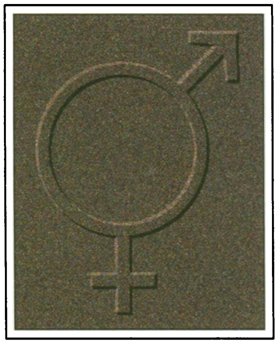
SEXUAL SELECTION—I

Swallows and Scorpionflies Find Symmetry Is Beautiful

It is the end of the mating season for barn swallows. All over North America and Europe, male swallows have been singing their twittering song as they pirouette through the air, their forked tails lending grace to the maneuvers, while females watch from perches on telegraph wires and barn roofs. But this romantic country scene is not quite the idyll it might appear. Each female is looking for the best male to choose as a mate and is equipped with the hard-hearted ability to measure up male quality—with one of the main criteria being the size and shape of a potential partner's tail. She follows two rules: the longer the tail, the better; and—surprisingly—the more symmetrical the tail, the better.



After years of being ignored in favor of study of the size of tails, crests, and other bizarre sexual ornaments of the animal world, the subtle cue of symmetry is now suddenly the topic of the moment in the study of sexual selection. By one of those coincidences that characterize science, two biologists on opposite sides of the globe have independently discovered that the key to solving an old argument of biology—how females choose males with good genes—may lie in symmetry. Measures of symmetry now look as though they could help settle the long-running argument between two groups of theorists over whether "runaway evolution" or "good genes" is the key force behind such extravagant male sexual displays as the peacock's tail and the nightingale's song.

One of the two researchers to emerge at the forefront of research on symmetry is Danish zoologist Anders Møller from Uppsala University, currently on sabbatical at University College, London. His new experiments—published in *Nature* (21 May, p. 238)—provide unexpected evidence that female swallows prefer male swallows, which have tails that are symmetrical as well as long. "I never expected that females would pay attention to symmetry," says Møller, "but they do." Males with symmetrical tails pair more quickly and hatch more offspring than competitors with asymmetrical tails.

The second researcher is ethologist Randy Thornhill of the University of New Mexico in Albuquerque, whose work will appear later this year in *Behavioral Ecology*. Thornhill has made an even more astonishing discovery. Among Japanese scorpion flies, females prefer the smell of a male with a symmetrical body to the smell of a male with an asymmetrical one—even when they cannot see the males.

ANIMALS ANIMALS/TERRY MURPHY

ANIMALS ANIMALS/STEPHEN DALTON

Evolutionary force? Female swallows look for mates with perfectly forked tails and scorpionflies prefer symmetrical bodies. The key question is whether these attributes denote "good genes" or the height of fashion.

"This was a very surprising result," says Thornhill. To mate successfully, scorpion flies must fight off other males and then lure females into copulation by offering them insects stolen from spiders' webs. But despite these challenges, "symmetry was a better predictor of male mating success in scorpion flies than size," says Thornhill. "In the field, symmetrical males won more fights and mated with more females.

But surprising as these results were to both Møller and Thornhill, when added to other recent research from Møller to be published in *Genetica*, they help to sort out a long-running dispute over which of two theories better explains the evolution of extravagant male ornaments.

The first of the theories descends from Charles Darwin. His answer to why peacocks have such fancy tails was simple: Peahens prefer to mate with peacocks with such ornaments. But that answer satisfied few of his contemporaries, who asked, quite reasonably, why?

The great University of Cambridge geneticist Ronald Fisher gave one ingenious answer to that question in 1930, in the form of a circular argument. Females prefer fancy-tailed males, he said, because females prefer fancy-tailed males: Any female who flouts the fashion and mates with a short-tailed male is likely to have short-tailed sons who will be ignored by the other females. By the early 1980s, after much mathematical modeling, principally by Russ Lande of the University of Chicago and Mark Kirkpatrick of the University of Texas, theorists had reached a consensus: The Fisher process worked, and even if a "fashion" began just as a tiny random preference, it could take on a life of its own, with "runaway evolution" taking it to bizarre extremes.

But biologists working out in the field were never entirely happy with the modeler's view that physiology was dictated by fashion, not adaptation. Instead, they tended to support the "good genes" theory: A male ornament is like a thermometer in a child's mouth, revealing the health, strength, or genetic fitness of the individual. That view evolved to its own extreme in Tel Aviv University ethologist Amotz Zahavi's "handicap theory" of 1975. He proposed that the very fact that a fancy tail was an encumbrance to a peacock was what made it valuable to the peahen as a criterion for choosing a mate. She knew that he had survived despite carrying such a handicap and that he therefore must be genetically superior.

Observations in the field certainly support the idea that ornaments can be a handicap; it is quite easy, for example, to catch a displaying peacock by sneaking up behind his outspread tail. But Zahavi's theory was ridiculed at first. Once more the mathematicians took over, and, although skeptical, Oxford University theorist Alan Grafen and others showed that Zahavi's idea can also work, so long as cheating is "expensive": The handicap—like the ponderous tail—must be a real one that only males with the best genes are capable of living with.

Impasse. Theorists say that either Fisher's theory or the good genes theory could explain the evolution of the peacock's tail. There is experimental evidence consistent with both, and none that distinguishes between them. Enter symmetry—a very special kind of trait with a long history of study by embryologists and classical geneticists.

"Symmetry is a reflection of how well development goes," explains Andrew Pomiankowski, an evolutionary biologist at University College, London, who works with Møller. "If you stress an organism basically in any kind of way, it becomes more asymmetric." During development, problems such as lack of food, disease, inbreeding, and almost any kind of genetic defect all disturb the delicate balance needed to produce a perfectly symmetrical adult. Asymmetry in the number of bristles on each side of a fruit fly's head has even been used as a measure of the genetic damage caused by inbreeding.


MATS PETTERSSON

Swooping in on symmetry. Anders Møller says he was surprised by the results of his research on swallows.

That the females of creatures as diverse as swallows and scorpionflies actually notice symmetry thus nicely confirms suspicions of its potential importance as a measure of an animal's health and genetic record. It also fits well with the views of "good gene" theorists who have definite evidence that animals pay attention to a measure that reflects genetic quality. But Møller goes further. He believes the symmetry of ornaments will reveal whether the ornaments evolved as "good gene" signals or fashion icons.

Along with his studies on swallows' preference for symmetrical tails, Møller also measured 181 swallows' tails and found a wholly unexpected relationship: The longer the tail, the more likely it was to be symmetrical. This is totally unexpected, for it breaks the general rule that the more any particular character deviates from the norm, the more asymmetrical it is likely to be—for example, swallows' wings that are exceptionally large or small are more asymmetrical than those that are just average.

Møller argues that this would never be predicted by Fisher's theory. Simply selecting for longer and longer tails will certainly produce longer tails, but they should also be more asymmetrical, for the additional stress of development will throw out the delicate genetic balancing act needed to maintain symmetry.

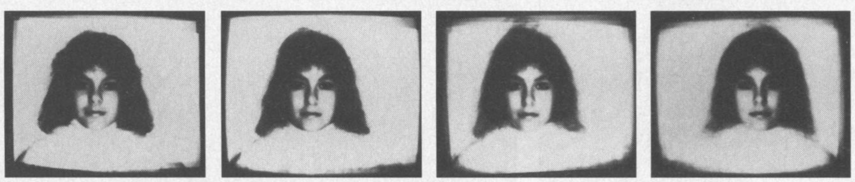
But the relationship between length and symmetry is just what would be expected from "good gene" theory. If a long tail is actually a kind of handicap that only the most genetically superior swallows can tolerate, that means that swallows with long tails are effectively announcing that they have good genes. And the birds with good genes, of course, are exactly the ones expected to have symmetrical tails: Long tails and symmetry then should go together because they both indicate good genes.

That is neat evidence for the "good gene" theory of sexual selection but Møller knows it will take more than a few swallows to convince Fisherians. He has since gone on with University College's Pomiankowski to examine sexual ornaments in five different species, measuring both size and symmetry. The result: Peacocks' tails, widow birds' tails, and beetle horns all fit the good-genes prediction—as they get bigger, they get less asymmetrical. But the feathers of pheasants and quetzals fit the Fisher prediction; as they get bigger they get more asymmetrical. In general, birds that are decorated with lots of different ornaments seem to be the products of Fisher's fashion-driven selection process while those with single ornaments are displaying the quality of their genes. In other words, both theories may be right: a satisfyingly symmetrical ending for a long evolutionary tale.

–Matt Ridley

Matt Ridley is a free-lance journalist who is writing a book on the evolution of sex.

No Better Than Average


JUDITH LANGLOIS

The more the better? Composite of four, eight, 16, and 32 faces.

Symmetry may not be just for the birds. Humans, too, may be susceptible to its charms, and the University of New Mexico's Randy Thornhill intends to look and see. He expects to find that facial symmetry and facial beauty are closely connected. "There's a tremendous amount of asymmetry in faces," he says, "and it probably reflects phenotypic quality. Everything we know about human attractiveness is consistent with symmetry being a factor." People with genetic or nutritional disadvantages during development probably end up with less symmetrical features.

There are already a few clues to what makes a face attractive. It has been known ever since Social Darwinist Francis Galton first did the experiment in 1883 that composite photographs of several faces laid on top of one another tend to be judged more attractive than any of the individual photographs that went into them. Two University of Texas psychologists, Judith Langlois and Lori Roggman, have recently modernized the experiment, digitizing images and adding them together with the aid of a computer. The result: Just as Galton said, the more faces that go into forming the average face, the more attractive it becomes.

Of course, a totally average face is also unusual—because, among other things, it is more symmetrical that any individual face. Is this the reason for its attractiveness? Thornhill hopes to find out. One prediction he is making is that humans will key in on one of the most complicated features of a face, such as the eyes, whose development is likely to be most sensitive to symmetry-altering developmental mistakes. If he is right, the eye will prove to be more than the "window of the soul" but a window to the quality of the genome itself.

–M.R.