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From Sexual Selection to Pest Control: Insights into Pupal Mating in Insects

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ABSTRACT

Pupal mating is an unusual but fascinating reproductive strategy observed in certain insect taxa, most notably Lepidoptera (e.g., *Heliconius* butterflies) and Diptera (e.g., *Opifex fuscus*). Unlike typical adult mating, pupal mating occurs when males copulate with females while they are still enclosed in the pupal case (pharate mating) or immediately upon adult emergence (teneral mating). This behaviour provides strong reproductive assurance for males, minimizes female mate choice, and promotes intense male–male competition for access to pupae. Ecologically, pupal mating influences population dynamics, species interactions, and chemical communication networks. From an applied perspective, understanding pupal mating behaviour offers novel opportunities for integrated pest management (IPM), natural enemy conservation, and enhancing ecological balance in agroecosystems. By disrupting or manipulating mating strategies, farmers and entomologists may gain alternative tools for pest suppression without relying heavily on chemical pesticides. This review synthesizes the mechanisms, evolutionary significance, ecological roles, and potential agricultural applications of pupal mating, highlighting its dual role in evolutionary ecology and sustainable pest management.

Keywords: Insect, reproductive behaviour, sexual selection and pupal mating behaviour

1. INTRODUCTION

Sexual selection, first elaborated by Charles Darwin in *The Descent of Man* (1871), is a fundamental evolutionary mechanism that explains the development of traits not necessarily tied to survival, but rather to reproductive success. Insects, which constitute nearly 80% of all described animal species,

provide some of the most striking and diverse examples of sexual selection. These range from acoustic courtship signals in crickets and katydids, to visual displays in fireflies and butterflies, and chemical pheromonal communication in moths (Symonds & Wertheim, 2014; Steiger & Stökl, 2014). One of the most remarkable and less common strategies observed in insects is pupal mating (also referred to as pharate or teneral mating). This behavior, particularly well-studied in *Heliconius* butterflies and some dipteran mosquitoes, occurs when males mate with females while they are still in the pupal stage, or immediately upon emergence, before females have fully hardened or acquired the ability to exercise mate choice (Deinert, Longino, & Gilbert, 1994; Estrada et al., 2010).

Pupal mating represents an extreme form of sexual selection and reproductive assurance. It enables males to secure fertilization before females are available to competitors, but it simultaneously removes female choice, leading to potential sexual conflict. This review provides a detailed overview of the concept, mechanisms, examples, ecological and evolutionary importance, and applied implications of pupal mating across insects, with emphasis on its role in pest control, ecological balance, and sustainable agriculture.

2. Concept of Sexual Selection and Pupal Mating Behaviour

2.1 Sexual Selection in Insects

Charles Darwin (1871) first articulated sexual selection as a driving evolutionary force acting through two principal pathways:

Intrasexual Selection (Male–Male Competition)

In this form, males compete with each other for access to mates or reproductive resources. This competition may take several forms, including direct physical combat, the use of specialized weapons, or post-copulatory mechanisms like sperm competition and mate guarding. For example:

- Horn battles in scarab beetles (*Onthophagus spp.*), where males use their large horns to rival competitors and control breeding tunnels that females use for laying eggs.
- Territorial contests in fig wasps, where males battle for control of mating areas to access females.
- Mate guarding and sperm competition are widespread strategies to ensure paternity after mating.

Males have evolved phenotypic traits such as large body size, horns, mandibles, and early sexual maturity that enhance their competitiveness. Stronger males often monopolize females and necessary breeding resources. The expression and effectiveness of these traits are often shaped by the intensity of male-male competition within populations.

Intersexual Selection (Female Choice)

Female mate choice is the counterpart to intrasexual competition, where females select mates based on preferred traits, which might indicate good genes, increased fertility, or direct benefits like nuptial gifts. Insects rely heavily on courtship signals such as:

- Acoustic signals like the songs of crickets.

- Bioluminescent flashes emitted by fireflies during night-time mate attraction.
- Sex pheromones in moths and butterflies, exemplified in species like *Bombyx mori* (silkworm moth), which use chemical signals for mate recognition and attraction.

Chemical communication is particularly important in insects, involving cuticular hydrocarbons (CHCs) and volatile pheromones. These substances serve as cues for reproductive status, kinship, and mate compatibility. CHCs may allow individuals to avoid inbreeding by recognizing close relatives, enhancing population fitness and genetic diversity. In systems featuring pupal mating, males detect chemical cues emitted by female pupae long before adult emergence, enabling them to locate, guard, and monopolize reproductive opportunities effectively. These chemical signals are vital triggers that facilitate early mate guarding behavior and reproductive success.

2.2 Pupal Mating: Mechanisms

Pupal mating is an unusual reproductive strategy where mating occurs during or immediately after the pupal stage of females, involving two main forms:

Pharate Mating

Here, mating happens while the female is still within the pupal case — the male inserts his reproductive organ (aedeagus) directly into the pupal case to copulate before the adult female has emerged. This form is relatively rare and represents one extreme in the timing of mating.

Teneral Mating

In this form, mating occurs immediately after adult emergence when the female's exoskeleton is still soft, and she has little or no ability to resist male advances. Mating at this vulnerable stage limits female choice, increasing male fertilization assurance.

Key Steps in Pupal Mating

1. **Detection**: Males use a combination of plant-associated volatiles and female-specific chemical cues to locate female pupae. Research in *Heliconius* butterflies has pinpointed compounds like linalool and linalool oxide as key attractants.
2. **Guarding**: After locating a female pupa, the male often guards it for multiple days. This guarding behavior involves blocking rival males and displaying aggressive postures. Studies on *Heliconius charithonia* detail such prolonged mate guarding as critical for male reproductive success.
3. **Copulation**: Copulation may occur within the pupal case (pharate mating) or immediately after female emergence (teneral mating). Males insert their aedeagus either into the pupal case or directly into the female reproductive tract post-emergence.
4. **Post-Mating Assurance**: Males transfer spermatophores containing sperm and nutrients, and often deposit anti-aphrodisiac pheromones or mating plugs. These serve to reduce the female's attractiveness or prevent remating with other males, ensuring the guarding male's paternity.

2.3 Examples Across Insect Orders

Lepidoptera

The order Lepidoptera (butterflies and moths) provides some of the most well-studied examples of pupal mating behavior, especially within the genus *Heliconius*.

- *Heliconius charithonia*, *H. erato*, and *H. hewitsoni* are classic examples of species exhibiting pupal mating. In these species, males locate female pupae and aggressively guard them, sometimes for several days, competing with rival males to secure mating access. Mating occurs either by inserting the abdomen into the pupal case before female emergence ("pharate mating") or immediately after emergence when females are vulnerable and soft-bodied ("teneral mating"). This behavior is considered a form of sexual coercion as females have limited ability to resist male advances during this period (Deinert et al., 1994; Estrada et al., 2010).
- In contrast, the butterfly Dryas iulia shows males guarding pupae, but mating mostly occurs post-emergence rather than via true pupal mating, making it a facultative behavior.

Diptera (Mosquitoes and Flies)

- Opifex fuscus, a mosquito species, exhibits a form of pupal mating where males clasp onto the pupae that float at the water's surface and mate with females as they emerge (Craig, 1967). This behavior enables males to secure mates quickly at emergence.
- The medically important mosquito species Culex pipiens exhibits *teneral mating*, where males mate with females immediately after adult emergence, although *pharate* mating is rare in this species.

Coleoptera (Beetles)

- Beetles generally show *teneral mating* behavior rather than true pupal mating. Males mate with females immediately after they emerge from the pupal case when they are still soft-bodied and less resistant. True pupal mating (mating while females are still pupae) is rare or absent in beetles (Eberhard, 1996).
- Examples include dung beetles and other species that display post-emergence mating and sometimes prolonged mate guarding.

Trichoptera (Caddisflies)

- Guarding of female pupae by males has been observed in some caddisfly species, although full *pharate mating* within the pupal case has not been extensively documented or remains unclear.
- The behavior is thought to be related more to guarding female emergence sites and less to direct pupal mating, but detailed studies remain limited in this order.

3. Ecological and Evolutionary Significance

3.1 Reproductive Assurance and Sexual Coercion

Pupal mating guarantees that males secure reproductive success by inseminating females before they become capable of resistance or mate choice (Thurman et al., 2018). This early mating assures paternity without female cooperation, significantly increasing male fitness in competitive environments. However, this strategy limits female autonomy, restricting mate choice and representing sexual coercion. Consequently, this may reduce genetic variation within populations as female choice, an important driver of genetic diversity, is curtailed.

3.2 Male–Male Competition and Mate Guarding

In species exhibiting pupal mating, such as *Heliconius charithonia*, males engage in intense mate guarding and physical competition over female pupae (Deinert et al., 1994). The presence of rival males results in aggressive contests requiring endurance, strength, and strategic guarding behavior. While successful males achieve high paternity assurance, the energy invested and increased exposure to predators and parasitoids create significant costs, highlighting an evolutionary trade-off between reproductive success and survival.

3.3 Role in Speciation

Variation in mating strategies—specifically pupal mating versus adult mating—among closely related *Heliconius* species plays a notable role in reproductive isolation (Beltrán et al., 2007). These different strategies reduce hybridization and gene flow between species, thus promoting speciation. Behavioral isolation driven by mating timing and mechanisms has been shown to be an important prezygotic barrier in these butterflies.

3.4 Chemical Ecology

The reproductive behaviors in pupal mating are mediated by complex chemical signaling. Female pupae emit volatile compounds such as linalool and dihydroedulan that attract males and facilitate sex recognition (Estrada et al., 2010). These chemicals enable males to detect and discriminate among pupae, promoting effective mate searching and guarding. The co-evolution of such chemical cues and mating strategies reflects an intricate relationship between ecological context and reproductive behavior.

3.5 Ecological Trade-offs

While mate guarding increases mating success, it also increases the predation risk for guarding males and vulnerability of the pupae to parasitoids. Such ecological pressures balance the benefits gained through increased reproductive assurance. Furthermore, the reduction in female choice resulting from pupal mating may decrease genetic diversity in the population, potentially diminishing adaptability to environmental changes or emerging threats.

Applied Importance in Pest Control and Agriculture

4.1 Implications for Pest Control

Pupal mating behavior in insects offers predictable and targeted opportunities for pest control interventions. Because males often cluster around pupae, these sites become visible, consistent targets for control measures. Approaches can include:

- Stage-Specific Control: Targeting the pupal stage with biological agents such as parasitic wasps or chemical treatments can disrupt mating success by killing or incapacitating emerging adults before reproduction occurs (Machtinger et al., 2015).
- Limitations of Sterile Insect Technique (SIT): SIT relies on releasing sterile males to compete for mates. In species with pupal mating, SIT effectiveness may be reduced unless sterile males can locate and monopolize female pupae early, preventing fertile males from fertilizing females (Papathanos et al., 2009). This requires specialized strategies to synchronize sterile male releases with pupal availability.
- Predictable Intervention Points: As pupal sites are often clustered (e.g., fly larvae developing in manure), pest managers can deploy biological control agents or insecticides more efficiently in these "hotspots" to maximize impact and reduce pesticide use.

4.2 Ecological Balance and Natural Enemy Conservation

Male guarding behavior increases the vulnerability of pupae to natural enemies, particularly predators and parasitoids. This has beneficial ecological implications for pest regulation:

- Boost to Natural Enemies: Pupal parasitoids such as *Trichogramma* spp. (egg parasitoids) and *Telenomus* spp. effectively exploit the pupal stage in agricultural pests and filth flies, helping regulate populations naturally (Machtinger et al., 2015).
- Augmentation Programs: Release of commercially produced pupal parasitoids can augment natural populations, improving biological control without chemical reliance. Such parasitoids require suitable environmental conditions and host availability for success, and compatibility with integrated pest management (IPM) strategies (Machtinger et al., 2015).
- Conservation of Beneficial Species: Ecological farming practices that reduce broad-spectrum insecticide use support natural enemies, enhancing their pest-suppressive roles around pupal stages.

4.3 Usefulness for Farmers

Understanding pupal mating aids farmers and pest managers in several ways:

- Pest Forecasting: Knowing pupal mating timing enables prediction of adult emergence and peak mating periods, assisting in timely application of control measures (biological or chemical).
- Cost-Effective Control: Targeting the pupal stage with biological control agents reduces the need for repeated chemical sprays, lowering costs and environmental impacts.

- Sustainable Pest Management: By promoting habitat conservation and ecological balance, farmers encourage natural enemy populations that regulate pests effectively, improving long-term crop and livestock health (Machtinger et al., 2015).

5. CONCLUSION

Pupal mating is a rare yet highly significant reproductive strategy in insects, especially Lepidoptera and Diptera. It represents an extreme form of sexual selection where males monopolize immobile females, ensuring reproductive assurance but limiting female choice. Ecologically, it is linked to male–male competition, chemical communication, and even speciation. From an applied perspective, pupal mating has important implications for pest control, ecological balance, and sustainable agriculture. By understanding this behavior, researchers and farmers can better design integrated pest management (IPM) programs that conserve natural enemies, optimize biological control strategies, and reduce pesticide reliance. Ultimately, pupal mating illustrates how deep insights into insect reproductive ecology can contribute both to evolutionary biology and to practical agricultural benefits.

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