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Nuptial Gifts in Insects: Evolution and Significance in Insect's Reproductive Success

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ABSTRACT: Nuptial gifts, which are non-reproductive nutritional materials transferred to females from males during courtship and mating, play a significant role in sexual conflict among conspecifics. These gifts can range from nutritious prey materials to glandular secretions, providing direct rewards to females by boosting their reproductive success and offspring viability. However, they can also be detrimental, as some gifts may manipulate female behavior or reduce their remating opportunities, thereby benefiting males at the expense of female fitness. Recent studies have highlighted the dual nature of these gifts, suggesting that while they may serve as a mating effort to secure copulation, they also function as paternal investments that nourish both females and their progeny. The interaction between sexual selection and the evolutionary dynamics of nuptial gifts continues to be a topic of debate, with research indicating that the benefits and costs associated with these gifts can vary significantly across different species and contexts. Understanding the complexities of nuptial gifts and the sexual conflict surrounding them is crucial for elucidating the evolutionary strategies employed by both sexes in mating systems.

Keywords: Nuptial gifts, Sexual conflicts, Insect reproduction, Male ejaculates, Seminal fluids.

INTRODUCTION

Earlier it was thought mating in insects to be a sexually cooperative act but Williams during 1966 critically analyzed the mating adaptations in insects and predicted mating to be "An evolutionary battle of the sexes" where "Genic selection will foster a skilled salesmanship among males and an equally well-developed sales resistance and discrimination among females". This William's notion of sexual selection recognized sexual conflict (Darryl 2008). It becomes prominent when males and females have differing optimal fitness strategies related to reproduction, especially regarding mating frequency and methods, which might lead to an evolutionary arms race between the sexes. It is also called sexual antagonism because in some interaction one sex get benefits other get harmed. For instance, because of the anatomical variations between the sexes, multiple matings may be advantageous to males but detrimental or dangerous to females. (Reinhardt *et al*., 2003). For instant, in decorated crickets, *Gryllodes sigillatus*, the spermatophore that a male transfers during mating includes a gelatinous spermatophylax which is consumed by female, delaying her removal of the sperm-filled ampulla. Male fertilization success increases with the length of time females spend feeding on the spermatophylax, while females may benefit by prematurely discarding the spermatophylaxes of undesirable males. This sexual conflict should favour males that produce increasingly appealing spermatophylaxes, and females that resist this manipulation (Gershman *et al*., 2013). In addition, the chase-away sexual selection model, which situates inter-sexual conflicts in the context of female resistance, sensory exploitation, and the evolution of secondary sexual characteristics, suggests that an evolutionary arms race is developing (Holland *et al*., 1998). Chase-away selection states that persistent sexual conflict produces an environment where the development of male secondary sexual traits and the frequency of mating are slightly correlated with the level of resistance exhibited by the female (Danchin *et al*., 2008). Nuptial gifts are nothing but the materials eaten or beneficial substances absorbed by the female during mating from the male *viz*., prey, various male body parts, hemolymph, salivary gland secretions, uric acid, minerals, ions like sodium and zinc, water, defensive compounds etc. (Andersson, 1994). These nuptial gifts are classified into endogenous gifts and exogenous gifts based on male perspective and oral gifts, seminal gifts and transdermal gifts based on female perspective (Lewis and Adam 2012). These gifts have a positive effect on female fitness resulting in increased fecundity, lifespan and defense against predators (Andres *et al*., 1999). For example, in *Aedes aegypti,* male reproductive gland substances increase female fecundity and blood feeding frequency, resulting in dramatic increases in fitness (Villarreal *et al*., 2018). The energy transferred by male in the form of spermatophylax equaled to 20% of energy content of the male whole body (Christian *et al*., 2005). In some insect female's gifts can also have either negative effect (reduced net fitness and lifespan etc.) or no effect at all while the nuptial gifts for male functions as mating effort and parental effort. The nuptial gifts in insects mainly act as energy source for female when the food from sources is limited. Sexual conflict takes two major forms:

Inter-locus sexual conflict: They arises from the interaction of antagonistic alleles at one or more loci in males and females, with the conflict often centering around differing optimal mating rates between the sexes. In most animal species, males invest fewer resources in offspring compared to females, leading to the evolution of male adaptations aimed at inducing females to mate more frequently. A well-documented example is the seminal fluid of *Drosophila melanogaster*, that serves the male's interests by up-regulating female egg-laying rate and reducing her desire to re-mate with another male, but also has the detrimental effect of shortening the female's lifespan, thereby reducing her fitness (Chapman *et al*., 2003).

Intra-locus sexual conflict: This kind of conflict involves a tug-of-war between sexual selection favoring one sex and natural selection working on both sexes. For instance, in zebra finches, bill color serves as a key example. While such ornamentation can be costly to produce, it plays a crucial role in mate choice but also increases vulnerability to predators. The alleles responsible for such phenotypic features are subject to antagonistic selection. This conflict is often resolved through elaborate sexual dimorphism, which helps maintain sexually antagonistic alleles within the population. Evidence suggests that intra-locus conflict may significantly constrain the evolution of various traits. (Arnqvis and Rowe 2005). Sexual conflict can lead to a perpetual cycle of antagonistic coevolution between the sexes. This cycle begins with the evolution of male traits that favor reproductive competition and persistence, which reduce female fitness. In response, females may develop counter-adaptations that reduce the costs imposed by these male traits, a process known as female resistance. As female fitness increases, the cycle continues, with each sex evolving traits to achieve their optimal reproductive strategies at the expense of the other sex (Holland *et al*., 1998). This ongoing evolutionary arms race reflects the differing fitness interests of males and females and highlights the importance of inter locus sexual conflict in shaping the coevolution of sexual traits.

Female tactics to minimize or avoid mating expenses, rather than concentrating on obtaining adaptive rewards like good genes from high-quality males, are what largely impact animal mating relations. In fact, any potential genetic advantages from remating are likely insufficient to offset these costs. A central aspect of this perspective is the sexual differences in the optimal number of copulations with various partners. Since males typically gain more from each additional mate than they lose in mating costs, they are likely to seek a higher number of different mates compared to females. This discrepancy can lead to conflict over remating rates, where males may coerce non-virgin females into mating while trying to limit their rematings with rival males. In response, females have evolved strategies to counteract such coercion (Darryl , 2008). Males of internally fertilizing species often produce ejaculates containing other substances in addition to sperm. These substances can serve as mate guarding mechanisms by inhibiting female remating through physical and physiological means. For example, in the ground beetle *Leptocarabus procerulus*, seminal fluids act as both mating plugs that physically obstruct the female genitalia and substances that induce a refractory period, reducing female receptivity (Yamane *et al.*, 2015). However, females have evolved counter-adaptations to these male tactics. They can expel the mating plugs and delay the onset of refractory behavior. Despite these female defenses, the interplay between the physical and physiological functions of male seminal substances can still lower female remating rates during the critical post-mating period important for male fertilization success (Yamane *et al*., 2015).This interplay of male defensive strategies against female resistance may represent an adaptation that has arisen from the ongoing evolutionary arms race between males and females. As males evolve new tactics to monopolize females, females in turn develop counter-adaptations, leading to the perpetual cycle of antagonistic coevolution (Cordero-Rivera 2017). The example highlights how sexual conflict can drive the evolution of complex reproductive strategies in both sexes, as each attempt to maximize its own fitness at the expense of the other. This dynamic interaction is a key driver of the incredible diversity of mating systems observed in animals (Krasnec *et al*., 2012; Hosken and Stockley 2005; Takami *et al*, 2008).

Evolutionary origins of nuptial gifts. Sexual conflict over remating rates may have led to the evolution of large male ejaculate meals in some species. The hypothesis suggests: Originally, males-controlled females through chemical ejaculation, which prevented female remating and reduced sperm competition. Through the metabolization of these ejaculate components, females developed resistance to this male compulsion. The ejaculate components then evolved into direct material benefits (seminal gifts) for females as ejaculates increased in size through a "coevolutionary arms race between the sexes" (Arnqvist and Nilsson 2000). It has been suggested that males in some orthopterans (such as crickets and katydids) evolved oral glandular gifts to divert their partners once females began consuming the spermatophore prior to complete insemination. These gifts include: The spermatophylax attached to the spermatophore, which is a proteinaceous meal provided from male external glands. Sperm partitioning into numerous tiny spermatophores that are transported during multiple matings, each of which serves as a nourishing food source for the female while enabling the male to finish insemination (Laird *et al.*, 2004).

Nuptial gifts and its classification. Proteins, carbohydrates, lipids, peptides, uric acid, amino acids, minerals, water, anti-aphrodisiac pheromones, antipredator defensive compounds, and neuroendocrine modulators that alter the recipient's physiology are examples of materials consumed or advantageous substances absorbed by one sex during mating. These nuptial gifts play a significant role in reproductive behavior and animal mating systems (Piascik *et al*., 2010; Lewis and Adam 2012). Behavioral, ecological, and evolutionary research has paid relatively little attention to nuptial gifts, nevertheless, in comparison to more obvious sexually chosen features like male decoration or weaponry. Male reproductive investment is increased by nuptial presents, which lowers male mating rates and affects courting dynamics and sexual size dimorphism. Selection forces influence both the donors and the recipients of gifts, influencing the biological makeup and structure of wedding presents as well as the gift-giving behaviors. Nuptial gifts also play a critical role in dynamic coevolutionary interactions between the sexes, connecting the resource budgets of males and females at the nexus of sexual selection, nutritional ecology, and life-history evolution (Piascik *et al*., 2010; Lewis and Adam 2012). There are many different types of animal nuptial presents, including as food offerings, male body parts, salivary gland secretions, hemolymph, seminal fluid, spermatophores (packages carrying sperm generated by male reproductive organs), and love darts. As an example, male scorpion flies gift females with dead insects or secretions from their larger salivary glands, which are sexually dimorphic (Carayon 1964; Thornhill 1981; Cumming 1994; Austad and Thornhill 1986; Lack 1940; Mougeot *et al*., 2006). Certain kinds of ground crickets have unique spurs on their hind legs from which the females ingest hemolymph. During mating, males of many animals, including most insects, mollusks, salamanders, crustaceans, annelids, and leeches, give females spermatophores with varying biochemical compositions. Animals with distinct sexes are not the only ones that may give nuptial gifts; several hermaphrodites inject substances during copulation to cause physiological reactions in their mates. Furthermore, not every gift-giving is a masculine trait; male heteropteran Zeus bugs, for instance, feed on glandular secretions supplied by females (Lewis and Adam 2012).

Animal gifts are remarkably diverse, not only amongst various insect species but even within individual clades. For example, spermatophores are widespread in the Lepidoptera order of insects, whereas they are rare in the Diptera and nonexistent in the Coleoptera. Certain males in the Lampyridae family of beetles (fireflies) create complex spermatophores, while males in other species transmit free (unpackaged) ejaculates. Orthopteran nuptial gifts exhibit an astounding spectrum of diversity, even beyond spermatophores. Another noticeable characteristic is the remarkable flexibility in gift-giving behavior shown in some tribes. Male *Panorpa* scorpion flies (Mecoptera: Panorpidae), for example, use several forms of gifts in their mating rituals. In *P. cognata*, a male's nutritional state influences his gift-giving behavior; well-fed males exude salivary masses that females ingest during copulation, whereas malnourished males provide a dead arthropod instead. Similarly, in certain empidid dancing flies (Diptera: Empididae), males can voluntarily offer females with a dead prey insect. (Lewis and Adam 2012).

Classification

Based on method of gift production. A. Endogenous gifts: These are manufactured by males themselves. E.g. Food items, spermatophylaces, hindwing secretions etc.

B. Exogenous gifts: Externally procured food items, such as seeds or prey, are gathered by males and transferred to females. Examples include seeds (Carayon 1964), insect prey (Thornhill 1981; Cumming 1994; Austad and Thornhill 1986), and courtship feeding (Lack 1940; Mougeot *et al*., 2006).

Based on gifts absorption by the recipient

A. Oral gifts: Oral gifts are absorbed by the female digestive system. For example, hemolymph from the tibial spurs of ground crickets (Piascik *et al*., 2010), spermatophylax of katydids and crickets (Gwynne 1997), and salivary secretions of *Panorpa* scorpion flies (Engqvist 2007). *Drosophila nebulosa*'s anal secretions (Steele, 1986), tree crickets' meta-notal secretions (Brown 1997), and sexual cannibalism in red-backed spiders and mantids (Elgar and Schneider 2004).

B. Genital gifts: These are absorbed by the female reproductive system, including both unpackaged secretions from male reproductive glands (conveyed in liquid seminal fluid) and those enclosed in discrete packages (spermatophores). Examples of spermatophores include those found in salamanders, lepidopterans, mollusks, copepods, crabs, and spiders (Mann 1984), as well as seminal fluid proteins in *Drosophila* spp. (Chapman 2008; Markow 2002; Wolfner 2007), love darts in land snails (Koene and Schulenburg 2005), and setal gland injection in earthworms.

Transdermal gifts: These are injected through the skin into the partner's body. E.g. Intradermal spermatophore implantation in Squid (Hoving and Laptikhovsky 2007) and Leeches (Mann 1984) and haemocoelic injection of seminal fluid in Bed bugs (Stutt and Siva-Jothy 2001).

Focal species studies of gifts

Exogenous oral gifts: Exogenous oral gifts are food items that males catch or collect and are likely to include nutrients that contribute to female metabolic reserves. As a result, these gifts are projected to confer net fitness benefits to females, as indicated by greater lifetime fecundity. From the male perspective, these gifts are expected to improve male fitness throughout numerous selection episodes (Vahed, 2007). First, because females can assess these gifts (either visually or through taste) prior to mating, exogenous oral gifts are likely to improve a male's ability to attract and successfully mate with females. Second, since females remain stationary while feeding, food gifts may facilitate the initiation of copulation. Third, as females consume these gifts during copulation, these gifts are expected to increase both the duration of copulation and the quantity of sperm transferred.

Endogenous oral gifts: This category includes a wide range of compounds generated by male salivary, reproductive, and other glands, as well as parts or the entire male body, which females ingest prior to, during, or following copulation. For example, females of *Oecanthus nigricans* tree crickets (Orthoptera) feed on proteinaceous secretions produced by glands placed on the males' backs. Similarly, female true flies (Diptera) and scorpionflies (Mecoptera) ingest male salivary secretions, whilst female Allonemobius ground crickets drink hemolymph from specific spurs on the males' hind legs. Females in many katydids and crickets (Orthoptera) ingest spermatophylax, a gelatinous part of the spermatophore generated by the male reproductive glands. Additionally, sexual cannibalism is observed in many mantids and orb-weaving spiders, where females kill and consume males either before or after insemination (Elgar and Schneider 2004). In these cases, the male body serves as an endogenous oral gift, and when given involuntarily, these gifts can negatively impact male fitness.

Endogenous oral gifts are expected to have varying impacts on females due to their distinct sources. These gifts, which include substances generated by male salivary, reproductive, and other glands, as well as portions of the complete male body, can provide major nutritional benefits. While some endogenous gifts, such as hemolymph or male body parts, may contribute to female nutrient budgets in the same way that exogenous gifts of prey or other food items do, glandular gifts are especially beneficial because they provide specialized dietary supplements.These unique glandular gifts may provide nutrients that are otherwise scarce in female diets, such as macronutrients (proteins, fats, and carbs), micronutrients (sodium, zinc), and defense chemicals (cantharidin, pyrrolizidine alkaloids, and cyanogenic glycosides). For example, male cockroaches (Dictyoptera: Blattidae) deliver endogenous oral gifts that serve as a vital nitrogen source for females and their eggs. In many cockroach species, males store uric acid in their accessory glands before packaging it into spermatophores, which females eject and ingest after mating. In other roach species, females feed directly on uric acid, which is generated by male glands. According to sexual conflict theory, male glandular gifts may evolve to benefit men while severely impacting female fitness (Arnqvist and Rowe 2005). This can set off a cycle of reciprocal sexual coevolution in which females acquire systems to digest or neutralize manipulative chemicals delivered by males (Arnqvist and Nilsson 2000). However, Gwynne (2008) contends that oral presents are less likely to contain manipulative compounds since these substances may disintegrate while passing through the digestive system. As a result, endogenous oral gifts can vary greatly, including nuptial gifts that may have a favorable, negative, or neutral impact on female fitness. When females may scrutinize endogenous oral presents, such as secreted salivary masses, males may perceive these gifts as exogenous gifts that improve male mating success, extend copulation duration, and potentially increase the quantity of sperm transmitted. For instance, in spiders, sexual cannibalism occurring post-insemination can benefit the male by prolonging copulation, thereby boosting sperm transfer and his share of paternity, while also enhancing female fecundity and offspring survival. In the case of orally ingested glandular gifts, like the spermatophylax in orthopterans, males may evolve to include phagostimulants to make their gifts more appealing to females. Additionally, selection pressures might lead to changes in the composition of male gifts to slow female consumption rates, allowing more time for sperm transfer. For example, many crickets and katydids produce spermatophylaxes with a sticky, gelatinous texture that inhibits rapid ingestion by females, thereby increasing the likelihood of successful sperm transfer (Vahed, 2007).

Endogenous Genital Gifts: Endogenous genital gifts are substances produced by male reproductive glands and transferred to females through seminal fluid or spermatophores, where they are absorbed via the female genital tract. These gifts likely evolved from the need to prevent sperm loss or desiccation, but they have multiple evolutionary origins and trajectories. Like orally ingested glandular gifts, these male reproductive products can provide essential nutrients that may be scarce in female diets. For instance, nuptial gifts can target female-specific requirements for vitellogenesis, potentially enhancing reproductive success. Research, across various insect orders, including Orthoptera, Lepidoptera, and Coleoptera, has shown that substances from endogenous genital gifts, such as amino acids, zinc, phosphorus, and sodium, are incorporated into female somatic tissues and eggs. A notable example is found in lepidopteran males that engage in puddling behavior to obtain sodium, a nutrient often lacking in their diets. Males store sodium in their reproductive glands and transfer it to sodium-rich spermatophores during mating. In the moth *Gluphisia septentrionis*, a single spermatophore can contain more than half of the male's salt concentration (Smedley and Eisner 1996). Females subsequently transmit this salt to their eggs, increasing larval survival rates, as observed in the skipper *Thymelicus lineola* (Pivnick and McNeil 1987). Furthermore, male reproductive glands can act as storage for protective chemicals derived from their food. These substances are then delivered to females via spermatophores or seminal fluid, providing protection from predators and microbial dangers. Cantharidin in *Neopyrochroa flabellata* beetles, pyrrolizidine alkaloids in *Utetheisa ornatrix* moths, cyanogenic glycosides in various *Heliconius* butterflies, and vicilin-derived peptides in Callosobruchus maculatus cowpea beetles are all examples of protective chemicals. Thus, endogenous genital gifts play an important role in improving female reproductive success while also providing protective advantages. Some components of endogenous genital gifts may indeed have detrimental effects on female fitness. Gwynne (1986) found that the spermatophores of *Requena verticalis* are twice the size necessary for complete sperm transfer. This suggests that while these gifts can enhance reproductive success, they may also represent an excessive investment. Furthermore, it was observed that when females consumed nutrients from spermatophylaxes, their egg size increased, indicating that courtship feeding in this species functions as a form of paternal investment.In a subsequent study, Simmons *et al*. (1993) noted that male *R. verticalis* increased sperm quantity in the ampulla while reducing spermatophylax size in response to heightened sperm competition. Gwynne (1988) further demonstrated that the nutrients provided by sires positively impacted offspring development using genetic markers and radioactive labels.In *D. melanogaster*, seminal fluid proteins have been shown to enhance female oogenesis and oviposition, increase sperm storage and utilization, and reduce female remating rates and lifespan (Chapman,2008). Despite the significance of these secretions, much remains unknown about their nature across various taxa. Recent studies have begun to characterize the composition of seminal fluid in species such as *Aedes* mosquitoes, crickets (*Gryllus* and *Allonemobius*), *Heliconius* butterflies, flour beetles (*Tribolium*), and honeybees. Many male gifts also contain anti-aphrodisiacs that lower the likelihood of female remating. While selection pressures may favor the inclusion of such substances to mitigate sperm competition, these anti-aphrodisiacs can negatively impact female net fitness by reducing remating rates below optimal levels. Thus, endogenous genital gifts are complex mixtures shaped by multiple selective forces. It has been argued that the composition of male ejaculates is primarily selected to manipulate female reproductive physiology, often resulting in a net fitness cost for the female recipients (Arnqvist and Rowe 2005).

Endogenous Transdermal Gifts: Endogenous transdermal gifts encompass male seminal and glandular products that are transferred and absorbed outside the female's digestive or reproductive systems, notably during extragenital insemination in bedbugs. In the bedbug (*Cimex lectularius*), male ejaculates contain not only sperm but also antioxidants, micronutrients, and antibacterial compounds (Reinhardt *et al*., 2003). This method of hypodermic injection of seminal products is prevalent among simultaneous hermaphrodites, such as leeches, sea slugs, and polyclad flatworms. Another category of transdermal gifts includes allohormones, which induce direct physiological responses in the recipient. These substances can be injected through the skin of a mating partner during copulation, allowing male products to bypass the digestive and reproductive tracts, where various components might otherwise be degraded. A similar mechanism is observed in the land snail *Helix aspersa*, where males use a calcareous dart coated with allohormones produced by a mucus gland. These allohormones inhibit sperm digestion and enhance sperm storage in the female. As with other endogenous gifts, the evolution of transdermal gift production may favor the inclusion of compounds that benefit males while potentially being detrimental to female fitness. This complex interplay of benefits and costs highlights the intricate dynamics of sexual selection and reproductive strategies in various species.

Table 1: The gifts and their role in different insects across the order.

Taxa	Male donation	Fecundity	Rate of oviposition	Egg weight	Egg survival	Female survival	Reference
Coleoptera							
Mellontha melolontha	Spermatophore/ seminal nutrients	+					Landa (1960 and 1961)
Bean Weevil *Acanthoscelides obtectus*	Sperrnatophore/ seminal nutrients						Huignard (1983)
Caryedon serratus	Sperrnatophore/ seminal nutrients	+					Boucher and Huignard (1987)
Lytta vestcatoria	Cantharidin					+	Sierra *et al*. (1976)
Diptera							
Drosophila mojavensis	Seminal nutrients	+					Markow and Krebs (1990)
Aedes aegypti	Seminal nutrients					+	Villarreal *et al*. (2018)
Mecoptera							
Bittacus spp.	Arthropod prey					+	Thornhill and Alcock (1983)
Panorpa spp,	Arthropod prey/salivary mass					+	Thornhill (1979)
Lepidoptera							
Colias eu ytheme	Seminal nutrients	+	+			+	Boggs and Wait (1981)
Heliconius spp	Seminal nutrients						Boggs and Gilbert (1979) Boggs (1981)
Danaus plexippus	Seminal nutrients						Boggs and Gilbert (1979)
Dyar julia	Seminal nutrients						Boggs (1981)
Euphydyas spp	Seminal nutrients						Jones *et al*. (1986)

Plodia interpunctella	Seminal nutrients						Greenfield (1982)
Utetheisa ornatrix	Pyrrolizidine alkaloids				+		Eisner and Meinwald (1987)
Ithomia agnosia	Pyrrolizidine alkaloids				+	+	Brown (1984)
Heliothis virescens	Zn						Engebretson and Mason (1980)
Thymelicus lineola	Na+				+	+	Pivnick and Mcneil (1987)
Orthoptera							
Xertoblatta hamata	Uric acid		+				Schal and Bell (1982)
Blattella germanica	Uric acid						Mullins and Keil (1980)
Melanoplus sanguinipes	Spermatophore	+			+		Friedel and Gillot (1977)
Chorthippus brunneus	Spermatophore	+	+				Butlin *et al.* (1987)
Oecanthus nigrzcarnis	Metanotalsecretions		+				Bell (1979)
Anabrus simplex	Spermatophylax	+					Gwynne (1984)
Requena verticalis	Spermatophylax	+		+	+		Gwynne (1988)
Gryllus bimaculatus	Spermatophore			+	+		Simmons (1988)

CONCLUSIONS

Most oral gifts, such as prey or glandular products, provide direct benefits to females. These gifts are crucial for female nutrition, particularly when food from other sources is scarce, often leading to increased mating rates. For instance, the availability of nutrients from these gifts can enhance female reproductive success, as evidenced by studies showing that females are more likely to mate when they can access these resources. Additionally, some seminal contributions from males also offer direct benefits. These contributions may include chemicals that serve defensive roles against natural enemies, as well as essential nutrients. Evidence suggests that when females receive these gifts, they can improve their reproductive outcomes, which further supports the idea that these gifts are beneficial. Overall, the interplay between male gifts and female fitness illustrates the complex dynamics of sexual selection and resource allocation in mating strategies.

FUTURE SCOPE

This area is rich with potential due to the complex interactions between male and female reproductive strategies, the ecological implications of gift-giving behaviors, and the evolutionary dynamics involved. Understanding the ecological context in which nuptial gifts are exchanged can be a significant area of study. The chemical composition of nuptial gifts and its effects on female fitness present another promising research avenue. The study on the molecular level interactions involved in this kind of behavior could be a potential tool for managing some of the harmful insects such as mosquitos and flies.

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REFERENCES

Andersson, M. (1994). *Sexual selection*. Princeton University Press.

Andres, G., Carmen, R., Maria, E. and Thomas, E. (1999). Sexually transmitted chemical defense in a moth (*Utetheisa ornatrix*). *Proceedings of the National Academy of Sciences, 96*(10), 5570–5574.

Arnqvist, G. and Nilsson, T. (2000). The evolution of polyandry: Multiple mating and female fitness in insects. *Animal Behaviour, 60*, 145–164.

Arnqvist, G. and Rowe, L. (2005). *Sexual conflict*. Princeton University Press.

Austad, S. N. and Thornhill, R. (1986). Female reproductive variation in a nuptial-feeding spider, *Pisaura mirabilis*. *Bulletin of the British Arachnological Society*, *7*, 48–52.

Bell, P. D. (1979). *Mate choice and mating behaviour in the black horned tree cricket, Oecanthus nigricornis (Walker)* (Master's thesis, University of Toronto).

Boggs, L. (1981). Selection pressures affecting male nutrient investment in heliconiine butterflies. *Evolution, 35*, 931–940.

Boggs, L. andGilbert, L. E. (1979). Male contribution to egg production in butterflies: Evidence for transfer of nutrients at mating. *Science, 206*, 83–84.

Boggs, L. and Watt, W. B. (1981). Population structure of pierid butterflies IV. Genetic and physiological investment in offspring by male Colias. *Oecologia, 50*, 320–324.

Boucher, L. and Huignard, J. (1987). Transfer of male secretions from the spermatophore to the female insect in Curyedon serratus: Analysis of the possible trophic role of these secretions. *Journal of Insect Physiology, 33*, 949–957.

Bownes, M. and Partridge, L. (1987). Transfer of molecules from ejaculate to females in Drosophila melanogaster and *Drosophila pseudobscura*. *Journal of Insect Physiology, 33*, 941–948.

Brown, K. S. (1984). Adult-obtained pyrrolizidine alkaloids defend ithomiine butterflies against a spider predator. *Nature, 309*, 707–709.

Brown, W. D. (1997). Courtship feeding in tree crickets increases insemination and female reproductive life span. *Animal Behaviour*, *54*(6), 1369–1382.

Butlin, R. K., Woodhatch, C. W. and Hewitt, G. M. (1987). Male spermatophore investment increases female fecundity in a grasshopper. *Evolution, 41*, 221–224.

Carayon, J. (1964). Un cas d'offrande nuptiale chez les Heteropteres. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences*, *259*, 4815–4818.

Chapman, T. (2008). The soup in my fly: Evolution, form and function of seminal fluid proteins. *PLoS Biology*, *6*(7), e179.

Chapman, T., Arnqvist, G., Bangham, J. and Rowe, L. (2003). Sexual conflict. *Trends in Ecology & Evolution, 18*(1), 41-47.

Christian, V. C., Michener, R. and Kunz, T. H. (2005). The energetics of trading nuptial gifts for copulations in

katydids. *Physiological and Biochemical Zoology, 78*(3), 417-423.
Cordero-Rivera, A. (2017). Sexual conflict and the evolution of genitalia: Male damselflies remove more sperm when mating with a heterospecific female. *Scientific Reports, 7*, 7844.
Cumming, J. M. (1994). Sexual selection and the evolution of dance fly mating systems (Diptera: Empididae). *The Canadian Entomologist*, *126*(6), 907–920.
Danchin, E., Giraldeau, L. A. and Frank, C. (2008). *Behavioural Ecology.* Oxford University Press.
Darryl, T. G. (2008). Sexual conflict over nuptial gifts in insects. *Annual Review of Entomology, 53*, 83-101.
Eisner, T. and Meinwald, J. (1987). Alkaloid-derived pheromones and sexual selection in Lepidoptera. In Pheromone Biochemistry (pp. 251-269). Academic Press.
Elgar, M. A. and Schneider, J. M. (2004). Evolutionary significance of sexual cannibalism. In P. J. B. Slater (Ed.), *Advances in the Study of Behavior* (Vol. 34, pp. 135–163). Academic Press.
Engebretson, J. A. and Mason, W. H. (1980). Transfer of 65Zn at mating in *Heliothis virescens.Environmental Entomology, 9*, 119-121.
Engqvist, L. (2007). Nuptial gift consumption influences female remating in a scorpionfly: Male or female control of mating rate? *Evolutionary Ecology*, *21*(1), 41–61.
Friedel, T. and Gillot, C. (1977). Contribution of male-produced proteins to vitellogenesis in *Melanoplus sanguinipes.Journal of Insect Physiology, 23*, 145-151.
Gershman, S. N., Hunt, J. and Sakaluk, S. K. (2013). Food fight: sexual conflict over free amino acids in the nuptial gifts of male decorated crickets. *Journal of Evolutionary Biology*, *26*(4), 693-704.
Greenfield, M. D. (1982). The question of paternal investment in Lepidoptera: Male-contributed proteins in *Plodia interpunctella. International Journal of Invertebrate Reproduction, 5*, 323-330.
Gwynne, D. T. (1984). Sexual selection and sexual differences in Mormon crickets (Orthoptera: Tettigoniidae, *Anabrus simplex*). *Evolution*, *38*(5), 1011–1022.
Gwynne, D. T. (1986). Courtship feeding in katydids (Orthoptera: Tettigoniidae): Investment in offspring or in obtaining fertilizations? *American Naturalist, 128*, 342-352.
Gwynne, D. T. (1988). Courtship feeding and the fitness of female katydids (Orthoptera: Tettigoniidae). *Evolution*, *42*(3), 545–555.
Gwynne, D. T. (1988). Courtship feeding in katydids benefits the mating male's offspring. *Behavioral Ecology and Sociobiology, 23*, 373-377.
Gwynne, D. T. (1997). The evolution of edible "sperm sacs" and other forms of courtship feeding in crickets, katydids and their kin (Orthoptera: Ensifera). In J. Choe & B. Crespi (Eds.), *The evolution of mating systems in insects and arachnids* (pp. 110–129). Cambridge University Press.
Gwynne, D. T. (2008). Sexual conflict over nuptial gifts in insects. *Annual Review of Entomology*, *53*, 83–101.
Holland, B. and Rice, W. R. (1998). Perspective: Chase-away sexual selection: Antagonistic seduction versus resistance. *Evolution, 52*(1), 1-7.
Hosken, D. J. and Stockley, P. (2005). Sexual conflict. *Current Biology, 15*(14), R535-R536.
Hoving, H. J. T. and Laptikhovsky, V. (2007). Getting under the skin: Autonomous implantation of squid spermatophores. *Biological Bulletin, 212*(3), 177–179.
Huignard, J. (1983). Transfer and fate of male secretions deposited in the spermatophore of females of *Acanthoscelides obtectus* Say. *Journal of Insect Physiology, 29*(1), 55-63.
Jones, K. R., Odendaal, F. J. and Ehrlich, P. R. (1986). Evidence against the spermatophore as paternal investment in checker spot butterflies (*Euphydryas*: Nymphalidae). *American Midland Naturalist, 116*(1), 1-6.
Koene, J. M. and Schulenburg, H. (2005). Shooting darts: Co-evolution and counter-adaptation in hermaphroditic snails. *BMC Evolutionary Biology, 5*, 25.
Krasnec, M. O., Cook, C. N. and Breed, M. D. (2012). Mating systems in sexual animals. *Nature Education Knowledge, 3*(10), 72.
Lack, D. (1940). Courtship feeding in birds. *The Auk*, *57*(2), 169–178.
Laird, G., Gwynne, D. T. and Andrade, M. C. B. (2004). Extreme repeated mating as a counter adaptation to sexual conflict? *Proceedings of the Royal Society of London. Series B: Biological Sciences, 271*(1545), 402-404.
Landa, V. (1960). Origin, development and function of the spermatophore in the cockchafer (*Melolontha melolontha* L.). *Acta Societatis Entomologicae Cechoslovacae, 57*, 297-316.
Landa, V. (1961). Experiments with an artificial spermatophore in the cockchafer *Melolontha melolontha. Acta Societatis Entomologicae Cechoslovacae, 58*, 297-301.
Lewis, S. and Adam, S. (2012). The evolution of animal nuptial gifts. In *Advances in the Study of Behavior* (Vol. 44, pp. 53-97).
Mann, T. (1984). *Spermatophores: Development, structure, biochemical attributes and role in the transfer of spermatozoa*.
Markow, T. A. (2002). Female remating, operational sex ratio, and the arena of sexual selection in *Drosophila* species. *Evolution, 56*(8), 1725–1734.
Markow, T., Gallagher, P. and Krebs, R. (1990). Ejaculate-derived nutritional contribution and female reproductive success in *Drosophila mojavensis* (Patterson and Crow). *Functional Ecology, 4*, 67.
Mougeot, F., Arroyo, B. E. and Bretagnolle, V. (2006). Paternity assurance responses to first-year and adult male territorial intrusions in a courtship-feeding raptor. *Animal Behaviour*, *71*(1), 101–108.
Mullins, G. K. and Keil, C. B. (1980). Paternal investment of urates in cockroaches. *Nature, 283*(5745), 567-569.
Piascik, E. K., Judge, K. A. and Gwynne, D. T. (2010). Polyandry and tibial spur chewing in the Carolina ground cricket (*Eunemobius carolinus*). *Canadian Journal of Zoology*, *88*(10), 988–994.
Pivnick, K. A. and McNeil, J. N. (1987). Puddling in butterflies: Sodium affects reproductive success in *Thynelicus lineolu. Physiological Entomology, 12*(4), 461-472.
Reinhardt, K., Naylor, R. and Siva-Jothy, M. T. (2003). Reducing a cost of traumatic insemination: Female bedbugs evolve a unique organ. *Proceedings of the Royal Society B: Biological Sciences, 270*(1531), 2371-2375.
Schal, G. and Bell, W. J. (1982). Ecological correlates of paternal investment of urates in a tropical cockroach. *Science, 218*(4569), 170-172.

Sierra, J. R., Woggon, W. D. and Schmid, H. (1976). Transfer of cantharidin (1) during copulation from the adult female *Lytta vesicator* (Spanish flies). *Experientia, 32*(2), 142-144.

Simmons, L. W. (1988). The contribution of multiple mating and spermatophore consumption to the lifetime reproductive success of female field crickets (*Gryllus bimaculatus*). *Ecological Entomology*, *13*(1), 57–69.

Simmons, L. W., Craig, M., Llorens, T., Schinzig, M. and Hosken, D. (1993). Bushcricket spermatophores vary in accord with sperm competition and parental investment theory. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 251*(1330), 183-186.

Smedley, S. R. and Eisner, T. (1996). Sodium: A male moth's gift to its offspring. *Proceedings of the National Academy of Sciences of the United States of America*, *93*(2), 809–813.

Steele, R. J. (1986). Courtship feeding in *Drosophila subobscura.* I. The nutritional significance of courtship feeding. *Animal Behaviour*, *34*(4), 1087–1098.

Stutt, A. D. and Siva-Jothy, M. T. (2001). Traumatic insemination and sexual conflict in the bed bug Cimex lectularius. *Proceedings of the National Academy of Sciences*, *98*(16), 5683–5687.

Takami, Y., Sasabe, M., Nagata, N. and Sota, T. (2008). Dual function of seminal substances for mate guarding in a ground beetle. *Behavioral Ecology, 19*(6), 1173-1178.

Thornhill, R. (1976). Sexual selection and paternal investment in insects. *American Naturalist, 110*(973), 153-163.

Thornhill, R. (1981). Panorpa (Mecoptera: Panorpidae) scorpionflies: Systems for understanding resource-defense polygyny and alternative male reproductive efforts. *Annual Review of Ecology and Systematics*, *12*, 355–386.

Thornhill, R. and Alcock, J. (1983). *The evolution of insect mating systems.* Harvard University Press.Thornhill, R. (1976). Sexual selection and paternal investment in insects. *The American Naturalist*, *110*(97), 153–163.

Vahed, K. (2007). All that glisters is not gold: Sensory bias, sexual conflict and nuptial feeding in insects and spiders. *Ethology*, *113*(2), 105–127.

Villarreal, S. M., Pitcher, S., Helinski, M. E. H., Johnson, L., Wolfner, M. F. and Harrington, L. C. (2018). Male contributions during mating increase female survival in the disease vector mosquito *Aedes aegypti*. *Journal of Insect Physiology, 108*, 1-9.

Williams, G. C. (1966). *Adaptation and natural selection.* Princeton University Press.

Wolfner, M. F. (2007). "S.P.E.R.M." (seminal proteins (are) essential reproductive modulators): The view from *Drosophila*. *Society for Reproduction and Fertility Supplement, 65*, 183–199.

Yamane, T., Goenaga, J., Rönn, J. L. and Arnqvist, G. (2015). Male seminal fluid substances affect sperm competition success and female reproductive behavior in a seed beetle. *PLoS One, 10*(4), e0123770.

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