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The American Naturalist, Vol. 124, No. 3. (Sep., 1984), pp. 309-323.

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TRUTH IN ADVERTISING: THE KINDS OF TRAITS FAVORED
BY SEXUAL SELECTION

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Submitted December 17, 1982; Revised July 11, 1983; Accepted February 22, 1984

Ever since sexual selection was first described by Darwin (1871), biologists have recognized the importance of the phenomenon but have had difficulty in understanding how it operates. Sexual selection is that special form of natural selection which is responsible for the evolution of traits that promote success in competition for mates. It is particularly important in polygamous breeding systems in which individuals of one sex, usually female, invest many more resources in gametes and often also in parental care, and individuals of the other sex, usually males, compete to mate with these females (Bateman 1948; Trivers 1972). Sexual selection can take two forms. On the one hand it can favor the evolution of traits, such as those related to fighting ability, which increase success in direct competition with other males for mates. On the other hand, it can lead to the evolution of characteristics, such as those involved in courtship displays, which make males more attractive to females.

Although strikingly sexually dimorphic characteristics, such as the antlers of deer, the plumes of birds of paradise, and the elaborate displays of bowerbirds have been attributed to sexual selection, the precise mechanisms responsible for the evolution of these traits have remained the subject of much debate. There are two main hypotheses. Fisher's (1930) runaway selection model proposes that sexual selection will favor females that choose mates on the basis of any trait that confers an initial survival or reproductive advantage. This process will continue, resulting in simultaneous exaggeration of the trait and enhanced female choice, until the trait reduces survival of males to the point that this outweighs the advantages of increased reproductive success. This model assumes that the advantages and disadvantages conferred by the trait are confined to the sex (male) that expresses it, and that sexual selection is a special form of directional selection that ultimately tends to oppose natural selection for traits related to survival.

Zahavi's (1975) handicap hypothesis also proposes that sexual selection favors the exaggeration of traits which promote male reproductive success at the expense of survival. Females choose mates with such traits because their demonstrated ability to survive despite such a handicap indicates the overall fitness of their genotypes. Under this model both male and female offspring tend to inherit

the superior genetic qualities of their male parents, but because the sexual traits are not expressed in females, only males inherit the handicap.

Several recent papers (e.g., Davis and O'Donald 1976; Maynard Smith 1976; Zahavi 1977; Bell 1978; Andersson 1982; Hamilton and Zuk 1982; Kirkpatrick 1982) discuss the problems with these models and some develop explicit genetic models to overcome some of the difficulties. Most of these models, however, retain an essential dichotomy between the effects of sexual selection for mating success and natural selection for survivorship. Also, by focusing almost exclusively on female choice, they ignore the fact that the same male traits that serve as the basis for female choice are often used in direct male-male competition for mates. More importantly, these models generally fail to account for the fact that females choose males on the basis of traits that appear to have low heritability, because variation in their expression among males is determined primarily by age, environmental factors, and phenotypic vigor (but see Zahavi 1977; Andersson 1982; Nur and Hasson, *in press*).

Here, we develop the idea that sexual selection favors the evolution of costly, phenotypically variable traits whose expression reflects the survivorship and vigor of males and hence their overall genetic quality. We call this the "truth in advertising" hypothesis. It has been suggested repeatedly by empirical studies of animal breeding systems (see references below) and has been developed conceptually in the handicap models of Zahavi (1975, 1977), Andersson (1982) and Nur and Hasson (*in press*). Our treatment differs from these, however, in pointing out that the cost of honest advertisements need not always be expressed as a handicap to survival. We explore the consequences of these ideas for the evolution of sexual traits and consider in detail two examples, antlers of deer and nuptial color of fishes.

THE TRUTH IN ADVERTISING MODEL

The essence of this model is that sexual selection favors the evolution of phenotypic traits that vary in such a way that their expression is highly correlated with overall genetic fitness. This is shown in figure 1, which illustrates the case in which both the expression of the trait and overall fitness are assumed to be normally distributed within the population. For such a case it is clear that directional sexual selection resulting from differential reproductive success of males exhibiting extreme exaggeration of the trait will also result in directional selection for increased overall fitness in proportion to the degree of positive correlation between the two variables. Such sexual selection is a potent evolutionary force which acts through differential male reproductive success to enhance the effects of natural selection to maintain and increase the fitness of the population. Differential male reproductive success can be a consequence of direct male-male competition or female choice or some combinations of these two factors. The advantage to females of choosing males of high fitness as fathers for their offspring will favor the evolution of male traits that maintain a high correlation between the extent of their phenotypic expression and overall genetic quality. It will also favor the evolution of females that exhibit such discrimination in their choice of mates.

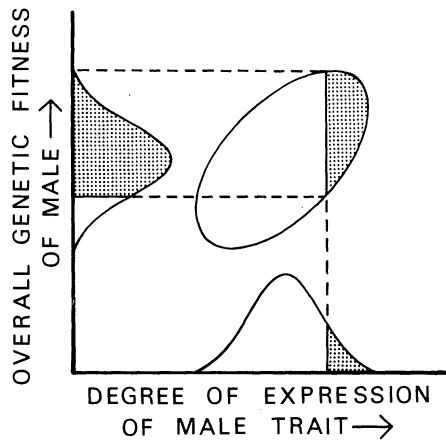


FIG. 1.—Graphical model of sexual selection by truth in advertising. As presented here, the model assumes that both expression of the sexual characteristic and overall fitness are quantitative traits, distributed normally among males. If there is a significant positive covariance between these two variables, females that mate with males with extreme expression of the sexual trait will be choosing individuals of superior overall genetic quality (as indicated by the shading).

The model makes three basic assumptions. (1) There is variation in male sexual traits which provides the basis for differential male reproductive success as a result of female choice and/or male-male competition. This is substantiated by numerous empirical studies of animal breeding systems. Males vary in the expression of sexual traits and those individuals with the most exaggerated traits tend to win contests with other males and be selected as mates by females (see examples beyond).

2. There is a significant variation in overall genetic fitness among males which, by definition, can to some extent be inherited by both their male and female offspring. Such variation may result from the accumulation and segregation of deleterious alleles as well as from the possession of favorable combinations of genes. Although theoretical population geneticists may argue about the kind and amount of this variation, we simply note that any form of evolution by natural selection requires the existence of such variation in the population.

3. There is a positive correlation among males between their overall genetic fitness and the degree of expression of their sexual traits. The reliability of the trait as an estimator of genetic quality is proportional to the degree of this positive covariance. Such a correlation will occur if the traits that influence reproductive success are phenotypically plastic and vary both within individual males and among males in the population so as to reflect age, health, social status, and resistance to predators and disease. Thus differences among males in the expression of their sexual traits honestly advertise differences in phenotypic quality and vigor that also reflect differences in genetic quality. When several traits simultaneously play a role in sexual selection, their patterns of expression should be highly intercorrelated, because all of them should be correlated with overall fitness (but see discussion of invariant traits beyond).

The model stresses that sexual selection favors the evolutionary development and ontogenetic expression of those male traits that most accurately reflect the heritable qualities of the entire male genome. Such traits should exhibit two general characteristics. First, there should appear to be little heritable variation in the male sexual traits themselves, because most of the variability should be correlated with age and environmental effects such as nutritional status, social position, and parasite load. In fact, heritability in the strictest sense should be very low and it should be difficult to change the expression of the trait by artificial selection under laboratory conditions, where all environmental effects (including age and interactions between individuals) are held constant. Nevertheless, under natural conditions the expression of the trait should be heritable in the broad sense that there should be a significant positive correlation between the degree of expression of the trait in males and in their male offspring and also between the selectivity of mates in females and in their female offspring. The magnitude of these covariances will reflect the extent to which overall fitness is heritable so that parent and offspring fitnesses tend to be positively correlated. This resolves an apparent paradox between the tenet of theoretical population genetics that continued directional selection should rapidly exhaust additive genetic variance, and empirical observations of breeding systems that variation in sexual traits persists despite continual differential reproductive success of individuals exhibiting the most exaggerated expression of these traits. Such variation is maintained and a significant proportion of it remains heritable because it reflects variability in the entire genome not simply in a relatively small number of genes coding specifically for a sexual characteristic.

A second general feature of sexually selected traits is that they are costly for individual males to produce and maintain. This costliness is essential to maintain the honesty of the advertisement. Males demonstrate the overall quality of their genome by displaying traits that indicate that they have acquired essential resources, survived to an advanced age, avoided their enemies, and bested their rivals in combat. The honesty of advertisement and the operation of sexual selection is facilitated by gene-environment correlations and interactions. Thus, to the extent that environmental resources are limiting, there will be a tendency for individuals of superior genotypes to be more successful in intraspecific competition, to be found in the better habitats, to have access to more resources, to develop more exaggerated sexual traits, and to achieve higher reproductive success.

The truth in advertising model has a number of empirically testable consequences. We hesitate to call these predictions because observations supporting them have already been reported in the literature. Nevertheless our treatment provides the basis for reinterpreting existing data as well as for rigorous testing with new observations and experiments. Among the important consequences of the model are: (1) Sexually selected traits should be highly correlated with phenotypic vigor and components of Darwinian fitness such as growth rate, predator avoidance, disease resistance, and competitive ability. Consequently these traits reflect the abilities of males to survive as well as to be successful in mating. (2) The traits are costly in the sense that their expression requires

expenditure of limited energy and other resources that otherwise could be allocated to other structures and functions. (3) Continued strong directional sexual selection will not exhaust the total variability in the heritable component of the trait, because the variation among males is the result of the expression of the entire genome. Consequently, males with the most exaggerated sexual traits should consistently experience the highest reproductive success. (4) Genotype-environment interactions and correlations should enhance the effect of sexual selection and hence should contribute significantly to the observed variation among males in sexual traits. (5) The Darwinian fitness of both male and female offspring should be positively correlated with the degree of expression of sexually selected traits in their fathers. (6) In many organisms both direct male-male competition and female choice are important components of sexual selection, and the same traits should often be employed both in intermale contests and courtship displays. Their effective use in direct aggressive contests between males is one mechanism that maintains the honesty of sexual traits. (7) When several different traits are important in sexual selection, their expression should be highly correlated among males. All of these traits should be so highly correlated with male reproductive success that it will often be difficult to determine the extent to which the outcomes of direct intermale competition and female choice depend on particular attributes. (8) Some exaggerated male traits, such as large body size and structures used in fighting, may confer advantages in intraspecific competition, not only with other males for mates, but also with individuals of both sexes for limited resources such as food and shelter. In these cases increased expression of the trait should enhance rather than compromise male survival.

Several of the above points are also consistent with other models of sexual selection. None of them, however, are necessary consequences of Fisher's (1930) concept of runaway selection, and point 5, in particular, is directly contrary to the predictions of Fisher's model. Zahavi's handicap principle and subsequent treatments of sexual selection based on this concept (Zahavi 1975, 1977; Trivers 1976; Halliday 1978; Clutton-Brock and Albon 1979; West Eberhard 1979; Thornhill 1980; Andersson 1982; Dominey 1983; Nur and Hasson, in press), have emphasized that the exaggerated expression of sexually selected traits is costly, is an honest advertisement of genetic quality, and consequently is positively correlated with the fitness of male and female offspring (points 1, 2, and 5). In the present treatment we have shown that the truth in advertising model is also consistent with other phenomena that are related to sexual selection, especially the genetic and environmental bases of variation in sexual traits (points 3 and 4) and the relationships between the traits used in attracting mates and in male-male competition (points 6 and 7).

The most important point that we make, however, is that sexual traits which honestly advertise male genetic quality need not reflect a trade-off between enhanced reproductive success and reduced survival, and consequently need not be handicaps in the sense of Zahavi and subsequent authors (point 8). We do not disagree that certain sexually selected traits, such as long plumes and bright nuptial colors, may increase attractiveness to females at the expense of an increased risk of predation (Selander 1972; Endler 1980). However, virtually all

previous treatments of honest advertisement have assumed a necessary trade-off between the expression of male sexual traits and survivorship (e.g., Zahavi 1975; Andersson 1982; Nur and Hasson, in press). We believe that this assumption is unnecessary and misleading. Many male traits, such as large body size and weapons, may confer an advantage in intraspecific competition for resources as well as for mates, and hence may enhance both survivorship and reproductive success. Reduction or absence of these attributes in females may reflect the necessity to invest a large proportion of their limited resources directly in offspring (Trivers 1972), rather than any inherent disadvantage of these traits. Empirical studies support this interpretation. For example, Packer (1983) attributes the possession of horns in females of the larger antelope species to their function as weapons in defense against predators. Additional examples of the role of deer antlers in female caribou and in male deer during the nonbreeding season are discussed in the next section.

EXAMPLES

The literature on polygamous breeding systems is so extensive that it is possible to find isolated observations which, especially if taken out of context, could be construed to support almost any mechanism of sexual selection. We believe, however, that most of the evidence is consistent with the truth in advertising model and not with existing alternative hypotheses such as Fisherian runaway selection. This is best demonstrated by evaluating the variety of information available for a few well-studied breeding systems. Here we examine the expression and function of two kinds of male sexual characteristics: antlers of deer and nuptial coloration of fishes.

Antlers of Deer

One of the most thoroughly studied examples of male secondary sexual characteristics in mammals are the antlers of deer (Family Cervidae, Order Artiodactyla). Perhaps the best data on the development and function of antlers have been obtained for the North American elk (*Cervus canadensis*) and the closely related European red deer (*Cervus elaphus*). The following points are relevant. (1) There is great phenotypic variability in antler size and branching pattern. Most of the variation is a function of age, health, and environmental factors (Clutton-Brock et al. 1982).

2. Antler size and the number of tines increase linearly with age up to 5 to 7 yr, increase more gradually until age 12, and decline in senescent individuals more than 13 to 16 yr old (Flook 1970; Geist 1982). Antler size also varies with social status (Bartos and Hyanek 1983; Geist 1982) and with nutritional condition. Clutton-Brock et al. (1982) report a dramatic decline in mean antler size of red deer correlated with an increase in population density, and presumably with increased competition for food.

3. The production of antlers is costly. Antlers are produced and shed annually. Metabolic requirements of stags are greatest during the peak of antler growth in late summer, when they are substantially greater than those of pregnant and

lactating hinds (Anderson 1976). Bubenik (1982) estimates that to produce even a modest set of antlers (14 kg) approximately five and three times the normal daily rates of calcium and phosphorus intake, respectively, are required during the 2 mo of most rapid antler growth. Mineral requirements must be substantially greater for those individuals which produce the largest antlers (20–24 kg).

4. Antler size is closely correlated with both body weight and the frequency of roaring displays during the rut. All three of these traits are important in sexual selection. They are so closely correlated with each other and with reproductive success that it is difficult to separate their independent effects (Clutton-Brock and Albon 1979; Clutton-Brock 1982; Clutton-Brock et al. 1982; Geist 1982). However, Lincoln (1972) has shown experimentally that stags tend to decline in social status following removal of parts of their antlers.

5. Antlers apparently play important roles in male threat displays, combat, and in female choice, although the relative importance of the latter is debated (Geist 1971, 1982; Clutton-Brock 1982; Clutton-Brock et al. 1982). Social dominance among stags and the ability to defend and mate with hinds is related to body size, frequency of advertisement by roaring, and development and use of antlers. Often reproductive competition between males is resolved by threat displays which involve roaring and the display of antlers and the body profile, but combat is frequent and costly. Of Russian stags found dead in the field, 13% had died of wounds received in combat (Heptner et al. 1961). Among Scottish stags 25% show some sign of damage and 6% are permanently injured in fighting each year (Clutton-Brock et al. 1979).

6. Antler size is correlated with social status during the nonbreeding season. Males with larger racks have differential access to limited resources, and this in turn promotes maintenance of health, growth, avoidance of predators, and production of larger antlers and enhanced reproductive success in the subsequent breeding season (Appleby 1980; Geist 1982). This is an example of a genotype-environment interaction and correlation.

7. The data of Clutton-Brock et al. (1982) provide no evidence for a trade-off between survival and reproductive success in male red deer that might be attributed to a handicapping effect of large antlers. Male reproductive success per year after reaching prime reproductive age, is, if anything, positively correlated with lifespan, and lifetime reproductive success definitely is positively correlated with longevity. Furthermore, there is no significant difference between males and females in age structure or age-specific mortality rates, even though fighting often results in serious injuries to stags.

8. In caribou and reindeer (genus *Rangifer*) females possess well-developed antlers. Although the function of these structures is poorly understood, this seems to provide an example of a costly trait that cannot be considered a handicap because it apparently contributes to the survival of both sexes as well as to male reproductive success (see also Packer's [1983] discussion of horns in female antelope).

These observations are consistent with the assumption that large antlers and the associated traits of large body size and frequent roaring reflect the overall genetic quality of stags which should benefit both male and female offspring. Two addi-

tional kinds of evidence provide more direct support for this relationship. (1) Social dominance, which is correlated with antler size, appears also to be positively correlated with genetic heterozygosity in elk (Craig and Baruth 1965). Both antler size and body weight are associated with multilocus heterozygosity in white-tailed deer, *Odocoileus virginianus* (Smith et al. 1983). The adaptive significance of genetic heterozygosity is debated, but these correlations support the view that it is positively related to fitness.

2. Clutton-Brock et al. (1982) show one way that male sexual traits of red deer affect their female offspring. Antler size and body weight of mature stags is positively correlated with their antler development and body size as yearlings. Antler size of yearlings is influenced by their birthdate. Yearlings with smaller than average antlers tend to be born after the mean calving date of the population. It follows that sexual selection for large antler size also selects for early calving time in females because females which calve late tend to produce smaller offspring which will have smaller antlers and lower reproductive success at maturity. Presumably some other form of selection, such as the stress of pregnancy during the winter, acts on females to counterbalance this effect and results in a net normalizing selection for calving date.

Nuptial Coloration in Fishes

Kodric-Brown's investigations of the factors influencing female choice and male reproductive success in fishes provided many of the observations which have led us to develop these ideas about sexual selection. Among the characteristics of the breeding systems of fishes, especially freshwater forms of the families Cyprinodontidae and Poeciliidae, are the following features of nuptial coloration. (1) Although the particular color patterns of males are under precise genetic control (Haskins et al. 1970), the degree of phenotypic expression of these traits is highly variable. This is perhaps best seen in pupfishes (*Cyprinodon*) in which the development of nuptial coloration depends upon possession of a breeding territory (an example of a gene-environment interaction), and varies even within individual territorial males from minute to minute and day to day (Kodric-Brown 1978, 1983).

2. Brightness of nuptial coloration is positively correlated with body size, territory quality, frequency of agonistic displays, and fights with other males, and with female choice in pupfishes (Kodric-Brown 1977, 1978, 1983). In fact, male traits affecting female choice are so highly intercorrelated that it is difficult to separate their individual effects, even by means of controlled manipulative experiments. Many of the motor patterns used in agonistic displays toward other males are also important components of courtship (Barlow 1961; Liu 1969).

3. Development of intense nuptial coloration and associated breeding behavior reflects ability to avoid predators and to acquire limited food resources. Endler (1980) has shown by means of both field observations and laboratory experiments that variation among populations of guppies in the pattern of brightness of nuptial coloration is related to risk of predation. In habitats where piscivorous fishes or shrimps are present, predation is such a severe source of mortality in males which

contrast in color with their backgrounds, that breeding coloration reflects a compromise between female preferences for bright colors and the advantage of being inconspicuous to predators. Red and yellow carotenoid pigments are important components of the nuptial coloration of guppies (Endler 1980; A. Kodric-Brown, in prep.). Since these pigments are synthesized from carotenoids acquired in the diet, the expression of red and yellow colors reflects the ability of males to capture the invertebrates which are the source of these substances (an example of a gene-environment correlation). Such foraging proficiency should benefit female as well as male offspring because carotenoids are an important constituent of eggs (Fox 1976). Thus expression of red and yellow pigments is an honest advertisement because only vigorous males can build up high concentrations. Similarly, the bright blue iridescent colors of breeding male pupfishes are not subject to cheating because they accurately reflect physical condition which is continually tested in combat with other males.

Thus in fishes, in which female choice can clearly be shown to play an important role in breeding behavior, sexual selection has resulted in characteristics of nuptial coloration that are similar in many ways to the antlers of deer. Nuptial coloration is an honest advertisement because it is phenotypically variable, is costly to produce and maintain, and reflects the overall phenotypic vigor and presumably the genetic quality of the males.

DISCUSSION

The idea that sexual selection favors the evolution of traits that honestly advertise the phenotypic and genetic quality of males is not new. Empirical biologists studying the breeding systems of a wide variety of polygynous species have long noted that females consistently choose to mate with the most vigorous males, clearly suggesting some kind of truth in advertising mechanism (e.g., Geist 1966, 1982; Trivers 1976; Halliday 1978; Clutton-Brock and Albon 1979; Rutowski 1979, etc.). Zahavi (1975) provided a conceptual basis for these observations by pointing out that in order for an advertisement to be honest it must be costly. Theoretical biologists, on the other hand, have seemingly continued to prefer to elaborate on Fisher's idea of runaway selection, in part because of the logical problems in defining a genetic mechanism that would maintain adaptive variation in male sexual traits (e.g., Davis and O'Donald 1976; Maynard Smith 1976; Bell 1978; Lande 1980, 1981; O'Donald 1980, 1983; Kirkpatrick 1982; Arnold 1983). Recently, however, several explicit mathematical models of truth in advertising mechanisms have been advanced (Hamilton and Zuk 1982; Andersson 1982; Nur and Hasson, in press).

We attempt to provide here a synthetic conceptualization of the interrelationships among the diverse phenomena associated with sexual selection. In particular, we provide a counterpoint to Arnold's (1983) recent treatment, which also attempts to reconcile theoretical and empirical perspectives, but which advocates a Fisherian mechanism. As pointed out earlier, Fisherian selection fails to make most of the predictions that are direct consequences of the truth in advertising model, and most of these predictions are supported by a large body of consistent

empirical data on the antlers of deer, the nuptial colors of fishes, and other sexual traits that we have not discussed for lack of space. By developing rigorous and realistic models of Zahavi's handicap principle, Andersson (1982) and Nur and Hasson (in press) provide an important first step in developing sound analytical models of the truth in advertising mechanism. However, several important theoretical issues remain to be resolved.

Virtually all treatments of sexual selection, from Darwin to the present, have emphasized a fundamental dichotomy between sexual selection, which favors the evolution of traits that promote successful competition for mates, and natural selection, which favors the evolution of traits that contribute to other aspects of reproduction and especially to survival. We believe that this dichotomy, which seems to have reinforced the idea that sexually selected traits must reflect a trade-off between promoting mating and handicapping survival, is unfortunate and misleading. We recognize that all organisms have a limited supply of energy and other resources so that allocation to present reproduction may reduce longevity and future reproduction (e.g., Schaffer 1974; Stearns 1976). Nevertheless, the currency of evolutionary adaptation is fitness, the product of fecundity and survivorship, and selection will consequently tend to favor traits that maximize this quantity by increasing both survival and reproduction. Thus it is not surprising that some sexually selected traits, such as the antlers in deer and large body size in many animals, rather than being handicaps, actually promote survival by enhancing intraspecific competitive ability and predator resistance. Although other traits, such as long plumes in birds and bright colors in many animals, may jeopardize long-term survival at the expense of reproduction in males, these traits are no more handicaps than those involved in the production and care of offspring which result in similar trade-offs in females. In fact, the essence of the truth in advertising mechanism is that it is a special form of natural selection. It operates differentially on breeding males to promote the evolution of the same kinds of traits, those correlated components of fitness that are the basis of the honest advertisement, that are favored by other mechanisms of natural selection operating on females and nonbreeding males.

A largely unrecognized consequence of the truth in advertising mechanism is that it provides a potentially important explanation for the evolution and maintenance of sex. Williams (1975) pointed out that in most higher organisms, in which males contribute only genes to their offspring, a parthenogenetic female, which produced only female offspring, over evolutionary time would leave twice as many descendants as a sexual female which produced equal numbers of male and female offspring. Williams called this the 50% cost of sex, and Maynard Smith (1978) noted that it might more precisely be called the 50% cost of producing males. The truth in advertising hypothesis implies that this cost is overcome, at least in part, by the advantage of males in contributing more fit genes to their offspring than their mates. Since in polygynous breeding systems a much smaller proportion of males than of females contribute as parents to the next generation, and these successful males also tend to be those of highest overall fitness, the average quality of genes contributed by fathers will be higher than of mothers. Trivers (1976) recognized this and suggested that if the average fitness of genes

contributed by the male parent were twice that contributed by the female parent, this would be sufficient to offset the cost of males and hence to prevent the increase of parthenogenetic clones. Trivers' conditions seem unnecessarily restrictive. Given the apparently low rate of viable parthenogenetic mutations, it seems necessary to postulate only a small advantage each generation in order to account for the gradual elimination of parthenogenetic clones in competition with their sexual relatives over evolutionary time. In polygynous species, the differential intensity of selection on males resulting from sexual selection should result both in more rapid evolution in response to directional selection and in the maintenance of a narrower range of variability (because of more severe selection against deviant phenotypes) in response to stabilizing selection.

Up to this point, we have considered the effects of sexual selection only on those polygynous breeding systems in which males do not contribute resources or care to their offspring. Sexual selection is also important in other breeding systems, such as monogamy. To the extent that the fitness of offspring depends on male parental investment and care, sexual selection will favor females that choose mates on the basis of traits that honestly advertise the ability of males to make these contributions; the relative importance of male genetic quality will be reduced concomitantly. The differential action of selection on males will also be reduced as the parental investment of the two sexes becomes more equal, and these material contributions of males will compensate for their diminished genetic quality (compared to polygynous males) in accounting for the maintenance of sexual reproduction.

In developing the truth in advertising model, we have shown why it is consistent with the commonly observed pattern of intraspecific variation among males in sexual traits: that there is substantial variability among individuals, and the expression of the traits reflects differences in phenotypic vigor and genetic quality rather than variation in the genes that code directly for the traits themselves (see also Andersson [1982]; Nur and Hasson, in press). It is less obvious how this model accounts for two other patterns of variation in sexual traits frequently observed in empirical studies: on the one hand, the maintenance of substantial variation, including polymorphisms, in the genes coding for sexual traits; and, on the other hand, the almost invariant nature of certain other traits. The existence of genetic variation in sexual traits is well documented. For example, there is significant heritable variation in antler size and configuration within and between populations of elk and deer (Harmel 1983; Templeton et al. 1983; Bubenik 1982). Similarly, there is genetic variation in nuptial coloration within and between natural populations of guppies (Haskins et al. 1961; Endler 1980). We can account for this variation in two ways. First, some of this variation may not be related to differences in male quality, and hence will not be subject to directional sexual selection which would tend to eliminate it. For example, details of the different branching patterns of the antlers of elk and red deer are probably unrelated to male vigor, although antler weight and number of tines are not. When alternative traits are not correlated with overall male quality, frequency-dependent selection can produce and maintain polymorphisms (O'Donald 1980). An apparent example of this in nuptial coloration of fishes is the reproductive advantage of rare male color morphs in guppies (Farr 1977).

A second explanation for genetic variation in sexual signals is that, to the extent that different genotypes differentially allocate resources to attributes used in mating, it might not be advantageous for all males to have the same genotype. It is easy to imagine that the optimal pattern of allocation might vary spatially between habitats. For example, since the ability to produce large antlers in deer and elk varies among habitats which provide forage of different nutritive value (Smith et al. 1983; Geist 1982), it would not be surprising if these differences selected for different patterns of allocation of resources to antlers. McKaye and Barlow (1976) have shown that dimorphic male nuptial coloration in a population of fishes (*Cichlosoma citrinellum*) is maintained by differential selection of alternative morphs in different microhabitats.

Many alternative male breeding strategies that are associated with differential expression of sexual traits, however, probably do not reflect heritable differences in the traits themselves. To the extent that maximal expression of these traits honestly advertises overall genetic quality, males that are incapable of making the investment required for maximum expression of traits will be at a disadvantage, because females choosing such mates will be selected against. Nevertheless, we would expect these males to engage in behavior that would enable them to achieve some reproductive success (Constantz 1975; Gross 1982). Thus, alternative male reproductive strategies, such as attempts at sneak copulations in many organisms, including deer and fishes, often can be interpreted simply as young or inferior individuals making the best of a bad situation.

It must also be recognized that some sexual traits exhibit virtually no variation among males. Perhaps the best examples are the bright color patterns of many male passerine birds, including highly polygynous species such as manakins. (D. McDonald, personal communication). An explanation for such essentially invariant traits that is consistent with the truth in advertising mechanism is being modeled by D. McDonald and D. Thompson (personal communication). They suggest that the invariant trait represents a constant cost, analogous to the ante in betting games, that males must pay to compete successfully for females. Consequently most mature males in good condition will express the trait to the same degree; but to the extent that resources that can be allocated to reproduction are limited and vary among males, the necessity of paying the ante will exaggerate differences among males in resources that could be devoted to other sexual traits such as courtship displays. This model predicts that invariant traits should enhance the honesty of the variable traits with which they are always associated and which provide the actual basis for female choice.

The quantitative details of the truth in advertising model will have to be developed before it will be possible to specify precisely the conditions under which this mode of sexual selection can operate. The effectiveness of sexual selection will depend on at least three things: (1) the degree of correlation (covariance) between the expression of the sexual trait and overall fitness; (2) the extent to which the variations in male quality can be inherited by both male and female offspring. (In this regard it is encouraging to note that Partridge's [1980] experiments on *Drosophila* suggest that opportunity for females to choose among competing males confers a significant advantage upon the offspring; also, Ander-

son et al. [1979] have attributed the substantial variation in allele frequency between local populations of *Drosophila* to differential reproductive success of males); (3) the advantages to females of choosing genetically superior males to father their offspring, which must outweigh any costs (measured in terms of time, energy, etc.) of female choice (Parker 1983). Continued interplay of mathematical theory and empirical studies will be necessary to resolve these problems and to test rigorously the predictions of the Fisherian and truth in advertising models.

SUMMARY

The truth in advertising model describes a mechanism of sexual selection to account for the evolution of the kinds of traits used by males of polygynous species to compete for and attract mates. Sexual selection favors the display of male traits that vary phenotypically within and among individuals in such a way as to maintain a positive correlation between the degree of expression of the traits and overall genetic fitness. Because the exaggerated expression of these traits requires allocation of limited resources to reproduction, it reflects age, nutritional condition, social status, and resistance to predators and pathogens. It is advantageous to females to choose as mates individuals with such exaggerated traits (and also those that have won aggressive bouts with other males) because these traits honestly advertise desirable attributes that can be passed on to both male and female offspring. By stressing the relationship between sexual traits and overall male fitness, this model deemphasizes the traditional dichotomies between the effects of sexual selection and natural selection and between female choice and male-male competition as mechanisms of sexual selection. Necessary conditions and predicted consequences of the truth in advertising mechanism are illustrated with examples of antlers of deer and nuptial coloration in fishes.

ACKNOWLEDGMENTS

We are grateful to numerous students and colleagues for discussing the ideas presented here. We especially thank R. E. Michod, D. McDonald, and D. B. Thompson for numerous discussions which shaped and influenced our ideas on sexual selection, and for critically reading and making helpful comments on two earlier versions of the manuscript.

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