A Most Private Evolution

Dumb Designs for Sex: Evolutionary biology walks on the weird side

By Susan Milius

Maybe female seed beetles have their own what-the-bleep exclamation. Even for insects, it's difficult to imagine any other reaction to a male *Callosobruchus maculatus* beetle's sex organ, which has spikes.

"It jumps to mind as something quite dumb," says evolutionary biologist Göran Arnqvist of Uppsala University in Sweden, who for much of the past eight years has studied seed beetle sex.

Male beetles of several *Callosobruchus* species have sharp edges on their sperm-delivery organs. The females' ducts grow a bit of extra toughening but not enough to make sex safe from the risk of injury. After many tests, Arnqvist has concluded that the genital excesses aren't good for the species as a whole. These seed beetles would have less-damaging sex — and would produce more babies — if males lost their edges.

Discussions of evolution often glorify the beautifully apt forms: orchids with nectar recesses just the right length for the tonguelike structure of a certain moth, or harmless butterflies with the same wing colors as a poisonous neighbor. Yet the most dramatic examples of the power of evolutionary theory may come from the strange and ugly stuff — biology too dumb to have been designed.

Trying to understand counterintuitive sexual parts and habits follows in the best of scientific traditions. As Charles Darwin worked up his ideas on evolution, he pondered male phenomena that looked useless, or even harmful, for surviving. Outsized horns on male beetles puzzled him, as did male birds with gorgeous plumage.

Out of this consternation came his insight into a process he called sexual selection, which he distinguished from natural selection. There may be survival of the fittest, but there's also survival of the sexiest.

Today the sex-related selection process doesn't get much attention outside scientific circles, but it's a powerful tool for making sense of downright peculiar stuff. Arnqvist and other biologists are expanding Darwin's framework, exploring the counterintuitive aspects of sex from flirtation to family life. And theorists are discussing female behavior that Darwin never recognized, or perhaps just didn't care to discuss in print.


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obscurely coloured and destitute of all ornaments, whilst the males are probably the most highly decorated of all birds, and in so many ways, that they must be seen to be appreciated. The elongated and golden-

Fig. 49. Spathura underwoodi, male and female (from Beclard).

Ridiculously long tail feathers don't make sense for survival of the fittest, so Darwin developed the idea of sexual selection to explain features such as the impractical plumage of some male birds (hummingbird pair illustrated in *Descent of Man*).

Not-so-natural selection

When Darwin first put his full idea of natural selection into print, he knew it wasn't enough.

In 1859, he argued in *On the Origin of Species* that organisms best adapted to their environment survive in greater numbers and leave more offspring than do their less fit neighbors. Thus more suitable traits gradually replace clunkier versions.

Yet antlers on stags and tails on peacocks could hardly be adaptations to the environment. Both antlers and tails may be so familiar that it takes a minute to summon a sense of their absurdity. They're huge. They must drain energy to produce. There's no way they improve agility in locomotion or foraging.

"The sight of a feather in a peacock's tail, whenever I gaze at it, makes me sick!" Darwin wrote in a letter to the botanist Asa Gray, albeit in a whimsical paragraph. Nauseated or not, Darwin was willing to step beyond survival of the fittest.

He devoted a few pages in the *Origin* to introduce sexual

selection as a sort of wild oats younger brother of natural selection. Sexual selection, as Darwin formulated it in the sixth edition of *Origin*, depends "not on the struggle for existence in relation to other organic beings or to external conditions, but on a struggle between the individuals of one sex, generally the males, for possession of the other."

Antlers evolved as stag-on-stag weaponry for fights over a female, he argued. Males also compete in contests "of a more peaceful character," he wrote. Extravagant plumage, singing and what he called "strange antics," such as bird acrobatic displays, bedazzle a female into choosing one male over his rivals.

What's good for bedazzling can be bad for survival, of course. Darwin made a glancing allusion to the conflict in his 1871 work, *The Descent of Man, and Selection in Relation to Sex*. There he admits that peacock tails wow the peahens but could be slightly harmful to the male.

Today's tales

Harm may be part of the charm, although debate continues on how supersized, shimmery tails evolved. The year 2008 proved a lively one for peacock studies, as a long-term line of research met a challenge from a new one.

Three independent studies in the past 20 years have found that tails matter. For example, Marion Petrie of Newcastle University in England and a colleague turned the same birds from hotties to notties and back again by clipping some of the eyespots out of the males' tails and then reattaching the finery. The females probably weren't counting male spots, but were choosing males that displayed a greater density of spots, according to similar tests by Adeline Loyau, now at France's CNRS Moulis station.

Peahens' interest in eyespots could have arisen for no particularly practical reason, Petrie and Loyau speculate. Their idea draws on the concepts of sensory bias and sensory exploitation, which deal with an apparent arbitrary silliness at the heart of sexy traits. Sure, a blue spot now burns hot with allure. But biologists puzzle over why a purple stripe didn't evolve instead.

In this scenario, basic arbitrary-looking evolutionary directions (blue not purple, long tail not wide eyes) actually were arbitrary as far as mate choice goes. For some reason that had nothing to do with reproduction, females might have tended to notice a particular color or shape or motion.

Let's imagine it was a blue spot. Males exploit that predisposition as guys with even a modest dot attract extra female attention. If the female bias gets inherited along with male coloring, then off go the males in an evolutionary race for bigger, better, bluer blues.

That was the beginning in the peacock's tale. At some point, the story goes, tails grew so fancy they posed a handicap for males. Growing the best tail or keeping it flossy or managing a little sprint despite its weight demanded energy or vitamin-rich food or something otherwise limited. And in animal communication, that's when fashion starts to mean something.

What's called the handicap principle comes from the Israeli biologist Amotz Zahavi, now retired from Tel Aviv University, who thought about how creatures judge each other's quality.

Suppose the peacock's tail signals, "Hey, honey. I'm the best bird, and you need me right now." Such a tail stays reliable as a badge of quality across generations only if good tails present a handicap that not all individuals can overcome, Zahavi suggested. A robust bird can pay the cost and still look good. A puny bird can't compensate for the loss, and looks like a second-rater. The tail signal honestly indicates quality.

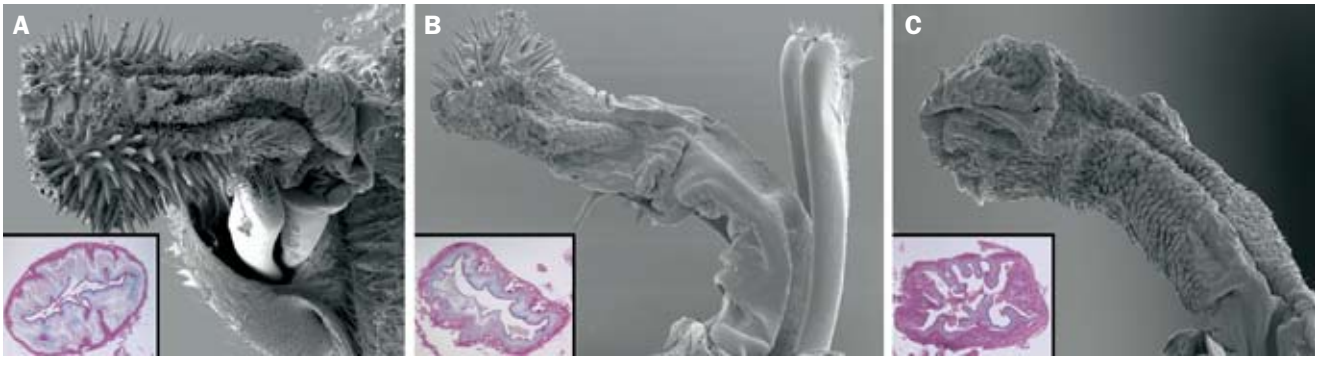
A signal with no cost, Zahavi argued, means anybody could waggle a full rainbow rear. Everybody could signal "best bird." The signal would lose its utility and fade away over generations, or never evolve to begin with.

Darwin said the peacock's tail is at least slightly harmful. Maybe it has to be.

Petrie and others have been taking this signaling idea further, testing to see whether the tail might signal good genes or some true benefit for a female who mates with a showy male. It sure isn't help with the chores and the chicks. Peacocks do only the most basic task of fatherhood.

In a jolt after years of research linking female preferences to tail feathers, readers of the journal *Animal Behaviour* were startled to learn in April that a seven-year study of feral peacocks in a park near Shizuoka, Japan, found no sign that females were

Male and female seed beetles engage in evolutionary arms races that appear to harm the species as a whole. Species with spinier, more dangerous male genitals (most extreme of three species at left) also have tougher walls in the female reproductive tracts (inset, cross section for each species).



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choosing males based on their tails. Neither eyespot number, tail symmetry nor tail length correlated with a male's success or his health, reported Mariko Takahashi of the University of Tokyo and her colleagues.

Loyau, Petrie and two other researchers responded in the November issue with ideas about why the new study doesn't agree with old research. For one thing, the researchers point out, the studies took place on opposite sides of the world. Other animal studies have recently detected what's called adaptive plasticity in mate choice, or differences in how various groups of females of the same species choose mates. What's a useful signal in one environment may not matter much in another. Also, Loyau says, "If we really want to understand, we need to study peacocks in the wild."

One commentary isn't going to settle a matter that's been under study since it nauseated Darwin, though. The Japanese experiment's challenge to years of experiment, theory and assumption is "sure to prove controversial," predicts Louise Barrett, one of the journal's editors.

For kicks

Plausible explanations for a dazzling but impractical tail don't make sense for injurious genital spikes. Beetle genitalia look more like instruments of war. The latest research suggests warfare may be the point.

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As Arnqvist puts it, "Unless you have perfect monogamy, there are conflicts of interest." When a male and a female can take different strategies in mating, their best interests often differ. What's good for the goose in terms of how often to mate, with whom and for how long probably won't be best for the gander.

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When the researchers removed females' legs so they couldn't kick, males persisted around six minutes. The sexes appear to disagree about how much is enough.

Female beetles' kickoffs probably are not a way of reducing contact with wimpy males that can't stand a drubbing, Siva-Jothy says. Female seed beetles look as if they have genuine cause to minimize mating. The longer an encounter lasted, the more rips and tears Siva-Jothy and Crudgington found in the female reproductive tract. And as additional evidence of harm, females that mated only once during the experiment lived longer than females that mated twice.

Those harmful male sex organs in the beetles "look like medieval torture instruments," Arnqvist says. Yet such a device may not have evolved through any direct benefit of its power to injure. Instead, injuries are probably side effects, Arnqvist contends. He and his colleagues have tested for potential direct benefits for the male, including what's called the "terminal investment."

In a terminal investment, a mauled creature facing an uncertain or shortened life span throws all resources and effort into the current batch of young. A dad with no guarantee he'll sire one of mom's future clutches will certainly benefit if he can get her to make an all-out investment in his offspring right then.

It's not an easy idea to test. Exactly mimicking the damage of mating isn't possible, so Arnqvist and his colleagues inflicted other injuries, including body punctures or cuts on wings, after a group of females had mated. The injured females actually laid fewer eggs than intact moms, so Arnqvist dismissed the idea of a terminal investment bonus for the males. Also the damaged females tended to mate again sooner than usual, so the damage doesn't look like a roundabout way of foiling rivals.

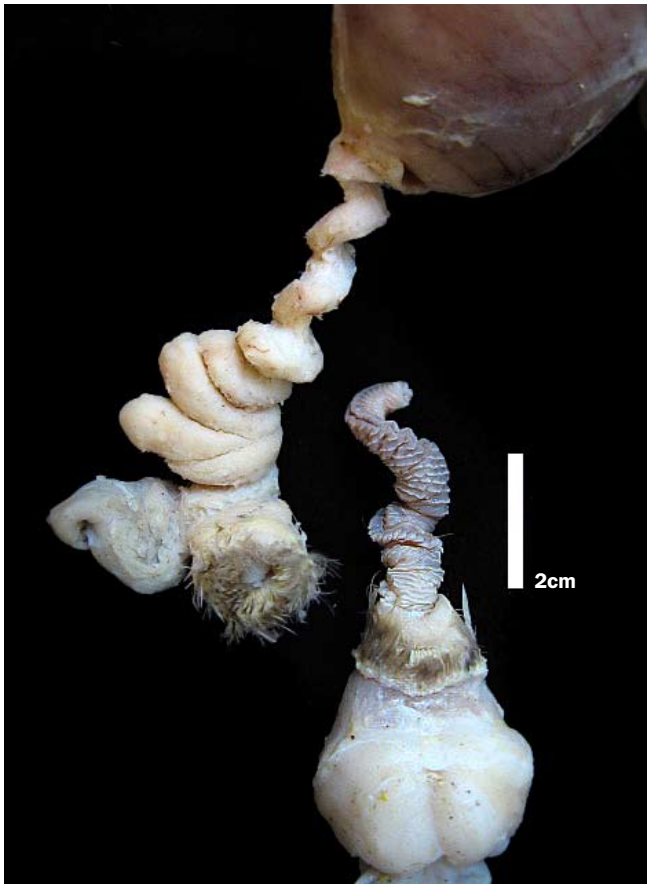
To explain how the sharp edges of a seed beetle arose without direct benefits, Arnqvist proposes that some quirk of male physiology, such as an irregular surface to improve anchoring, injured females incidentally. The risk of such injuries favored females with tougher plumbing, which in turn favored spikier males. So seed beetle anatomy, he argues, could derive from an ongoing arms race between the sexes. Even if the conflict harms the species.

Similar harm, and possibly arms races, could be smoldering far beyond seed beetles. "Being an entomologist, I know of hundreds of insect groups with male genitalia that have this appearance," Arnqvist says.

Some male insects deploy bundles of spines, knives and even full-fledged swords. Male bedbug organs look like a stiletto, and "they literally use it as a stiletto," Arnqvist says. Females' reproductive tracts do have external openings, but male bedbugs usually just stab through some spot in the body wall and let the sperm swim from there.

Birds have evolutionary arms races too, says Patricia Brennan of Yale University.

Most birds don't have insertable parts, achieving fertilization by the so-called cloacal kiss. It's just his-to-hers contact of cloacae, the all-purpose openings of reproductive and excretory systems. Male ducks, however, belong among the 3 percent of male bird species with a phallus, and some duck



Mallard duck anatomy shows signs of an escalating battle of the sexes. The male has a long phallus (bottom), but the female's genitals (top) corkscrews in the opposite direction.

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organs extend a full 40 centimeters.

In the mallard and long-tailed duck, males deploy at unusual length "what looks like a weird tentacle with bumps and ridges," Brennan says.

Female duck anatomy hadn't received as detailed a look until Brennan spent some time in Tim Birkhead's lab at the University of Sheffield. Female mallards and long-tailed ducks have a correspondingly intricate reproductive tract "like a maze," Brennan says.

In studying 16 species, she found that if the male had a long and elaborate phallus, the female had intricate genitals too. The sexes' intricacies seemed at odds with each other, however. Males spiraled counterclockwise (from the base) but female reproductive tracts antagonistically curved clockwise (from the outer opening). Blind pouches along the female tracts looked like traps for sperm.

A classic arms race is what Brennan and Birkhead proposed in *PLoS ONE* in May 2007 to explain the mismatched genitalia. Males of the extra-long species are more likely to try forcing themselves on females than are less elaborated males. Thus females might have benefited from countermeasures against unsuitable matings. A maze that proves navigable only when a female cooperates and relaxes could have provided some control, but it would also favor the evolution of even more extreme males.

"These kinds of evolutionary races are costly," Brennan says. "You would have been better off without this conflict in the first place, but you can't stop investing because you're already in the war."

There's chemical warfare too, says William Rice of the University of California, Santa Barbara. Male fruit flies dope their seminal fluids with a cocktail of additives that revs up the female so she devotes extra resources to the eggs. Never mind that it shortens her life and therefore shrinks the total number of offspring she can produce.

Possible high quality offspring won't make up for the loss in quantity, Rice and his colleagues report in the November *Journal of Evolutionary Biology*. They tested the idea that mating with a male carrying superb genes might, over the course of generations, give a female enough extra grandkids and great-grandkids to compensate for her initially small brood.

Yet breeding experiments showed that good genes don't help enough, the researchers conclude. At most, females mating with a superior male might get a modest increase in the number of their offspring's descendants. The uptick isn't big enough to compensate for the downside of drugged sperm. This evidence and earlier work show fruit flies paying a toll for their battle of the sexes. "It's clearly bad for the species," Rice says.

Even hermaphrodites can have battles of the sexes. Conflicts arise when everybody tries to play the guy instead of the girl, according to ongoing work by Nico Michiels and Nils Anthes of the University of Tübingen in Germany.

Just why it would be better to be "male" has inspired much theorizing about sperm being energetically cheaper than eggs to produce. Anthes, though, does the accounting in different terms. He sees conflicts looming if one sex, usually the male, benefits from virtually unlimited matings while the other sex rapidly reaches some limit. Females, for example, might be able to produce only so many eggs in a lifetime, so matings to fertilize even more eggs wouldn't be useful.

Whatever drives the conflicts, researchers see what looks like a lot of antagonism out there. In the small marine flatworm *Pseudoceros bifurcus*, two flatworms stand up on the hind parts of their bodies, stick out both their penises (each worm has two) and jab them at each other. Worms bend and dodge as any duelists would, trying for a hypodermic strike that injects sperm anywhere on the opponent's body. Bouts sometimes last 20 minutes.

In the flatworm *Pseudobiceros bedfordi*, ejaculate dissolves its way through skin and can leave scars. A full frontal splash can dissolve the recipient into two pieces, although the flatworms do regenerate lost body parts.

The latest battle that Michiels and Anthes have documented "turned out to be quite spectacular," Anthes says. Hermaphroditic *Siphopteron quadrispinosum* sea slugs stab at each other with a sharp spike on the side of the penis. When one

Combining both sexes in one body doesn't eliminate conflict. Two hermaphroditic marine flatworms (*Pseudoceros bifurcus*) struggle for the male role in a duel (top) to be the first to inject sperm into the opponent's body (middle). Sperm from *Pseudobiceros bedfordi* can dissolve through skin, but too big a splash corrodes the recipient into fragments (bottom).

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slug gets spiked in the head region, it slows down and stops dueling. "They look pretty sleepy," Anthes says. The spiker is apparently injecting some kind of sedative that allows unilateral insemination, Anthes and Michiels reported in 2007 in *Biology Letters*.

Counterintuitive reproductive strategies continue even into parenthood. Consider the penduline tits (*Remiz pendulinus*). In any given nest, the mother and/or the father often desert and start a second family, says Tamás Székely of the University of Bath in England. A single parent can still raise chicks to adulthood, given the right location, but sometimes both parents desert. In this case, the chicks starve. In populations across Europe, about a third of egg clutches die from abandonment, Székely and his colleagues have found.

To make sense of this, Székely describes a competitive desertion arms race between male and female tits. Each sex can increase its number of offspring by starting another nest with a new partner, as long as the old partner stays around to care for the previous clutch.

As the optimal time for desertion nears, when all eggs have been laid, female tits behave as if they're trying to keep their current mate from seeing the true number of eggs. Females confront a male at the nest opening and fuss at him furiously.

Whether this loss of a third of clutches ends up as a bad thing for the species overall will take more research, says István Szentirmai at Őrség National Park in Hungary. But he speculates that the strategy limits the species to insect-rich places like wetlands, where a single parent can catch all the necessary baby food.

Mothers certainly didn't run off with other males in *On the Origin of Species*. Darwin acknowledged that males of various species take more than one mate but said hardly anything about such shocking behavior (to mores of the era) in females. So one of the biggest developments in the theory of sexual selection has been the recognition that females in many species aren't monogamous, says Jeanne Zeh of the University of Nevada, Reno.

"It's molecular genetics," says David Zeh, also at Reno. Once DNA analysis could identify the true fathers of offspring, biologists could see widespread challenges to old ideas of females as the choosy, monogamous sex. That idea opens the way for much entertaining science.

And another major shift, as illustrated in the arms races, has been the recognition that sexual competition continues into the depths and details of the reproductive tracts. "[Darwin] spoke only about mating," Arnqvist says. Now scientists have created a whole discipline called sperm competition that takes the struggle for access even further.

Reproduction in the modern view isn't particularly pretty. With medieval torture instruments, mazes and corkscrews, drugged sperm and arms races everywhere, reproduction looks more like war than love. All in all, it's easy to wonder if sex itself was such a great idea.

But that's another story. ■