

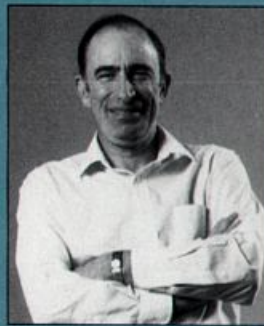
Widowbirds look like small airplanes towing huge banners, and on the ground the bird seems as if it could use the sort of help that queens once got from small children carrying the trains of their royal gowns.

ONE OF THE MOST interesting sights for a birder in Africa is a male Long-tailed Widowbird in breeding plumage. Whether it is doing its undulating courtship flight, simply flying by, or hopping along the ground searching for seeds, the bird's ridiculously long tail is a source of instant astonishment. In flight, the widowbird looks like a small airplane towing a huge banner, and on the ground the bird seems as if it could use the sort of help that queens once got from small children carrying the trains of their royal gowns. Widowbirds are weavers, but the males with their long tails superficially resemble males of several species of African whydahs, brood parasitic finches. The females of both groups are inconspicuous and have "normal" short tails. Male widowbirds and whydahs have a very good reason for evolving their vast caudal impediments: They help the birds get mates. Females fancy the long-tailed males.

The preference of female widowbirds was demonstrated through an elegant series of experiments by Swedish ornithologist Malte Andersson. He captured males and modified the lengths of their tails with scissors and glue. Males with both supplemented and bobbed tails and "control" individuals (ones whose tails had been snipped and glued back on without changing

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BIRDING FOR FUN



Sexual Selection

Illustrations by Darryl Wheye

their length) were released, and their mating success studied. The widowbirds are polygynous—one male normally mates with more than one female. It turned out that the males with the artificially lengthened tails persuaded significantly more females to settle in their territories than either the short-tailed males or the controls. The poor bob-tails had the least mating success of all.

The importance of tail length is not limited only to exotic birds of the African savanna. In similar experiments, another Swedish ornithologist, Anders Møller, manipulated tail-length in Barn Swallows, which unlike the widowbirds are monogamous. He found that males with lengthened tails were able to obtain mates earlier and fathered second clutches more frequently.

More than twice as many young fledged from their nests in a single season than from the nests of males with artificially shortened tails. In addition, females preferred males with artificially enhanced tails as partners when they copulated with other than their mates ("extra-pair copulations").

If individuals with certain genetically-controlled characteristics reproduce more than those with others, biologists say that natural selection is occurring. When one sex prefers certain kinds of individuals as partners, and those kinds are genetically different from others of

their sex, they become agents of sexual selection. It was Charles Darwin who originally proposed that the so-called secondary sexual characteristics of male animals—such as the elaborate tails of peacocks, the colorful expandable throat sacs of grouse, the bright plumage and melodic songs of many male passerines, large racks in bull mooses, deep voices in men—evolved because females preferred to mate with individuals that had those traits. In the widowbirds, whydahs, and swallows, the evidence clearly indicates that female choice has caused sexual selection, and has led to the evolution of long-tailed males.

Since the females apparently prefer the males with the longest tails, why haven't male widowbirds, whydahs, or swallows evolved tails of even greater length? Why hasn't the process led to six-inch weavers with sixty-inch tails? The obvious answer is that plain old natural selection counters sexual selection. Male widowbirds in breeding plumage do not even look airworthy, and dragging their lengthy ornament around must make them much more vulnerable to predators. Male Barn Swallows also pay a price for sexual success. Møller discovered one of the costs of their long tails: Birds with experimentally lengthened tailfeathers captured smaller, less profitable prey, and their plumage showed signs of dietary deficiency. In short, a balance exists between selective forces: At the point where the costs of lengthening the tail balance the benefits, selection no longer favors individuals with longer tails.

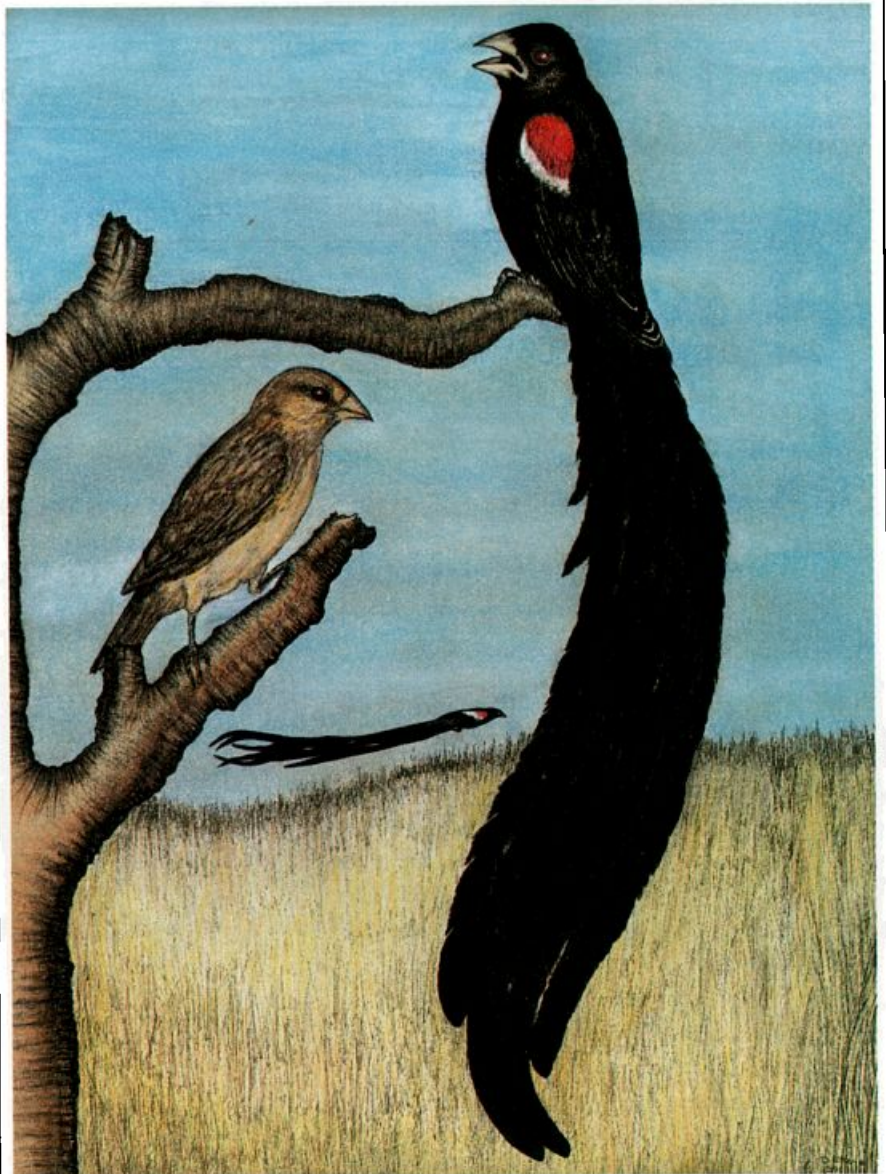
Sexual ornaments do not, however, necessarily reduce the chances of an individual surviving. In pheasants, experimental manipulation of the length of spurs on the legs of males has shown that long spurs are attractive to females. The length of a male's leg spurs is also a good indi-

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cator of whether or not an individual will survive the winter. In a similar vein, behaviorists W.D. Hamilton and M. Zuk have proposed that males possessing bright and elabo-

rate plumage and able to put on prolonged displays (including long, complex, and variable songs) are relatively free of parasites and disease. Resistance to those afflictions could have a genetic component, in which case the male would be a very desirable mate. Support for that notion has been found in correlations in both Europe and North America between parasite infection and bright male coloration and in experimental work showing that artificially infected Red Jungle Fowl (*Gallus gallus*) had duller colors than uninfected birds (even though parasite load did not affect traits like bill size and body weight). Support for



A male Long-tailed Widowbird in breeding plumage.



Breeding plumage of the polyandrous female Red Phalarope (left) is far brighter than that of the male (right).

the notion that disease-free males are better songsters has not been found, however. Rather, it has recently been shown that there is no relationship between song quality

Female phalaropes compete for the plain-colored males, who will incubate her eggs and tend her young.

and parasite infection. Future tests of the Hamilton-Zuk hypothesis could include investigation of whether the most decorative males and the most elaborate displays are found in areas where pathogens and parasites pose the greatest threats to avian populations.

As evidence that sexual selection for bright coloration is widespread, consider the reversal of normal sexual differences in the ornamentation of some polyandrous birds. There,

the male must choose among females, which, in turn, must be as alluring as possible. Consequently, in polyandrous species, the *female* is ordinarily more colorful—*her* secondary sexual characteristics are enhanced. This fooled even John James Audubon and John Gould, who confused the sexes when labeling their paintings of phalaropes. Female phalaropes compete for the plain-colored males, who will incubate her eggs and tend her young.

Of course, females may choose among males (or vice versa) on the basis of quite impersonal characteristics. For example, female Red-winged Blackbirds and Marsh Wrens apparently use the quality of a male's territory as a basis for deciding whether or not to mate with him. Basically, if a choice is possible, individuals seemingly cue in on virtually any sign of genetic superiority in picking a mate. And in so doing, they help to guide the evolution of the opposite sex.

Further work is required to determine the details of mate choice in birds, and to settle many issues related to sexual selection. The effort required will be considerable, and suitable systems may be

difficult to find, but the results should cast important light on the evolutionary origin of many physical and behavioral avian preferences. We know remarkably little about the origins of sexual selection. Why, for example, do female widowbirds prefer long-tailed males? Possibly females choose such males because the ability to grow and display long tails reflects their overall genetic "quality" as mates—and the females are thus choosing a superior father for their offspring (as apparently are female pheasants when they pick long-spurred males).

Or the choice may have no present adaptive basis but merely be the result of an evolutionary sequence that began for another reason. Perhaps the ancestors of Long-tailed Widowbirds once lived together with a population of close relatives whose males had slightly shorter tails. The somewhat longer tails of males of the "pre-Long-tailed" Widowbirds were the easiest way for females to recognize mates of their own species. Such a cue could have led to a preference for long tails that became integrated into the behavioral responses of females. Although I am inclined to think the former scenario is correct, and that tail-length is a reflection of genetic quality, the data in hand do not eliminate the second possibility.

At one time, it was thought that the brilliant colors and sweet songs of male birds were designed by God to please human beings. We now understand that they evolved for a more earthy purpose, one more related to the function of singles bars than art galleries or symphony halls. ■

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