Why Guys Get Fancy

The diversity of private parts mystifies biologists

By SUSAN MILIUS

Common-sense mechanics just doesn't explain male genitalia. The male chicken flea, for example, procreates with a complex assemblage of extrusions, nubbins, curled growths, and whatsits that biologist William G. Eberhard has called "one of the marvels of organic engineering."

Yet, the main purpose of such anatomical exuberance seems to be simply to deliver sperm to where they can fertilize eggs. Do the basic requirements of the job warrant all the complex and diverse equipment found throughout the animal kingdom? Wouldn't a simple tube do?

Some male reproductive paraphernalia rank as "the most complex organs in the entire body," notes Eberhard of the Smithsonian Tropical Research Institute and the University of Costa Rica. In certain nematodes and flies, male sexual structures grow longer than the rest of the body. "It is just too fantastic to believe that such complicated machinery is necessary only to perform a mechanically simple function," Eberhard concludes.

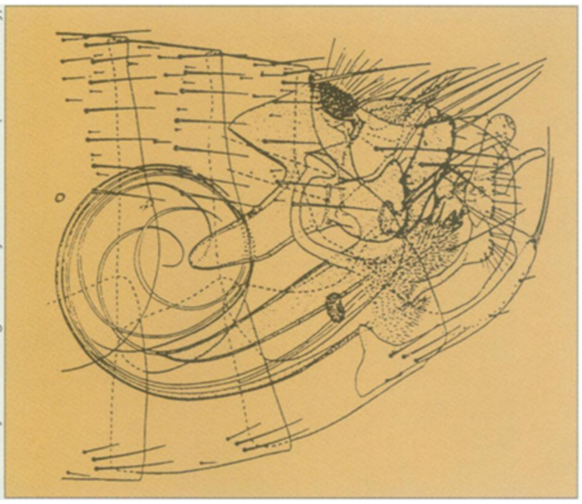
In his classic book *Sexual Selection and Animal Genitalia* (1985, Harvard University Press), Eberhard proposed an alternative explanation: that female choice drives the evolution of male genitalia in animals with internal fertilization. All the male's bumps, bristles, spurs, and wiggly bits have evolved as added attractions in the competition for fatherhood, private versions of the peacock's tail.

Now, Göran Arnqvist of the University of Umeå in Sweden has devised a way to test the female-choice idea against a time-honored rival, the lock-and-key hypothesis. The older idea explains diverse and complex genitalia as specialized lock systems that evolved as last-minute checks to tell Mr. Right Species from Mr. Wrong.

Arnqvist's test results, reported in the June 25 NATURE, strongly support Eberhard's idea of female choice and raise doubts about the lock-and-key model. The results have impressed students of male genitalia but have not settled the argument, particularly among biologists who call for more research on female anatomy.

From the microscopic to the massive, male genitals have been thoroughly studied. Taxonomists often depend on the genitals' distinctive shapes to tell one species from the next.

If taxonomists can use a character to identify species, that trait must evolve fast, notes Eberhard. "That is, it acquires a new form in each new species." This trend toward rapid divergence pops up in all major animal groups where internal fertilization predominates, he says.



Royal Entomological Society/British Museum(Natural History)

Do the mechanics of the job—transferring sperm to a female—really demand all the complex genital anatomy on the rear of a male chicken flea?

Debate over why male genitalia change so quickly dates back at least to the last century, when the lock-and-key idea ruled. Its followers described cases of oddball male shapes that nestle perfectly into female counterparts. However, the examples could fit other hypotheses, Eberhard says.

As an alternative, he proposes that females pick and choose among males, in some measure, by comparing their organs. A male with a more desirable trait, be it functional or fun or both, would father more offspring and spread the trait.

That extra something might be anything stimulatory, including traits that come into play only during copulation, Eberhard suggests. Traditional discussions of sexual selection faded out like old movies when the flirtation ended and the sex started. Yet, why should the pressure of selection stop then, asks Eberhard. "Events that happen later, after genitalic coupling [begins], can also be crucial in determining a male's reproductive success," he points out.

Invertebrates may not star in steamy movies, but they certainly behave as if stimulation matters during sex, Eberhard reports. He has found insect male behaviors that seem to have no purpose beyond their potential for titillation— rubbing, licking, rocking, shaking, singing, and so on—in 36 percent of the published descriptions of mating in 302 species.

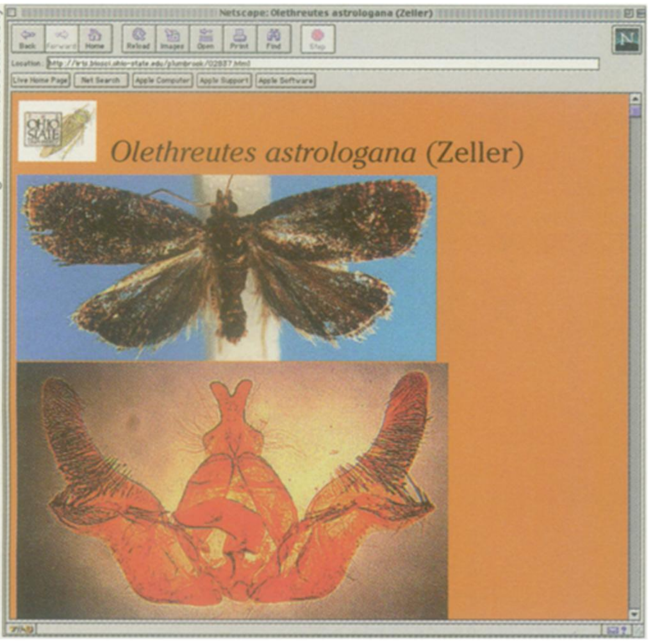
And the studies may underreport the sexy stuff, he notes. The fruit fly has been one of the most studied insects, but its "quite energetic" copulation was not described in the scientific literature until 1982. Among the 131 species Eberhard observed himself, 81 percent—more than twice the percentage in the literature survey—seem to titillate their partners.

Among butterflies of the *Erebia* genus, the spines and teeth on the male's genitalic valves do not seem to do anything practical, like gripping, but they do brush against the female's abdomen during copulation. Male azyine ladybird beetles have distinctive pairs of hairy bulblike structures, called parameres, that remain outside the female's body, tapping rhythmically against her.

Male genitals of the moth *Olceclostera seraphica* include special vibrating parts: a scraper and a file. Some researchers have proposed that the female of this species lacks conventional ears and essentially "hears" these vibrations genitally.

The millipede *Cylindroilus punctatus* spends several minutes rhythmically moving structures called gonopods, essentially modified legs, inside the female

Todd Gilligan/Ohio State University



To tell who's who among the Olethreutes moths and their relatives, taxonomists rely on male genitalia. Entomologist Norman Johnson has posted close-ups of male genitalia, as well as full pictures of the tiny moths, at the Plum Brook moth survey Web site at Ohio State University: http://iris.biosci.ohio-state.edu/plumbrook/plumbrok.html

before withdrawing them, filling them with sperm, and reinserting them. And among rhodacarid mites, which have species-specific structures to deliver their sperm packages, males spend up to 30 minutes with their mouthparts in a section of the female's reproductive tract before delivering sperm to another specialized female pore.

To test Eberhard's theory that female choice drives the evolution of such anatomy and behavior, Arnqvist combined an old-fashioned, comparative method with some fancy modern mathematics. "This is the first quantitative test of this [female choice] hypothesis," he says.

How can a person objectively judge other species' genitalia? Arnqvist took the novel approach of turning to an emerging field called geometric morphometrics. With one of its techniques, he was able to represent the outlines of the genitalia and other body parts of each species with a suitable mathematical function. "It's very handy," he says. In the 19 pairs of insect groups he chose, including butterflies, flies, and beetles, genitals indeed vary more from species to species than do legs or other structures.

If female choice were driving the rapid evolution that produces complex genitalia, he reasoned, then the structures would evolve faster among insects where females mate more than once. Such females get the chance for a complete comparison of the functioning genitalia of different males, and in essence, give the process of sexual selection an opportunity to work.

Comparing the mathematical representations of genital geometry, Arnqvist found the predicted relationship in 18 out of the 19 pairs of insect groups. Although each of the pairs had a common ancestor, the differences were nearly twice as great among the groups with multiple-mating females as among the once-is-enough insects. He considers this finding to be strong support for female choice.

"It's a really crisp, clear-cut result," comments Darryl T. Gwynne, who has studied insect genitalia at the University of Toronto in Mississauga, Ontario. However, he's not ready to throw away the lock and key in all cases.

Whatever force is powering the evolution of male genitalia, it has done an extraordinary job, Gwynne observes. "I get kind of frustrated when TV nature shows go on about the diversity of nature in birds' feathers and so on—people tend to ignore the 'lowly' insects. Even though the general public doesn't have coffee table books of insect genitalia, they're just as diverse."

One of Gwynne's favorite examples is the male cockroach's sexual gadgetry, with lots of moving parts that fold into a bristling cluster. "It looks like a Swiss army knife," he says.

Mike Siva-Jothy, head of the sperm competition laboratory at the University of Sheffield in England, notes that Arnqvist's paper is "certainly going to get up the noses of people who believe in lock and key." While the old hypothesis may not be flourishing at the cutting edge of theory these days, it's still taught, and "it's become sort of embedded in every biologist's psyche," Siva-Jothy says.

He praises Arnqvist's test for its clever simplicity. "When you see it you think, why didn't I think of that?" he says. However, he cautions that this quantitative test of female choice "supports the idea; it doesn't prove it."

Much of the other evidence for female choice is anecdotal, he notes, although some of the anecdotes do impress him. For example, he points out the case of a cluster of nematodes, each parasitizing a different primate. These worms diverged a long time ago, and because they stick to their own host species, the different species don't encounter each other. Even though they can hardly need specialized lock-and-key mechanisms, their genitalia nevertheless differ by species. Female choice does a much better job of explaining their anatomy, Siva-Jothy says.

Arnqvist's results agree with similar analyses on termites, roaches, and *Heliconius* butterflies that Eberhard himself has performed. Like Arnqvist, he compared species whose females mate only once to species whose females mate several times, although he did not use mathematical descriptions.

Eberhard, however, is a little cautious in embracing Arnqvist's test of his theory. "I should be wildly enthusiastic about the article since it constitutes a test that confirms some predictions from my own work," he says. But he is still evaluating the new data.

Among the tricky issues is the extreme difficulty of telling how many partners female insects really do have in the wild and whether human tests measure the aspects of male genitalia that matter to female insects.

In all this fuss about male genitalia, what about females?

Arnqvist notes, "We know very little about them because they're relatively difficult to measure." The crucial female anatomy tends to have more soft tissue than that of males, and key parts may depend on nerve functions that preserved specimens don't reveal.

Eberhard acknowledges the difficulties, but he says that in the several species he's studied, he agrees with "the general impression of many authors that female genitalia are often much less specific than male structures."

Patricia Adair Gowaty from the University of Georgia in Athens is not at all convinced that scientists know enough yet to make general pronouncements about female anatomy. She praises a 1995 paper in AMERICAN NATURALIST by Luther Brown of George Mason University in Fairfax, Va., and his colleagues. "They made the totally obvious point that variation in genital size of primates, especially penis length, is uninterpretable without more knowledge about female innards," Gowaty says. "I mean—duh."

Even when biologists can describe a female anatomical structure, who's to say the interpretation is right, Gowaty asks. In insects, for example, she says, are we really even sure that so-called sperm storage organs in females evolved to pamper and preserve sperm? "Maybe she's trying to kill them when she puts them in that 'sperm storage organ.'" The sperm that survive to fertilize eggs may not be coddled guests so much as prisoners that outwitted a death trap.

How more detailed knowledge of female innards could change current theories of sexual selection is hard to predict. Yet Gowaty won't be surprised if it inspires big shifts and rearrangements. Arnqvist's paper strikes her as "wonderful," but "this is all old-paradigm stuff," she says. It's time for the next Darwin. □