Quick guide

Nuptial gifts

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What are nuptial gifts? They are what it says on the label: the gifts that male animals transfer to females during courtship and mating, beyond the obligatory gametes. Chemically, nuptial gifts can contain proteins, uric acid, lipids, carbohydrates, allohormones, minerals, and anti-predator defensive chemicals. They come in diverse packages, such as food collected by males, salivary gland secretions, spermatophores (sperm-containing packages produced by male reproductive glands), and free ejaculates. One fundamental distinction can be drawn between endogenous gifts that are produced by the male himself and exogenous gifts males collect. In addition, oral gifts that are taken in through the female's digestive system are distinguished from seminal gifts that are deposited in the female's reproductive tract during mating.

Who gives nuptial gifts? As mentioned above, it's usually males, and they can belong to many animal groups, such as arthropods, molluscs, birds, and even humans. Because they show the most diverse gift types and transfer mechanisms, insects are probably the champions of nuptial gifts (Figure 1). Seminal gifts in the form of spermatophores are common in butterflies, moths, and beetles. In these groups, males typically deposit their spermatophore directly inside the female's reproductive tract. In most katydids (bush crickets) and crickets, males transfer a distinctive two-part spermatophore consisting of a sperm-containing ampulla connected to a part that remains outside called the 'spermatophylax'. While the sperm is moving into her reproductive tract, the female twists around to eat the spermatophylax. Female tree crickets also eat while being inseminated, in this case dining on secretions from a gland on the male's back. In some ground crickets, males even donate blood during mating by allowing a copulating female to chew on a specialized hindleg spur.

Spitballs?! Scorpionfly males can switch gifts depending on which condition they're in. When in good condition, they use enlarged salivary glands to produce one or several salivary masses, which the female consumes during sex. When in bad shape, the male instead offers a dead arthropod, which he may even try to steal back from the female after copulation.

What's in it for the females? Male spermatophores often provide limiting resources, like amino acids or sodium, that enhance a female's lifetime egg production and longevity. Some spermatophores also contain defensive chemicals that protect females and their eggs against predators. Gifts that females ingest, such as a male's spermatophylax, salivary mass or scavenged prey, have also been shown to provide a net benefit to females in terms of lifetime fitness.

And what about the males? Obviously, nuptial gifts and giving can only evolve if the males gain a net fitness benefit, as for them the gifts are costly to produce or find. In some cases, the benefits may play out before mating, as in scorpionflies, where displaying a gift will increase a male's chance of attracting, courting and coupling with a female. However, other gifts appear to have evolved mainly to ensure effective insemination of females. For example, katydid females consume the male's spermatophylax before removing and eating the ampulla, and this allows the full complement of sperm to be transferred. Many other oral gifts also allow males to maximize the number of sperm they transfer. Even after sperm have been transferred, nuptial gifts can benefit a male by increasing his paternity share when females are promiscuous. In fruitflies, katydids and scorpionflies nuptial gifts contain substances that reduce a female's receptivity to additional matings. While nuptial gifts also may boost female fecundity, from a male's perspective, such investment will only be beneficial if it increases the number of his own offspring.

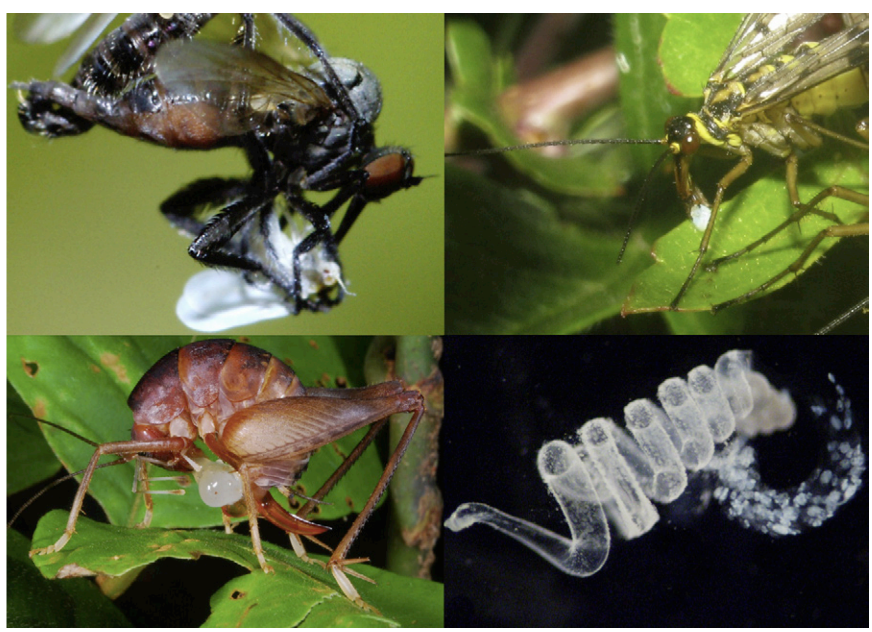

Figure 1. Nuptial gifts of insects.
An array of nuptial gifts provided by male insects. Top left: during mating, a female dance fly (Diptera: Empididae) feeds upon a dead insect provided by her mate (Photo: Rob Knell). Top right: a male scorpionfly (Mecoptera: Panorpodidae) secretes a white salivary mass that will be consumed by a female during mating (Photo: Arp Kruithof). Bottom left: after mating, a female camel cricket (Orthoptera: Rhaphidophoridae) consumes a gelatinous spermatophylax that the male has attached to her genitalia (Photo: Arthur Anker). Bottom right: a spermatophore manufactured by a firefly male (Coleoptera: Lampyridae) and transferred internally to the female reproductive tract.

So everybody's happy? Not necessarily. Although the term 'gift' may have a positive ring to it, female fitness may not only be enhanced, but also remain unaffected or even reduced by receiving nuptial gifts. The term 'Medea gifts' has been used to refer to gifts that reduce a female's lifetime fitness. *Drosophila melanogaster* males, for instance, transfer seminal fluid proteins that may accelerate current reproduction at the expense of a female's long-term fitness. Documented effects include reduced female receptivity, increased short-term ovulation and egg-laying rates and decreased life-span. Because such seminal gifts allow males direct access to the female reproductive system, they are more likely to benefit the giver while undermining the female's lifetime fitness.

What makes nuptial gifts so interesting? Giving and receiving nuptial gifts can clearly influence the reproductive success of both sexes. Yet, people are only beginning to explore the role such gifts play in the evolution of animal mating systems. When food resources are scarce or unrewarding, females may rely on males that can provide valuable gifts. Many insects stop feeding altogether once they become adults. In these capital breeders, nuptial gifts may have evolved as a way to balance reproductive costs between the sexes. Their position at the interface of sexual selection, nutritional ecology and life-history evolution is what makes nuptial gifts so fascinating.

Where can I find out more?

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Q & A

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Nilli Lavie is Professor of Psychology and Brain Sciences and leads the Attention and Cognitive Control group at the UCL Institute of Cognitive Neuroscience. She was previously at the MRC Applied Psychology Unit in Cambridge, following a Miller Institute postdoctoral fellowship in Anne Treisman's lab at UC Berkeley. She took her BA and PhD at Tel Aviv University. She is best known for her 'load theory' of attention, perception and cognitive control. Load theory provides a resolution of the 'early versus *late selection' debate about the effect of attention on information processing, a debate that endured four decades of intensive research before it was resolved; load theory has since been developed and extended to many areas of information processing (ranging from elemental perception processes, to awareness, emotion and control of behavior) in the intact human brain, in clinical populations and in other species.*

What attracted you to biology? Although at high school my main aim was to get by without doing homework, I did develop a deep interest in biology and relished any insights into how biological systems work, at all levels, from molecules to principles of homoeostasis and evolution. There was one exception though: fieldwork. I was no nature girl, nor did I have enough patience to sit back and observe. In preparation for the Biotope part of final exams, I made one short visit to my Biotope field and concluded that nothing happened! A few months later I picked up a few plants and tried to pass the Biotope viva based on textbook knowledge augmented by just these few plants. Inevitably this did not work too well… Fortunately, the Biotope was only a small component of the final exams and my biology teacher kindly did not allow it to blemish my final grade, so as not to detract from a potential future career in biology. When I applied to University, however, I discarded mainstream biology because the course involved too much fieldwork for me.

Did you plan to become a scientist in a different area? Not really, unless you accept science fiction as a form of science. Back then I planned to become an author and wrote a few synopses of possible novels. On a recent holiday I finally developed one of these synopses into the start of a novel. I looked into finding a literary agent but got distracted by my scientific work routine before finding one. In my next holiday I wrote a scientific review paper instead, so am coming to terms with the fact that fully pursing my scientific dreams just doesn't leave enough time to pursue other dreams.

What drove you to continue with University education? In Israel, my University application was purely driven by the opportunity to shorten my army service duty by several months. I only learned about this opportunity in the nick of time, just before the deadline, so hastily put in an application ticking the two courses I knew least about: philosophy and psychology. They seemed interesting, if only for being new to me; they also clearly involved no fieldwork: they fitted the bill. I was accepted to both and, failing to decide which I preferred, embarked on a dual-degree track.

And you found that you preferred psychology? Actually, during the first two years of the undergraduate course I enjoyed philosophy more than psychology. I chose the philosophy of science track and focused once again on biology (writing my bachelor thesis on the evolution of mind). I enjoyed the mix of studying in the daytime, while also being able to follow my other pursuits of fashion, indie rock music and Tel-Aviv nightlife (the first two I am still pursuing until this very day). I did pretty well in my studies, but excelled in the other pursuits, especially the nightlife. This, at least on paper (e.g. in the print media) appeared to be my true vocation, as I became a sort of a nightlifer/socialite and was regularly covered in the gossip columns (sometimes for my interesting outfits, but most of the times for the men I dated!). On the academic front, following two