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Overview of Thelytokous Parthenogenesis in Two Insect Orders: Diptera and Hymenoptera

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Abstract

Thelytoky is a type of parthenogenesis when unfertilized eggs only produce female offspring. Consequently, it prevents the need for females to find a mate for reproduction through automixis or apomixis. It allows them to successfully pass on their genetic material to their progeny, increasing the number of females. This phenomenon can occur through the genetic mechanisms of certain species or can be induced by infections from maternally transmitted endosymbiotic bacteria such as *Wolbachia*, *Rickettsia*, and *Cardinium*. Different Dipteran and Hymenopteran species reproduce via thelytokous parthenogenesis, but there is still limited information about this process. In this review, we provided a broad summary of the phenomenon of thelytokous parthenogenesis by referencing studies focusing on Dipteran and Hymenopteran species.

Key words: Automixis, apomixis, endosymbionts, arrhenotoky

1. Introduction

Thelytoky is derived from Greek words ‘female’ and ‘birth’. It can be described as a type of parthenogenesis. In this mechanism, unfertilized eggs develop into female offspring, whereas fertilized (diploid) eggs develop into females in parthenogenesis. Therefore, it enables females to transmit their genetic material to their offspring successfully, enhancing the number of females while eliminating the necessity of finding a mate for reproduction either through automixis or apomixis (Figure 1) (Normark and Kirkendall, 2009). In automixis, a normal meiosis process can be completed (Pearcy et al., 2011). Diploidy in females is restored through terminal fusion, central fusion, gamete duplication, or random fusion. In contrast, apomixis lacks meiosis entirely, resulting in diploid females that are considered clones of the mother (Du et al., 2023). If females do not fertilize their eggs or if there is an increased prevalence of sterile females due to infection, the proportion of male individuals within the population can rise significantly. The thelytoky mechanism is essential for population maintenance in these situations because it permits the continued reproduction of female individuals without the requirement for fertilization (Jeong and Stouthamer, 2005).

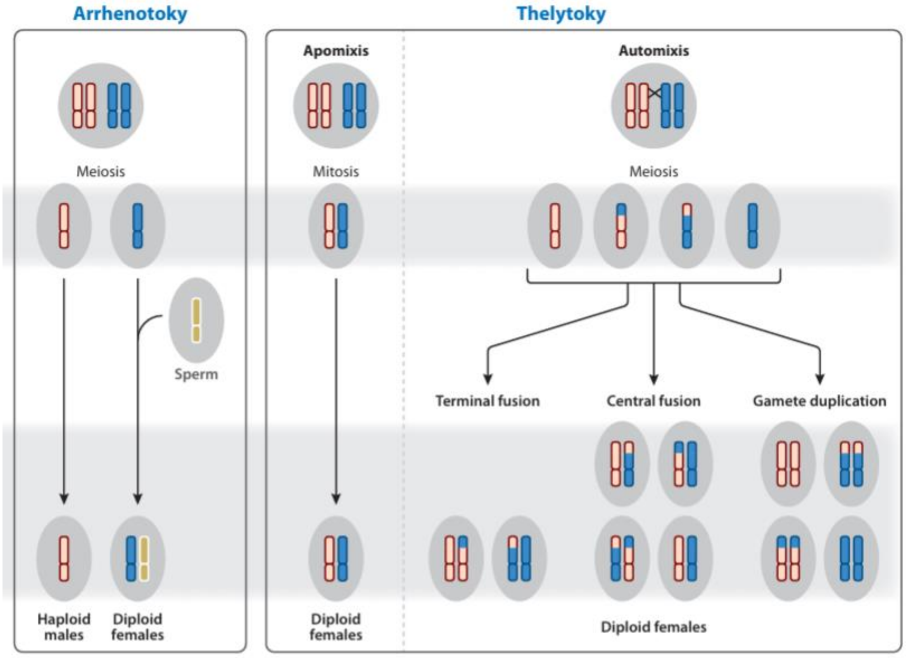

Figure 1. Types of reproduction (Rabeling and Kronauer, 2013)

Thelytokous eusocial insects provide a unique model for evaluating inclusive fitness theory. Colonies of obligatory parthenogenetic species tend to have cooperative functioning as a single 'superorganism' with minimal appearance of individual selfish behavior. However, initial research suggests that even in thelytokous species dominant in clonal lineages, social conflicts and worker policing behaviors are prevalent. This phenomenon is likely due to the presence of multiple clonal lineages within colonies (Rokas et al., 2002). Thelytoky is observed in several hymenopteran taxa including Apoidea, Ichneumonoidea, Tenthredinoidea, and Vespoidea (Keller, 2007). Additionally, four thelytokous ant species are also known: *Pristomyrmex punctatus* (formerly *P. pungens*), *Cerapachys biroi*, *Cataglyphis cursor*, and *Platythyrea punctata*. *Among these*, *P. punctatus* and *C. biroi* are obligatory thelytokous species, whereas *C. cursor* and *P. punctata* exhibit facultative thelytoky (Jeong and Stouthamer, 2005). In addition to hymenopteran species, a substantial majority of dipterans also produce through parthenogenesis.

Thelytoky can occur under the control of the insect itself or be induced by endosymbionts. Shifts from arrhenotoky (produces haploid males from unfertilized eggs) (Figure 1) to thelytoky are frequently mediated by maternally inherited endosymbiotic bacteria including *Wolbachia*, *Rickettsia*, and *Cardinium* (Rokas et al., 2002; Pearcy et al., 2004; Du et al., 2023). However, thelytoky can also be genetically determined in some insects such as those belonging to the genus *Trichogramma* (Vavre et al., 2004). In this review, we discussed previous studies, the dominant viewpoints, and the genetic pathways of thelytokous parthenogenesis.

2. The Genetic Basis of Thelytoky

Thelytoky is a rare phenomenon in which female offspring develop from unfertilized eggs. It is associated with certain traits, such as early onset of egg-laying and the production of queen-like mandibular gland pheromones. The gemini transcription factor at the candidate locus on chromosome 13 is generally crucial for worker reproduction but does not solely regulate the parthenogenesis mechanism (Aumer et al., 2019). It was demonstrated that the two models of parthenogenesis (arrhenotoky or thelytoky) segregated in 1:1 Mendelian ratio under the control of a single recessive locus. Moreover, they stated that the thelytoky allele is not recessive but rather a dominant allele, and works together with a complementary arrhenotoky allele under strong selection in *A. mellifera*. Similarly, Jarosch et al. (2011) investigated potential genes linked to the thelytoky by analyzing chromosome 13 in Cape honeybee (*A. mellifera* *capensis*). They found that worker sterility is controlled by alternative splicing of a gene that is similar to the gemini transcription factor in Drosophila. Furthermore, they revealed a deletion of 9 bp in flanking intron downstream of exon 5 of gemini gene named as thelytoky associated element 1 (tae1). They also suggested a key molecular switch governing whether an unmated worker reproduces via thelytoky or arrhenotoky. In another study, Chapman et al. (2015) also identified 9 bp deletion in tae1 in African-derived honeybee populations, while it was absent in European-derived honeybee populations. They concluded that this deletion is not responsible for thelytokous parthenogenesis. In addition, their study revealed two novel tae alleles (tae2 and tae4).

3. Thelytoky Parthenogenesis in Hymenoptera

Hymenoptera includes approximately 200,000 identified insect species. Ants, bees, wasps, sawflies, etc. are found in this order. The origin of the thelytokous parthenogenesis mechanism in Hymenoptera is believed to have evolved through a convergent process from an ancestral arrhenotokous haplodiploid system (Leach et al., 2009; Kuhn et al., 2020).

Thelytoky was first described in *Apis mellifera capensis*. When capensis worker bees lay unfertilized eggs, the eggs typically develop into diploid female offspring through automictic thelytoky with central fusion. In automictic thelytoky, the reductive division of meiosis II occurs normally resulting in four haploid nuclei. Diploidy is then restored through one of several mechanisms and each of which produces different genetic outcomes (Huigens and Stouthamer, 2003). Furthermore, *Ceratina dellatorreana*, a tiny carpenter bee, has also been known to reproduce thelytokously. Thelytoky in the *C. dellatorreana* was found in an invasive population (Daly, 1966). In addition to bees, thelytoky is relatively common in ants. The number of known thelytokous ant species has significantly increased in recent years as more species have been investigated at the molecular level. Notably, thelytoky in ants also appears to be associated with invasive life history traits (Keller, 2007).

In Hymenoptera, thelytoky has a nuclear allelic basis, yet it is predominantly induced by infections with symbiotic microorganisms (Hagimori et al., 2006). The microbial induction of thelytoky stems from the cytoplasmic transmission of endosymbiotic bacteria and this relies exclusively on maternal inheritance. As these bacteria are not passed through males, male progeny production represents an evolutionary dead end for them. These endosymbionts have developed various reproductive manipulation strategies in their hosts, including male-killing, cytoplasmic incompatibility, feminization of genetically male individuals, and the induction of female parthenogenesis (Heinze, 2008).

There are three types parthenogenesis-inducing (PI) bacteria in Hymenoptera: *Wolbachia*, *Cardinium*, and *Rickettsia* (Jarosch et al., 2011). PI *Wolbachia* strains can be found in many different hymenopteran families, but they are especially prevalent in the superfamilies Chalcidoidea and Cynipoidea (Pearcy et al., 2011). *Wolbachia* induces thelytoky through gamete duplication, either by failure of chromosome segregation during the first mitotic anaphase or fusion of mitotic nuclei during the second prophase (Jarosch et al., 2011). Among Hymenoptera, PI *Cardinium* bacteria have been identified exclusively in wasps of the superfamily Chalcidoidea. These bacteria manipulate their proliferation by reducing or eliminating male production in their hosts, thereby inducing female-producing parthenogenesis (Croizer and Pamilo, 1996). Furthermore, the only known example of PI induced by *Rickettsia* was the eulophid parasitoid wasp, *Neochrysocharis formosa* in China and Japan (Hagimori et al. 2006; Yang et al. 2017).

3.2 Thelytoky Parthenogenesis in Diptera

The Diptera is one of the most well-known and popular insect orders. A significant portion of the dipteran reproduces via parthenogenesis. It has been observed that the adoption of thelytoky parthenogenesis by certain Diptera helps them avoid environmental challenges. During periods of extreme temperatures or high winds, the ability to fly in swarms and find mates may be restricted. In such cases, reproduction through parthenogenesis can help overcome these difficulties (Porter and Martin, 2011; Sperling and Glover, 2023).

Yagound et al. (2020) reported specific changes in protein-coding genes associated with the thelytoky. These were not observed in dipteran genomes but were also found in some ant and bee species. Therefore, it is proposed that another gene may be responsible for the thelytoky expression in dipteran species. Aumer et al. (2019) suggested that genes such as Ethr and mycC are strongly associated with the thelytoky allele, and because they are orthologous to ebony gene in Drosophila melanogaster. Therefore, they may play a role in thelytoky.

4. Conclusion

Thelytoky is a rare form of parthenogenesis observed only in certain species, and its genetic foundations have not yet been fully elucidated. In the initial studies, it was proposed that a single recessive locus controls the mechanism (Lattorff et al., 2005; Jarosch et al., 2011). Later, the expression of multiple loci was also considered (Chapman et al., 2015). The recessive locus hypothesis was eventually refuted due to the low number of microsatellites and the small sample size used in the studies (Aumer et al., 2019). Additionally, the thelytoky mechanism, particularly the role of *Wolbachia* and other endosymbiotic bacteria, is an important area that requires further investigation. The ability of endosymbiotic bacteria, especially *Wolbachia*, to trigger thelytoky by killing male individuals or manipulating sex determination is a significant strategy for enhancing their evolutionary fitness. The bacteria only trigger thelytoky in certain species and do not have similar effects in others. Therefore, it is essential to investigate the interactions between the bacteria and their hosts in greater detail. A thorough understanding of the thelytoky parthenogenesis mechanism could facilitate the development of genetically homogeneous populations and provide strategies for combating certain agricultural pathogens. Further molecular research in this field will enhance our understanding of the genetic factors underlying thelytoky.

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