Is Sexual Selection a Burden?

Two biologists challenge the traditional interpretations of sexually selected traits, which assume they can be a threat to survival

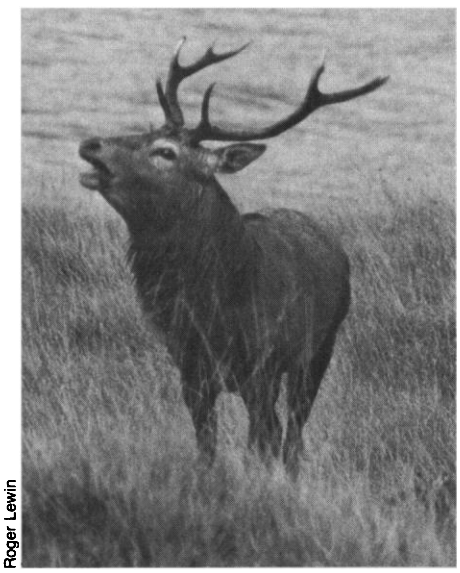
The phenomenon of sexual selection is the subject of much wonderment, confusion and disagreement among biologists. Some of the most spectacular manifestations of nature—such as the brilliant plumes of birds of paradise and the massive and elaborate antlers of the extinct Irish elk—are considered to be products of this type of selection, and as such often present problems. Most common is the apparent burden that such elaborations inflict on their bearers, and a lot of theoretical discussion has focused on attempts to explain this observation. Two researchers at the University of Arizona, Astrid Kodric-Brown and James Brown, have recently proffered an interpretation of sexual selection that appears to eschew this problem, mainly by suggesting that sexual traits are frequently not the burdens they seem (*1*).

In addition to seeing positive attributes in sexually selected traits outside the arena of improved access to mates, the Tucson researchers argue that the exaggeration of such traits is a reflection of the overall genetic fitness of the individual carrying them and therefore represent a "truth in advertising" display. For example, a red deer stag will sport an impressive set of antlers—which are important in combat with other males over access to females—only if the animal is generally fit in the Darwinian sense. A female mating with such a stag can be assured that her offspring will be sired by a fine set of genes.

Another problem that exercises evolutionary biologists is whether sexual selection, which has to do with access to mates, should be considered as separate from and complementary to natural selection, which concerns individual survival, or the "struggle for existence," as Darwin called it. Most biologists do treat the two as separate and distinct processes, principally because, contrary to natural selection, sexual selection appears to produce traits that can be maladaptive in individual survival. For instance, impressive though it is to peahens, the peacock's tail is undoubtedly a burden and potential hazard to its bearer.

Kodric-Brown and Brown, by contrast, consider the separation of natural and sexual selection as "unfortunate and misleading." Their heterodox position on this point stems in part at least from their consideration of many sexually selected traits as being aids, rather than handicaps, to survival. Success in reproduction and survival, they say, are partners in contributing to the currency of evolutionary adaptation—fitness. "In fact, the essence of the truth in advertising mechanism," they say, "is that it is a special form of natural selection."

Access to mates is a matter of competition in biology because it is the means by which genes are passed on to subsequent generations. The fact that for females reproduction is typically a more expensive affair than it is for males, who frequently contribute little more than the required gametes, means that competition for mates among males is intensified. Any characteristic that enables a male to mate with more females than his fellows enjoys greater reproductive success and therefore greater representation in the next generation. It is such characteristics that are the subject of sexual selection. And it was the fact that such traits often appear to be potentially injurious to survival that forced Darwin into a discussion of sexual selection as distinct from natural selection.



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Rutting red deer stag

Body size and antler size are important to stags for success in the annual rut. Both features are metabolically expensive to produce and depend on the animals being able to gain access to prime resources.

Sexual selection can be manifested in two forms: through the development of traits that are utilized in direct competition between males (such as fighting equipment and skills); and through the elaboration of features that make males more attractive to females (courtship and other displays). Biologists usually agree on the identity of sexually selected traits, but often dispute the precise mechanism by which they evolve. Currently there are two main interpretations: the runaway selection model and the handicap model.

The runaway selection model, which was first advanced by R. A. Fisher in 1930, focuses on the power of female choice in selecting a mate on the basis of any trait that confers an initial survival or reproductive advantage. Because of continued selection through the generations, such a trait eventually becomes extremely exaggerated, perhaps to the detriment of the bearer. At some point a balance is reached between reproductive advantage and burden on survival. In this model the selected trait can become uncoupled with the general fitness of the individual. In addition, the qualities associated with the exaggeration of the trait are confined to the male offspring.

In the mid-1970's Israeli biologist Amotz Zahavi proposed a more organismal approach, one that involves more than just the sexual trait being selected. Like the runaway selection idea, Zahavi's handicap hypothesis also proposes that sexual selection favors development of traits that promote male reproductive success at the expense of survival. But the difference is that the development of such traits is linked to superior genetic qualities in the males: the sexually selected traits must be costly to produce. In other words, Zahavi introduced the concept of honesty in advertising in sexual selection. Because sexually selected traits are linked to overall genetic fitness, both male and female offspring benefit from the filter of sexual selection, which again differentiates this viewpoint from the runaway selection model.

In spite of their differences, both the Fisher and Zahavi approaches accept that sexual selection will inevitably push males into the precarious position of jeopardizing their own survival, either going into massive metabolic deficit or becoming easy prey to predators. But, compared with the handicap hypothesis, the runaway selection idea is more accessible to mathematical modeling and has become the favored explanation of sexual selection among many theoretical biologists (*2*).

Kodric-Brown and Brown clearly favor Zahavi's position more than Fisher's. They stress the point that sexually selected characteristics should be only weakly heritable, so that their elaboration in any particular individual will reflect overall phenotypic vigor, in gaining access to resources for instance. The development of big antlers in red deer, for example, depends in large part on the animal's age and on superior nutrition. Similarly, the bright blue coloration required by pupfish males in order successfully to attract gravid females to their territory depends on their access to good quality food and on fighting displays. Large antlers in red deer and bright nuptial coloration in pupfish are examples of an interaction between genes and environment and as such represent truth in advertising, say the Tucson researchers.

Where Kodric-Brown and Brown depart from the handicap model is in saying that the elaborated sexual trait need not necessarily be a handicap. In focusing too narrowly on the reproductive function of sexually selected traits biologists too often overlook their potential contribution to improved survival, they argue. "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."

The Tucson researchers' definition of cost is therefore best seen as being broader than Zahavi's. Zahavi says that advertising must be costly to be honest, which is true. But Kodric-Brown and Brown believe that cost does not inescapably have to imply potentially reduced survival. They agree that some sexually selected traits, such as long plumes and bright nuptial plumes, may increase the risk of predation while enhancing attractiveness to females. But they insist that there is no "necessary trade-off between the expression of male sexual traits and survivorship."

Central to the Kodric-Brown/Brown argument is a considerable plasticity in development of sexually selected characteristics. The existence of some apparently invariant sexual traits, such as the bright color patterns of many male passerine birds, such as manakins, might therefore seem to challenge their hypothesis. Here, once again, they suggest that too narrow a vision has been used in assessing the factors involved in attracting females. The plumage should be regarded as a basic entry fee in the courtship game, after which other features in the overall display become crucial.

Kodric-Brown and Brown contend that biologists too often concentrate on just one or two obvious traits in mating behavior and overlook the real degree of complexity, including the manner in which it might be integrated with the animals' survivorship needs. The theoreticians point out that, so far at least, mathematical models have failed to substantiate the premises of the honesty in advertising hypotheses. "This short-circuits theoretical work on the topic," says Stevan Arnold of the University of Chicago. Kodric-Brown and Brown reply that this reflects an inadequacy of the inevitably simplified mathematical models, not that the proponents of the honesty in advertising position are misinterpreting the natural history observations they make.—**Roger Lewin**

References

1. A. Kodric-Brown and J. H. Brown, *Am. Nat.* **124**, 309 (1984).
2. S. J. Arnold, in *Mate Choice*, P. Bateson, Ed. (Cambridge University Press, New York, 1983), pp. 67–107.

Oncogene Linked to Cell Regulatory System

Analysis in yeast of the activity of the ras *oncogene suggests that it works through adenylate cyclase, a major cell regulatory enzyme*

The transforming protein produced by the *ras* gene, one of the two dozen or so oncogenes that have been implicated as possible contributors to cancer development, is an activator of the enzyme adenylate cyclase, at least in yeast. This result, which was presented by Michael Wigler of Cold Spring Harbor Laboratory at the Seventh Annual Bristol-Myers Symposium on Cancer Research, links the *ras* product to what may be the best studied of the cell's regulatory systems. Adenylate cyclase, which catalyzes the formation of cyclic AMP (cyclic adenosine monophosphate) from ATP (adenosine triphosphate), is activated when any of several hormones or neurotransmitters binds to specific receptors on the cell surface. The enzyme is an integral component of the system that transmits the hormonal signals from the membrane to the cell interior.

Robert Weinberg of the Massachusetts Institute of Technology characterized the work, an early example of the way in which the function of a potential cancer gene can be dissected in a simple eukaryotic organism, as "one of the milestones of cancer research." It grew out of last year's discovery by Deborah DeFeo-Jones and Edward Scolnick of Merck Sharp & Dohme Research Laboratories in West Point, Pennsylvania, and then by the Wigler group that yeast contains its own *ras* gene counterparts.

Many living species, including humans, rodents, and fruit flies, also carry *ras* genes. These genes are thought to be required in normal cells for the regulation of growth and differentiation, a hypothesis that is supported by their presence in such evolutionarily diverse species. However, the genes were first identified in animal cancer viruses that had picked up the genes during the course of infection. In contrast to the normal genes, those of the cancer viruses can cause the malignant transformation of cells. Identification of *ras* genes with the ability to transform in several types of human cancer cells has lent credence to the view that the genes may contribute to cancer development.

The activation of the transforming potential of the *ras* genes in cancer cells and the viruses has been linked to small structural changes in their protein-coding sequences. Analyzing the biochemical functions of the normal and transforming *ras* products, although a matter of intense interest, has proved difficult in the higher organisms. Identification of the genes in yeast cells opened the door to studies of *ras* functions by methods that are simply not applicable to mammalian cells. "Yeast has clearly emerged as one of the best systems for studying the mechanism of the oncogene's action because you can combine genetic and biochemical studies," Scolnick notes.

The Wigler and Scolnick groups have found that yeast contains two *ras* genes,