxonomic study of horned beetles of the genus *Blackburnium* (Scarabaeidae: Geotrupinae: Bolboceratini) (Howden, 1979) illustrates both intraspecific geographic variation in horns (e.g., in *B. angulicorne*) and interspecific differences in horns useful in the species-level classification of males. Females, on the other hand, show very little variation, as do non-sexually dimorphic characters of males other than genitalia (which may also be affected by sexual selection—Eberhard, in prep).

Similarly, the weapons and combat rituals of horned and antlered mammals show species-specific forms (see Mayr, 1974) and striking (clinal) geographic variation (Geist, 1971).

Non-Sexual Social Selection

Non-sexual social selection is selection involving competition for resources other than mates. A given character may be employed in both sexual and non-sexual social communication. For example, the "head-toss" of gulls occurs during food solicitation, courtship displays, and aggressive encounters (Hinde, 1970, p. 681). The purpose of this section is to provide evidence that non-sexual social selection is one important cause of rapid signal divergence, by citing examples in which species-specific or geographically variable characters are used in non-sexual social competition.

In mantis shrimps (stomatopod crustaceans) both males and females fight, using formidable weapons in the form of raptorial appendages specialized primarily for different modes of predation on other marine animals (Caldwell and Dingle, 1976). With these appendages stomatopods can break open the shells of clams, and (in some species) deliver lethal blows to conspecific competitors during territorial disputes. Among the structures specialized primarily (but not exclusively—see Schmitt, 1965) for intraspecific contests are the armor of the telson, or tail shell, which is modified as a defensive weapon to receive blows; and the meral spots, variously colored areas on the raptorial appendages that are conspicuous during threat displays. In accord with the predictions of social selection theory, these characters are (monomorphically) well developed in both sexes, and useful in the identification of closely related species (Manning, 1969; Caldwell and Dingle, 1976). The distinctiveness of the meral spot in sympatric species has been assumed to serve for species recognition (Caldwell and Dingle, 1976). But a striking positive correlation between the frequency of aggressive interactions (threat displays per minute) of a species and the prominence of its meral spots in six congeneric species (Caldwell and Dingle, 1976) indicates that meral spots have evolved importantly under social selection.

The same pattern holds in a number of groups of birds: species are sexually monomorphic for striking species-specific social-display morphology when both sexes participate in aggressive or territorial displays (Huxley, 1938, p. 426). Examples include toucans (*Ramphastos* and *Pteroglossus* species), whose enormous bills and bright facial markings may be used in ritualized agonistic behavior (see Skutch, 1958; Bourne, 1974); hummingbirds (*Amazilia* spp.) in which both sexes defend feeding territories (Wolf, 1969; Stiles and Wolf, 1970); colonial species of parrots (*Agapornis*) (Dilger, 1960); and jays (Brown, 1964). (For color plates documenting the predicted species-specificity in bright markings see Haffer, 1974, and Meyer de Schauensee and Phelps, 1978, on toucans and on hummingbirds; Dilger, 1960, and Forshaw, 1973, on parrots; and Davis, 1972, on jays.) The markings of monomorphically bright birds are unlikely to have evolved under sexual selection on males (with pleiotropic effect on females), as suggested by Darwin (1871). Most of these species (e.g., toucans, parrots, and jays) are monogamous for life, and pair formation may involve little or no display (see Dilger, 1960). The parrots studied by Dilger represent a series from solitary to highly social (group-living) species. Females most closely resemble males in the more social species, in which the females aggressively defend nest sites against intruding conspecifics regardless of sex. In the sexually dichromatic species, on the other hand, females confine their aggressive behavior mainly to attacks on other females, and males participate less in defense of the nest (Dilger, 1960, pp. 668–9). Similarly, toucans (*Selenidera*) that live as solitary pairs rather than in flocks are sexually dimorphic and have less exaggerated beaks than do more highly social toucans (*Aulachorhynchus, Rhamphastos*) (Meyer de Schauensee and Phelps, 1978). The trend toward monomorphic brightness in the more highly social species is as predicted in plumage signals if those species are more subject to selection (on both sexes) for successful social interaction within groups, and less strongly selected (primarily in males) for effective courtship. The species-recognition hypothesis is thrown in doubt in the case of parrots by the very large number of strikingly distinctive allopatric and island populations in this family of birds (Moreau, 1948; Forshaw, 1973; see discussion of "superspecies," below).

There is also a correlation between monomorphically bright signal coloration and territoriality by both sexes in some lizards (Ferguson, 1971), mammals (e.g., lemurs—Wilson, 1975, p. 530), and fish (Baylis, 1974). Jolly (1972, p. 155) describes lemurs as among the "showiest of mammals," comparing their species-specific signal pelage to the plumage of visually communicating birds. Some lemurs have undergone "extreme subspecific radiation," showing remarkable geographic variation in fur color and markings (Jolly, 1966, pp. 144–147), suggesting rapid evolution of these display characters. Although the functions of coloration in some reef fish (e.g., Chaetodontidae) are controversial (for a concise summary see Reese, 1975, pp. 38–39), there is no doubt that in some groups they have evolved under social selection (see Warner, Robertson, and Leigh, 1975). I suspect that much of the signal diversity in brightly colored and highly territorial reef species will prove explicable in terms of sexual and non-sexual social selection.

Severe non-sexual social competition occurs among temperate-zone wintering birds. In some species, individuals unable to hold territories generally perish (references in Rohwer, 1977). Experimental dying of the head and crown plumage has shown that the extent of black coloration communicated dominance status in winter hierarchies of Harris' sparrows (*Zonotrichia quereula*) (Rohwer, 1977; Rohwer and Rohwer, 1978). And this aspect of the plumage (also displayed in extreme form during the breeding season) is a key species-specific taxonomic character in North American species of the genus *Zonotrichia* (Robbins, Bruun, and Zim, 1966). It thus follows the prediction of rapid divergence under social selection. In the Harris' sparrow, individuals of both sexes and all age classes form flocks where they compete for resources within a single dominance hierarchy (Rohwer and Rohwer, 1978).

Completely non-sexual social selection occurs in the social insects. Within colonies of the social Hymenoptera (wasps, ants, and bees) only females compete for reproductive status, in contests involving both direct and ritualized dominance and sometimes mediated by pheromonal signals (see references in West-Eberhard, 1977, 1981). These contests result in very large differences in reproductive success between winners (egg-layers) and losers (non-egg-laying workers) (West-Eberhard, 1981). As predicted by social selection theory the aggressive rituals associated with this strong competition, like sexually selected displays, are complex and species specific in the few groups (*Polistes* wasps and stingless bees) where comparative data are available (see Sakagami, 1982; West-Eberhard, in press).

Additional Evidence

Both the degree of exaggeration of socially selected characters and their rate of evolution are expected to be functions of the intensity of social selection (Prediction 2, above). If this is so, there should be a positive association between degree of social specialization of a taxon and the rate of change in its socially selected characters.

Crane (1975, p. 534) recognized different degrees of social specialization among fiddler crabs: socially specialized species have more highly ritualized displays, longer and more complex or intense waving displays, more complex courtship, more time dedicated to territorial maintenance, and more striking male color change during display. As predicted, the subgenus *Celuca*, whose social behavior is the most specialized of the nine subgenera of fiddler crabs (Crane, 1975, p. 531), has undergone "explosive evolution" in the eastern Pacific, where it shows a far greater diversity of species and subspecies (recognized primarily on the basis of socially selected characters) than do the more primitively social subgenera. Of course such comparisons suffer from the difficulty of ascertaining how much of this divergence is due to different numbers and times of speciation-causing (isolating) events in the different subgenera, or to their age. A better test of the hypothesis that rate of divergence and speciation is accelerated by social selection would be to compare the amounts of divergence undergone by populations of different degrees of sociality after being split into allopatric isolates for a given known amount of time. Just such an experiment occurred with the last closing of a seaway through Central America near the end of the Pliocene (3 to 4 million years ago). This simultaneously divided eight species of *Uca* into pairs of populations isolated on the Pacific and Atlantic sides of the Isthmus of Panama (Crane found no evidence of fiddler migration through the Panama Canal). Two of them belong to the socially specialized subgenus *Celuca*; one to a "conservative" subgenus (*Boboruca*) resembling the most primitive social group (*Deltuca*); and five represent subgenera (*Uca, Minuca*) of intermediate and variable social specilization. As Crane pointed out, the classification of allopatric populations as "species" or "subspecies" is necessarily somewhat arbitrary. The important thing for the present comparison is the consistent application of the same criteria to the entire genus, so that the distinctions reflect consistent differences in degrees of divergence (especially, in socially selected features of the major cheliped and waving displays). Crane's taxonomic designations support the hypothesis that more strongly socially selected (specialized) populations evolve more rapidly: both of the most highly social species diverged in allopatry to the level of "species" (*batuenta/cumulanta*, and *limicola/leptodactyla*, on the Pacific/Atlantic sides, respectively), whereas the socially relatively unspecialized *U. thayeri* diverged only to the "subspecies" level (*t. umbratila/t. thayeri*). (Of the species of intermediate social specialization—subgenera *Uca* and *Minuca*—two diverged to the subspecies and three to the species level.)

Rohwer and Niles (1979) made a pioneer attempt to document the rapid evolution of a socially selected trait by studying plumage changes in male purple martins (*Progne subis*). During the period 1840 through the 1970s populations east of the Great Plains have become increasingly colonial due to the increased availability of favorable foraging areas (open fields) and artificial nest holes (martin houses). Rohwer and Niles hypothesized that this might produce evolutionary increase in female-mimicry (plumage dullness) of sub-adult males, which functions in social competition for mates. Although their measurements of museum specimens showed a trend toward increased dullness just short of statistical significance ($p \sim 0.15$), taken together their comparisons of eastern and western U.S. populations indicated a significant ($p = 0.011$) evolutionary effect of density-related geographic factors on subadult male plumage during a period of less than 150 years.

Both these analyses—of fiddler crabs, and of purple martins—would require further research to be considered definitive. But they suggest ways of documenting relative rates of change in socially selected characters using comparative study, in addition to Darwin's (1871) classical methods of (1) showing greater development of social versus non-social characters of the same species, and (2) showing greater variation in social versus non-social characters among different closely related populations (races or subspecies, and congeneric species).

The social-selection (but not the species-recognition) hypothesis is further supported by the occurrence of divergence in social signals within superspecies in a variety of taxa.

A superspecies is ". . . a monophyletic group of entirely or essentially allopatric species that are morphologically too different to be included in a single species" (Mayr, 1963, p. 499). That is, the populations of a superspecies have diverged beyond the subspecies to the species level as judged by taxonomists, with no or very little secondary contact. As such, they are "a particularly convincing illustration of the geographical nature of speciation" (Mayr, 1963, p. 501)—that is, of divergence occurring in isolation, and (by implication) without character displacement due to sympatry with related populations. Therefore, insofar as superspecies fit Mayr's (above) definition, they can be taken to illustrate divergence *not* likely to have originated in the species-recognition context.

Superspecies occur in many socially selected groups, including toucans (Haffer, 1974), birds of paradise (Mayr, 1963; Schodde and McKean, 1973), parrots (Keast, 1961), and fiddler crabs (Crane, 1975). In all of these groups the component species are distinguished primarily by divergence in socially selected characters, as pointed out above. Behavioral observations indicate that this divergence is certain to have been affected significantly by social selection. It cannot be attributed to selection for species recognition without giving more weight to hypothesized "lost neighbors" and selection in a very limited area of geographical contact, than to observed social interactions occurring throughout the species range and likely to be subject to strong selection.

Non-competitive signals (such as alarm call or anti-predator displays) often diverge less rapidly than competitive social signals. Some of them may be strongly selected to remain constant (Mayr, 1974). In one of the few available discussions of conservatism and lability in the evolution of different kinds of displays, Moynihan (1975) showed that three of the four kinds of cephalopod displays categorized as "conservative" (showing little variation among living species and even orders of cephalopods) are non-competitive startle reactions or alarm signals. By contrast, courtship displays are varied, even among closely related species. Moynihan hypothesized that conservative patterns are stable because they are adapted to influence a diversity of receivers (different age, size, and sex classes of the same species, or individuals of other species such as predators), with consequently severe limits on the kinds of signals that would be suitable to all. The contrasting rapid evolution of the competitive displays may be due to social selection. Similarly, in some birds with seasonal plumage change, drab winter or juvenile (camouflage) plumage is often less species-specific than the breeding (socially selected) plumage (e.g., in sandpipers, phalaropes, wood warblers, loons, and grebes—see Robbins, Bruun, and Zim, 1966).

In all of the above examples, the key characters for taxonomy at the species and subspecies levels have served to indicate the relative rapidity with which social characters evolve. Examples are therefore primarily limited to groups in which social competition happens to involve visible morphological characters or coloration. There must be many cases in which divergence important in social selection and speciation involves cryptic characters such as odor or behavior not usually observed by taxonomists (e.g., see Blaustein, 1981; Bornemissza, 1966; Bergstrom, Svensson, Appelgren, and Groth, 1981; and Blum, 1981, on the sex pheromones of mammals, scorpionflies, bumblebees, and ants, respectively). In such groups, taxonomic separation of biological species is often difficult until these characters are analyzed (see Alexander, 1962), and, in accord with the theory presented here, close study of living specimens should reveal divergence in the socially selected characters even when little or none is evident in morphology.

SPECIATION

The theory and examples given so far show a connection between social selection and rapid character divergence in isolated populations. Speciation is complete only when divergence is sufficient to lead to reproductive isolation. The question of how much genetic or phenotypic divergence is necessary to favor reproductive isolation between overlapping populations has never been resolved (Lewontin, 1974). (Electrophoretic studies of Hawaiian *Drosophila*—Carson, 1978—have exposed the inadequacy of using genetic distance to assign taxonomic status to different sexually selected populations.) The critical parameter is the degree to which the two sexes are incompatible or hybrids are at a disadvantage when male and female are from different populations, not simply the number of genes involved. Divergence in a critical signal could conceivably involve a small number of genes, yet have a disproportionately large effect on the sexual compatibility or competitive ability of hybrid offspring. For example, two species of Australian scorpionflies (*Harpobittacus*) that are scarcely distinguishable morphologically fail to pair in the laboratory due to divergent male sex pheromones (Bornemissza, 1966). The pheromonal divergence is almost certainly due to sexual selection rather than to selection for species recognition, since the two populations are known to have been completely allopatric since the Middle Cretaceous (Bornemissza, 1966). This seems to be a clear example of allopatric signal divergence under sexual selection leading to reproductive isolation and speciation without secondary contact and reproductive character displacement.

In general it seems reasonable to argue that if divergence can lead to speciation (reproduction isolation), then anything that accelerates divergence should tend to accelerate speciation—especially if characters critical to survival or reproductive success are concerned. It follows that social selection must often accelerate speciation in socially interacting organisms like those discussed in this article.

Spieth (1974) has remarked on the rapidity with which divergence and intra-island speciation is attained by lekking Hawaiian *Drosophila* compared to non-lek-forming subgroups, and has noted that in the lek species a single mountaintop has often served as a sufficient area to allow the evolution of a species. It is not surprising that many of the groups cited by Mayr (in press) to illustrate peripatric speciation (rapid acquisition of isolating mechanisms in small isolated populations) are groups often showing strong social or sexual selection (Hawaiian *Drosophila*, tropical birds, and lizards). As pointed out by Carson (1978), the distinctive sample of characters that happens to characterize such a small isolate (the "founder effect") could be enough to start the population on a new evolutionary direction under sexual selection.

When learning affects divergence it is difficult to generalize about the role of divergence on rates of speciation. In some species [e.g., white-crowned sparrows (*Zonotrichia leucophrys*), indigobirds (*Vidua* species), and Indigo buntings (*Passerina cyanea*)], individuals are so extremely flexible at mimicking local dialects and even songs of different species that it raises the possibility that learning retards, rather than promotes, the evolutionary (genetic) divergence of song. Instead, it suggests what Payne (in press) terms the "appealing" (but unproven) possibility that selection for flexibility under social competition in such species has led to the evolution of greater song learning ability, or intelligence. Indeed, it is probably no accident that the animals we regard as especially intelligent—e.g., crows and jays, dogs, porpoises, parrots, and primates—are also especially social (and hence subject to strong intragroup competition in which signal flexibility, mimicry, and other clever social manipulations may become highly advantageous) (see references in Alexander, 1979, p. 213).

But learning in some species seems to contribute to narrowness and rigidity (rather than flexibility) of breeding preferences. In white-crowned sparrows, for example, males learn songs in an early auditory-sensitive period (Baker, Spitler-Nabors, and Bradley, 1981), which would ordinarily mean that they could learn only the songs heard in their natal region. And there is a widespread tendency among social organisms to exclude outsiders, or at least to prefer to associate with members of their own flock or region on the basis of learned cues (Wilson, 1975). The extent to which this influences *mating* patterns is controversial (Bush, Case, Wilson, and Patton, 1977; Daly, 1981). Hardy (1966) hypothesized that the xenophobia, or clannishness of parrots—learned recognition cues, and their strong preference for pairing (in laboratory experiments) with members of the same flock, region, and species—may have contributed importantly to the rapid and superficial divergence of these birds, which never hybridize in the wild, yet like many other socially selected organisms (see below), when forced together in captivity can produce hybrids between species, genera, and even sub-families (Hardy, 1966, p. 80).

Sexually selected characters are often referred to as "superficial" (Sibley, 1957; Gilliard, 1969; Carson, 1978) in that conspicuous phenotypic differences can involve just a few genes (Carson, 1978). Two very distinctive varieties of the golden pheasant (*Chrysolophus pictus* mutants *obscurus* and *lutens*) are the results of single mutations (Gerrits, 1961). And interspecific and even intergeneric hybrids are common in sexually selected organisms in nature (Sibley, 1957; Mayr, 1963; Pace, 1974; Blackwell and Bull, 1978) and in captivity (Gerrits, 1961; Hardy, 1966). The great but superficial species diversity of orchids (indicated by ease of hybridization) may be due to a coevolutionary process like social selection involving flowers and pollinators. This kind of superficiality may render socially selected characters relatively useless in designating higher categories; few would deny the undesirability of the huge members of monotypic genera formerly recognized on the basis of socially selected characters in such groups as hummingbirds and birds of paradise (Sibley, 1957). At the species level, however, there is some justification for giving extra weight to socially selected characters because of their likely importance in effecting reproductive isolation.

The most notable result of social selection for the taxonomic studies of speciation is confusing variation. Darwin (1871) was impressed with the variability of sexually selected characters, and recognized it as being of several kinds: variation between the sexes (sexual dimorphism), which often makes it difficult to associate males and females of the same population in collections; geographic variation, making it difficult to ascertain the status (subspecific, specific, and generic) of allopatric populations; intrasexual and caste polymorphisms (e.g., high-low, or size-related dimorphisms, and immature vs. adult plumage of males), now seen to be associated with different mating or reproductive strategies (e.g., see Selander, 1972; West-Eberhard, 1979; Rohwer, Fretwell, and Niles, 1980; Eberhard, 1982); and individual variability, due to continuing selection (transient polymorphism of characters undergoing change, called "generative variability" by Darwin, 1859, p. 114). Taxa under sexual or social selection are thus commonly described as different groups. This problem is even more intractable for the systematist when variations are cryptic: for example, when there is biologically important but invisible divergence of behavioral, acoustical, or pheromonal characters without obvious morphological correlates. Conspicuous variation (e.g., in the acoutrements of visual displays) sometimes leads to inordinate "splitting" (elevation of geographic varieties to species rank) and to large numbers of allopatric and monotypic genera, whereas non-morphological variation leads to the opposite problem: lumping of variants, and unrecognized cryptic species.

One of the remaining controversies in speciation theory involves the significance of parapatric distributions, in which the borders of closely related species touch, often extensively and for long periods of time, without major overlap or massive hybridization (Mayr, 1982b). Parapatric distributions are reported in diverse organisms, including several of the socially selected taxa discussed in this article, such as birds of paradise (Gilliard, 1969), toucans (Haffer, 1974), parrots (Keast, 1961), lemurs (White, 1978, p. 89), and fiddler crabs (Crane, 1975). They must often have some ecological basis, with one species superior on each side of the boundary (Mayr, 1969), even though clear habitat or topographic barriers are not always visible to the human eye. As pointed out by Pace (1974, p. 73), however, maintenance of extensive contiguous distributions (e.g., see Pace, 1974, on leopard frogs) means that ". . . the limits of distribution of one member of any species pair are more clearly related to the presence of the other species than to any other feature of the physical or biotic environment, suggesting that significant, special interspecific interactions are involved in the biology of these species." What might the nature of these special interactions be? A combination of social-selection theory and classical ecological theory may hold an answer. When socially selected characters take the lead in speciation-related divergence, as suggested here, this implies that ecological divergence may sometimes lag behind. Niche similarity of allied species is expected to lead to competitive exclusion—elimination of one of the species from a region where it could exist alone, due to the competitive superiority of another species (see review by Hutchinson, 1975). Thus the low degree of ecological divergence of socially selected sibling species may particularly dispose them to parapatric distributions. And the aggressiveness and territoriality of socially competitive individuals, as well as the tendency to aggregate preferentially with conspecifics (e.g., in mating or nesting sites), may sometimes contribute to the maintenance of clearcut boundaries between species (e.g., see Diamond, 1973; Caldwell and Dingle, 1976). Gilliard (1969, p. 4) concludes that such a combination of ecological and behaviorial exclusion has affected the (parapatric) distributions and mating systems of closely related species of birds of paradise: "I found that the rapidly evolving polygynous 'genera' . . . usually behave somewhat like a semispecies in that they exclude each other ecologically; but the primary pressures of exclusion apparently involve the breeding grounds (the arenas), which they defend vigorously. . . ." Gilliard believes that these "exclusion pressures" may lead to the occurrence of generic tiering or layering of arenas at different heights within highland New Guinea forests, as well as to the (secondary) evolution of monogyny in some species and the evolution of bower construction behavior in some of those confined to the forest floor.

The evolution of divergent signals potentially serving as pre-mating isolating mechanisms can be an early rather than a late event in the speciation process in these groups; and divergence of social traits may be the basis of breeding incompatibility (hybrid disadvantage, or failure to interact as normal conspecifics) between populations that have diverged very little ecologically. Rapid divergence and speciation can thus conceivably occur between populations even when there is very little difference in their non-social environments.

CONCLUSION

The discovery in a taxon of species-specific social signals does not necessarily imply a primary species-recognition function. Social signals diverge in isolation, and can be elaborated independently of species recognition, even in sympatry with closely related species. Populations whose signals or appearance have diverged under social selection are preadapted for species recognition by the prior acquisition of species-specific markers, and need only be selected to distinguish them. If the diverged traits are so distinctive as to be severely disruptive to normal interaction, hybridization may not even occur upon recontact, and speciation (reproductive isolation) can be regarded as already complete. Any *assumption*, however, that even extravagant divergence under social selection would automatically have this result would be as invalid as the common but erroneous assumption that species specificity implies selection for species recognition.

The species-recognition hypothesis seems to have persisted as an explanation for divergence in social signals in many groups not because it was strongly supported by data, but because it was consistent with ethological and speciation theory at a time when sexual selection theory was largely forgotten. During that period biologists proved remarkably more creative at forcing the species-recognition interpretation upon contradictory data than they did at considering alternative explanations. Occasional attempts (e.g., Sibley, 1957) to revive Darwin's powerful arguments in support of sexual selection were not widely appreciated. The reasons for this would make an interesting study in the history of science.

Socially competitive characters, whether employed in a sexual or a non-sexual context, follow the same pattern of rapid divergence. This demonstrates the utility and wisdom of Darwin's (1871) painstaking insistence on the importance of the distinction between *natural* and *sexual* selection, as well as the importance of extending the latter category to include selection on non-sexual social characters. Only by making this distinction and applying Darwin's original generalizations regarding the special nature of sexual selection broadly (to all social competition) could one discover the common pattern in the evolution of beetles' horns, crabs' claws, pheasants' tails, toucans' beaks, birds' songs, and the dominance behavior of bees and wasps. The ideas presented here should eventually prove applicable to a very wide variety of organisms having behaviors and structures (e.g., complex genitalia and pheromonal signals) whose competitive functions are only beginning to be understood.

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