SCIENCE

This Common Butterfly Has an Extraordinary Sex Life

For the cabbage white, sex involves sperm packages of ungodly size, genitals that double as a souped-up stomach, and an unexpected set of chewing jaws.

By Ed Yong

Vagina dentata. It's a wonderful phrase. Vagina dentata. Ain't no passing craze. (Nathan Morehouse)

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Nathan Morehouse wasn't expecting to discover anything extraordinary when he started studying the cabbage white butterfly. Small, plainly colored, and common across six continents, it's a rather hum-drum member of a family known for its kaleidoscopic wonders. Morehouse calls it the "world's most vanilla butterfly," and he hadn't even planned to study it at all. He only did so because the butterfly he wanted to work with had gone through a population crash, and he needed a reliable replacement.

“It turned out to be one of the best choices of my career,” he says.

Over the last few years, Morehouse and his colleagues, including Nathan Clark who is also at the University of Pittsburgh, have shown that the sex life of a seemingly unremarkable butterfly is utterly remarkable. It features sperm packages of ungodly size. It involves genitals that double as a souped-up stomach. There’s even an honest-to-goodness vagina dentata.

Mating cabbage whites (Nathan Morehouse)

Let’s start with their color. The mostly white wings of the cabbage white reflect a lot of ultraviolet light, which we cannot see but the butterflies themselves can. To our eyes, they seem plain and drab, but to each other, the females are a gentle lavender hue, while the males shine with a brilliant royal purple. And Morehouse showed that the brighter the males, the more attractive they are to females. Why?

Partly, it’s because the strength of their colors reflect how fit they are. The patterns depend on proteins in the wings, and as caterpillars, these butterflies feed mostly on protein-poor food like cabbage and kale. Only the most successful individuals can eat

enough to create bright colors later on in life. And these same males also offer females more enticing gifts.

A cabbage white's ejaculate is very different from a human's. Rather than a blob of white gunk, it's a complex solid package called a spermatophore, which consists of a hard outer shell, soft nutritious innards, and a ball of sperm at the base. The male deposits this into a pouch within the female reproductive tract called the bursa copulatrix. Once inside, the sperm swim off into a second pouch—the female will later use these to fertilize her eggs. Meanwhile, she starts to break down the outer shell of the spermatophore to absorb the nutrients within. So, the spermatophore acts as a nuptial gift—a way for the male to nourish the mother of his future offspring, long after he flies away.

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As gifts go, the spermatophore is a substantial one. On average, each packet makes up an astonishing *13 percent* of the male's body weight. "Scientists who work on ejaculates will often show up to meetings with props," says Morehouse. "I've never had it in me to bring a five-gallon bucket along. But that's what we're talking about [if you scale it up to human size]. It's a water-cooler-sized ejaculate."

These gargantuan gifts are so nutritious that females use the proteins within them to make roughly half the eggs that they eventually lay. That's why they pick the most colorful males—these are the ones that offer the largest spermatophores.

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If males are ejaculating 13 percent of their body weight with each fling, that surely limits how often they can have sex in one lifetime. No one knows the exact number, but it's at least two or three. And if they're running low on resources, they start producing smaller spermatophores—and breaking down their flight muscles and internal organs. Elderly males actually digest their own innards to fund the construction of their giant ejaculates.

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It is far easier, by contrast, to work out how often the females have sex. That's because females can't fully digest the outer layers of the spermatophores, even after they have sucked all the nutrients out. Each female carries around the legacy of all her past sexual encounters, as withered husks sitting inside her genitals. If you dissect her, you can just count them. That's how Morehouse knows that most females mate two or three times, but some manage up to six.

> These insects have a reproductive tract that's more stomach-like than their own stomachs.

From a female's perspective, it's best to mate as often as possible, since each encounter brings a new packet of nutrients. But that's disastrous for a male, since the sperm of a subsequent suitor could displace his own. These contrasting incentives set up an intense battle of the sexes, in which females try to mate often, and males try to stop them. "It's this tug-of-war over who's in control of when the female can mate again," says Morehouse. But it's not a physical contest. It's an invisible one, which plays out inside the female's body through the chemistry of the spermatophore.

The female only mates again when she has drained her existing spermatophore of nutrients, which is why males have evolved to coat these packets in layers of extremely tough proteins. To analyze these layers, Morehouse and Clark's team first had to break them down. And they could only do that by boiling them in *concentrated sulfuric acid*. It's as though the cabbage white's nuptial gift is sheathed in nearly-indestructible wrapping paper.

A female butterfly has no access to sulfuric acid. Instead, she *chews* her way into the spermatophore using an organ called the signum, which sits inside her bursa. It looks exactly like a pair of toothed jaws, with a hinge in the middle. "I like to tell people that we found the vagina dentata, but it's in butterflies," says Morehouse. When a female takes up a spermatophore, her bursa clenches and contracts, and the signum flexes around its hinge. It takes between 24 and 36 hours of constant chewing to break into the spermatophore.

To help the signum along, the bursa also secretes a cocktail of proteases—the same enzymes that stomachs use to digest food. But Morehouse's colleague Melissa Plakke showed that the bursa produces 20 times the concentration of proteases as cabbage white caterpillars have in their guts. These insects have a reproductive tract that's more stomach-like than their own stomachs. And while all this is happening, the actual sperm get out of Dodge. Within minutes, they swim out of the bursa and into a separate pouch, so they're not degraded by the flood of digestive enzymes.

Many of these traits—the bursa, spermatophores, and signum—are common throughout butterflies and moths, but different species have elaborated them to varying extents. Consider the silk moth. Humans domesticated this species millennia ago to harvest the silk that its caterpillars make. By controlling its sex life, we have enforced monogamy upon it, nullifying the sexual conflict that exists in other butterflies. As a result, silk moth males now produce spermatophores that are more like time-release capsules—they dissolve on their own. The females, in return, produce far lower levels of proteases in their bursa. And silk moth sperm is lazy: it ambles its way out of the female's bursa over the course of hours.

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And wait, there's more! Clark's colleague Camille Meslin showed that the male doesn't transfer the spermatophore into the female as a ready-built package. Instead, he builds it *inside her body*. Using separate glands in his aedeagus—a penis-like organ—he first transfers the tough outer envelope, inflates it with the nutritious inner core, and caps the whole lot with sperm.

This staged process gives the female an opportunity to intervene. Meslin found that a quarter of the proteins in the outer layer are actually proteases that come from the female. By including these as soon as the spermatophore forms, she could give herself a head start in breaking it down, and shorten the gap between her next round of sex.

"Male ejaculates have so many dramatic effects: They can alter female physiology, lifespan, reproduction, and all kinds of behaviors like eating and sleeping," says Jen Perry from the University of Oxford. But these studies "show that what we often think of as solely a male trait is actually the product of both males and females. This is a really significant shift in perspective, from the idea of females being the recipients of large and complex chemical packages from males, to being active participants in shaping those packages."

Meslin also found that both the proteins that the males use to build the spermatophore, and the proteases that females use to infiltrate it, are evolving rapidly. "This is exactly what we would expect if there is an ongoing evolutionary arms race between the sexes," says Karim Vahed from the University of Derby.

There's likely more to this story left to unpack. For example, Laura Sirot from the College of Wooster wants to know if females can somehow evaluate males based on how tough their spermatophores are. Perhaps they can use that cue to work out if they want to fertilize their eggs with a recent mate's sperm. And what about the other chemicals within the spermatophore—do those affect the female's behavior in any way? "We've known for a long time that insect spermatophores are structurally complex (and some, like those of fireflies, are even beautiful), but this study makes clear that they're also quite biochemically complex," says Sara Lewis from Tufts University. "There's clearly a quietly intense sexual tug-of-war going on here," says.

"Quietly intense" is also an apt description for the cabbage white butterfly itself, given everything that Morehouse has discovered. And if Morehouse's name sounds familiar to you, it's probably because I talked to him in last week's story about jumping spiders that can see the moon with their telescopic eyes.

"One of the delights of studying backyard bugs is the opportunity to be reminded that magic is still all around us," he tells me. "Jumping spiders with telescope eyes are singing and dancing to impress their mates. That butterfly on your kale has a chewing jaw in its reproductive tract that helps it to regain control over its own reproductive timing. It is this ability of life to continually surprise us that brings me such joy as a scientist. And it's my hope that, in some small way, my work can return some childlike wonder to the daily lives of others. It is only through falling back in love with nature that we stand any chance of saving it."

ABOUT THE AUTHOR

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Ed Yong is a former staff writer at *The Atlantic*. He won the Pulitzer Prize for Explanatory Reporting for his coverage of the COVID-19 pandemic.