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Feature Article

Breeding Methods for Improving the Resistance of *Apis mellifera* to *Varroa* Mite (*Varroa destructor*)

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Abstract

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The Western honey bee (*Apis mellifera* L.) is an essential pollinator and contributes significantly to apiculture. Its health is crucial for food security and agricultural profitability. *Varroa destructor*, an ectoparasitic mite, poses the greatest threat to honey bee health by transmitting pathogens and disrupting development, which negatively affects agricultural productivity. Beekeepers used to control *Varroa* mites with miticides, but prolonged use has led to mite resistance and miticide residues in honey bee products. In addition to chemical control, social immune behaviors of honey bees, such as worker hygienic behavior can enhance the *Varroa* mite management by reducing pathogen and mite reproduction. This review explores the methods for breeding *Varroa* mite-resistant honey bees by: (1) assessing the health status of source colonies; (2) evaluating social immune behavioral competencies and gene expressions for selecting parental colonies; and (3) assessing the performance of social immune traits in progeny colonies. This breeding program will help improve Integrated Pest Management (IPM) strategies.

Key words: *Apis mellifera*, *Varroa destructor*, Social immune behaviors, Integrated pest management.

INTRODUCTION

Western honey bees (*Apis mellifera* L.), the primary species in global apiculture, produce honey, beeswax, bee pollen, and royal jelly. The Food and Agriculture Organization (FAO 2023) estimated that the value of honey and associated products exceeded USD 1,200 billion in 2023. Porto *et al*. (2020) valued eco-pollination services at USD 267–657 billion annually, with bees being the main pollinators crucial for food production and ecosystem sustainability (Hung *et al*. 2018; Khalifa *et al*. 2021). Bee-pollinated crops account for about one-third of the human diet and enhance both the quality and quantity of agricultural products such as coffee, cocoa, and almonds (Stein *et al*. 2017; Khalifa *et al*. 2021).

Honey bees are vital for human well-being and agriculture. However, their health is threatened by multiple factors, including ecto-

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parasites, pathogens, environmental conditions, beekeeper management, nutrition, and pesticide exposure (Johnson *et al*. 2010a; Olate-Olave *et al*. 2021; Ricigliano *et al*. 2022). The ectoparasite mite *Varroa destructor* (*Varroa* mite) feeds on the fat body and haemolymph of adult and larval honey bees, causing weight loss, shortened lifespan, and damage to reproductive ability. *Varroa* mites also transmit viruses that cause wing deformation in adult workers, posing a major threat to the beekeeping industry (Duay *et al*. 2002; Ritter 2006; Ramsey *et al*. 2019; Piou *et al*. 2022). Beekeepers often use miticides, such as synthetic pyrethroid compounds, to control *Varroa* mites. However, overuse has led to resistance in *Varroa* populations, resulting in reducing treatment effectiveness and complicating mite control, which can contribute to colony decline and reduced profitability (Johnson *et al*. 2010b; Avalos *et al*. 2024). Integrated Pest Management (IPM) approaches have been advocated in progressive agricultural countries to control *Varroa* mites. These approaches are based on pest and host biology and incorporate sustainable pest management techniques, including monitoring, risk prediction, control methods, pesticide toxicology, breeding programs, and regulatory management (van Alphen & Fernhout 2020; Jack & Ellis 2021).

Honey bees are eusocial insects and possess social immunity against pathogens and parasites. Social immunity includes behavioral, physiological, and organizational adaptations that reduce pathogen transmission within a colony (Cremer *et al*. 2007). To combat *Varroa* mites and associated pathogens, honey bees have developed hygienic and grooming behaviors. Hygienic behavior involves worker bees detecting and removing diseased, dead, or *Varroa* mite-parasitized brood from the colony. Grooming behavior involves bees using their mandibles and legs to remove *Varroa* mites from their bodies, sometimes attacking or killing them (Gilliam *et al*. 1983; Spivak & Reuter 2001; Evans *et al*. 2006; Morfin *et al*. 2021). These hygiene and grooming behaviors are heritable social immune responses that confer disease resistance in honey bee colonies (Spivak & Reuter 2001; Morfin *et al*. 2021). As mentioned above, breeding programs to improve *Varroa* mite resistance through social immunity are a next important step in IPM strategies. Beekeepers primarily maintain colonies for economic purposes and commonly use chemical treatments to control *Varroa* mites. While this approach has long been practiced in conventional farming, few have leveraged honey bees' social immunity. This review explores the breeding potential of social immunity to enhance *Varroa* mite resistance.

INTEGRATED PEST MANAGEMENT (IPM)

IPM for *Varroa* mites involves bee and mite biology, local regulations, and cooperation with beekeepers and the government. It uses pest population monitoring to establish control thresholds and evaluate treatment effectiveness. The life cycle of the *Varroa* mite consists of two phases: The phoretic (on adult bees) and the reproductive phase (within capped brood cells). Female mites prefer drone brood due to its longer development period, which allows for increased progeny production (Rosenkranz *et al*. 2010; Torres & Torres 2020).

The *Varroa* mite population monitoring measures can be divided into screening for mites on adult bees and detecting mites parasitizing capped brood cells. To monitor *Varroa* mites on adult bees, approximately 300 bees are mixed with powdered sugar, ethanol, or other chemicals, gently shaken to remove the mites, then sieved and counted to determine the parasitism rate per 100 bees (Rinderer *et al*. 2004; Dietemann *et al*. 2013). Compared to ethanol or chemical treatments, the sugar dusting method is gentler on bees. However, chemical treatments are more precise because they ensure the complete removal of all mites. Another method for counting *Varroa* mites is the sticky board

method, in which a sticky board is placed underneath a hive and separated from the bees by a layer of screen mesh. The number of fallen mites on the board can be counted regularly (Delaplane *et al*. 2005). Furthermore, parasite infection in brood cells is mostly assessed by removing drone larvae, because adult female mites prefer to parasitize drones, which often provide sufficient development energy for *Varroa* mite nymphs (Dietemann *et al*. 2013).

Monitoring measures can also be used to determine control thresholds for *Varroa* mites and the effectiveness of treatments. The threshold for *Varroa* mite population is set below the economic loss level, as the pest population continues to grow until treated. Various factors, including seasonal variation, geographic region, monitoring method, virus prevalence, and honeybee genetics, influence the determination of these thresholds. For instance, Morfin *et al*. (2024) reported that a *Varroa* mite infestation rate of 1% or higher, monitored through ethanol washing, resulted in higher colony mortality in the following spring compared to colonies with lower mite infestation rates in the fall in Canada. Similarly, Currie & Gatien (2006) established a 2% threshold for *Varroa* mite control on adult bees in the Canadian prairie region to prevent honey production losses. Additionally, Delaplane *et al*. (2005) found that colonies with the suppressed mite reproduction trait took longer to reach the control threshold compared to conventional colonies.

Varroa mite control treatments include physical and chemical methods. When *Varroa* mite levels are below the control threshold, physical treatments such as removing drone brood during inspections and using sticky boards on the bottom of the hive can help reduce mite reproduction (Rosenkranz *et al*. 2010; Dietemann *et al*. 2013). For mite populations that reach the control threshold, chemical treatments like synthetic pyrethroids (e.g. tau-fluvalinate and flumethrin) are recommended. However, resistance to these chemicals has been reported in various countries. Therefore, alternative miticides or organic acids are suggested for IPM strategies (Martin 2004; González-Cabrera *et al*. 2016).

In addition to human interventions, Spivak & Reuter (2001) observed that honey bee colonies exhibit social immunity by removing brood pathogens, thereby enhancing disease resistance. Morfin *et al*. (2021) further noted that hygienic behavior can improve a colony's resistance to *Varroa* mites. As a heritable social immune response in honey bees, hygienic behavior can serve as a trait for breeding healthy colonies, thereby increasing the efficiency of *Varroa* mite management.

SOCIAL IMMUNITY OF WESTERN HONEY BEE

Western honey bee is a eusocial insect that employs various defensive mechanisms against pathogens and parasites. These mechanisms include the innate immunity of the individual bees and the social immunity of the colony. Social immunity represents the collective efforts of individuals to limit the spread of parasites and pathogens, thereby protecting uninfected bees. Examples of social immunity of honey bees against *Varroa* mites include grooming and hygienic behaviors (Spivak & Reuter 2001; Harpur *et al*. 2019). Grooming behavior involves honey bees using their mandibles and legs to remove *Varroa* mites from their bodies. Invernizzi *et al*. (2015) found that Africanized honey bees were more successful at dislodging *Varroa* mites (65.9 ± 15.6%) than Italian honey bees (60.8 ± 20.0%) in petri dish tests, though the difference was not statistically significant. Additionally, Africanized honey bees exhibited a significantly higher tendency to injure *Varroa* mites (29.0 ± 8.6%) than Italian bees (17.7 ± 9.8%). Another study by Morfin *et al*. (2020) compared the expressions of *AmNrx-1* (neurexin) between Indiana mite-biter colonies and unselected Italian colonies. The Indiana mite-biter colonies showed higher *AmNrx-1* expression, a

greater proportion of mutilated mites and higher winter survival rates compared to unselected Italian colonies.

Hygienic behavior in bees refers to the ability of worker bees to detect and remove infected broods, as well as dead or unhealthy bees from the hive. Field studies have demonstrated that such behavior significantly reduces the prevalence of disease such as chalkbrood and American foulbrood, as well as the parasitic mite *V. destructor* (Gilliam *et al*. 1983; Spivak & Reuter 2001; Harbo & Harris 2009). The assessment of hygienic behavior can be conducted through the pin-killed brood test and the liquid nitrogen-killed brood test (Fig. 1). These methods involve killing 100–300 capped cells containing young pupae either by piercing the caps or by applying liquid nitrogen. After returning the treated frames to the hive for 12–30 h, the removal rate of the killed pupae is evaluated to determine the colony's hygienic behavior efficiency (Fig. 1A) (Büchler *et al*. 2013).

Masaquiza *et al*. (2021) reported that hygienic bee colonies exhibited a lower *Varroa* mite infestation rate on adult bees (3.47 ± 1.56%) and achieved the highest honey production (25.08 ± 4.82 kg hive^{-1}) compared to control colonies. Hawkins & Martin (2021) demonstrated that in hygienic colonies, approximately 40% capped cells artificially infested with *Varroa* mite were removed, which was higher than in control colonies. Additionally, the reproductive efficiency of *Varroa* mite in hygienic colonies was lower than in control colonies. Similar results were reported by Khan & Ghramh (2021); in hygienic colonies, the infestation rate of artificially infected *Varroa* mites in capped cells was (10.28 ± 0.86%), significantly lower than that of control colonies (22.78 ± 1.41%). These findings indicate that hygienic colonies possess a superior ability to detect and remove *Varroa* mite-infested brood.

Comprehensive studies of gene expression in hygienic and control colonies demonstrated that worker bees in hygienic colonies not only have higher gene expression of odorant binding proteins and gustatory receptors but also show increased expression of oxidative phosphorylation pathways in KEGG (Kyoto Encyclopedia of Genes and Genomes). These studies indicate

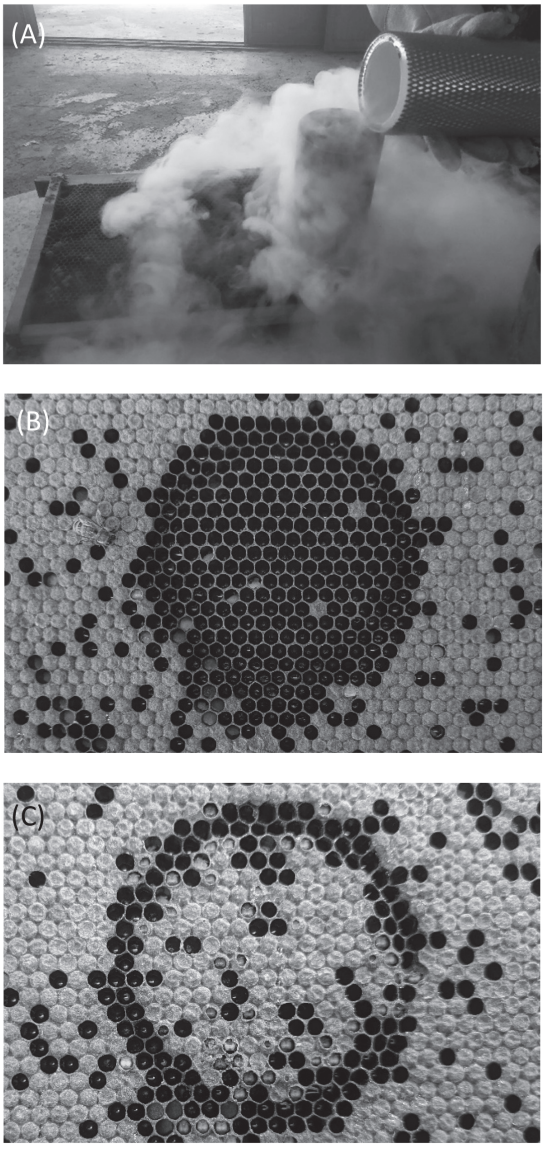

Fig. 1. Evaluation of hygienic behavior in bee colonies with liquid nitrogen. (A) Liquid nitrogen is poured into capped frames. (B) A hygienic bee colony removes dead pupae from the capped frame. (C) A non-hygienic bee colony fails to remove dead pupae from the capped frame.

that signal transduction mechanisms play an important role in inducing hygienic behavior in worker bees (Gempe *et al*. 2016; Morfin *et al*. 2023). Furthermore, worker bees from hygienic colonies have been demonstrated to express higher levels of odorant-binding proteins (OBP3, 16, and 18) on their antennae than those from control colonies. These proteins have an affinity for β-ocimene and oleic acid, which are abundant in 5th instar larvae and prepupae. When mature brood and prepupae were killed by liquid nitrogen, the exudation of β-ocimene and oleic acid induced worker bees to remove the dead brood and prepupae. These studies also found that deformed win virus (DWV, type A and B) titers were higher in control colonies than in hygienic colonies (Mondet *et al*. 2015; McAfee *et al*. 2018). Additionally, Guarna *et al*. (2015) demonstrated differential expression of *BM-40-SPARC* (secreted protein acidic and rich in cysteine Ca binding), Calcyclin-binding protein, and VAMP (vesicle-associated membrane protein) in descendant colonies. The studies indicated that social immunity behaviors are heritable and that biomarkers could potentially be used as indicators for breeding healthy bee colonies.

BREEDING MEASUREMENTS

In a breeding program aimed at enhancing social immunity in colonies, it is essential to monitor social immunity traits, such as grooming and hygienic behaviors, within a genetic resource colony pool. Additionally, monitoring *Varroa* mite infestation rates and virus titers is crucial for selecting parental colonies. *Varroa* mites can transmit the viruses through feeding on bee bodies, with these viruses being detectable in various bee tissues, including mucous glands, seminal vesicles, ovaries, fat bodies, and the midgut. During flight mating, viruses can be transmitted from semen to queens and subsequently to the eggs, leading to latent infections in the progeny colony (Fievet *et al*. 2006; Francis *et al*. 2013; Damayo *et al*. 2023).

Sex determination of honey bees follows the principle where females are diploid and males are haploid, depending on whether the eggs are fertilized (Heimpel & de Boer 2008). Inbreeding often results in the production of diploid males due to homozygosity of complementary sex determination (CSD) genes (Heimpel & de Boer 2008). However, these diploid males do not develop properly and are removed by worker bees, negatively impacting colony development (Ihle *et al*. 2025). Page & Marks (1982) developed a regression model to predict the emergence rate of diploid drone bees, suggesting that with 25 colonies as a genetic resource pool, the survival rate of the bee brood would drop to 85% after 40 generations. Maintaining genetic diversity in a bee breeding program is crucial to prevent the production of diploid drones caused by inbreeding, which decreases the colony productivity and health. This strategy supports breeding colonies with diverse strains, aiding adaptation to changing environmental conditions and disease pressures (Le Conte & Navajas 2008). Furthermore, maintaining diverse populations of lines in a genetic resource pool can provide valuable traits for breeding programs.

Honey bee queens are polyandrous and mate with several drones during one or more mating flights in drone congregation areas (DCAs) (Baudry *et al*. 1998). DCAs consist of sexually mature drones from various colonies, promoting genetic diversity among worker bees in the progeny colony (Baudry *et al*. 1998). This reproductive behavior of the queen causes colony characteristics to vary across generations and creates challenges in tracking paternal lineages.

In a breeding program against *Varroa* mites, it is recommended to rear drones from socially immune colonies for both natural mating and semen collection for artificial insemination (Seltzer *et al*. 2023). Harbo (1976) conducted a study on artificial insemination in

Western honey bees. Artificial insemination of honey bees requires a diluent to dilute the semen, protect the spermatozoa, maintain osmotic pressure, prevent microbial contamination, supply energy to the spermatozoa, and serve as an insemination medium. Ruttner & Drescher (1976) proposed the Kiev solution, followed by the development of a Tris buffer (Rhodes 2008) and a TES buffer (Hopkins *et al*. 2012). These formulations provide proteins to nourish the spermatozoa and reduce oxidative damage (Hopkins & Herr 2010; Rajamohan *et al*. 2020). Cobey (2007) reviewed studies comparing queens inseminated artificially with those mated naturally and found no significant differences in lifespan, fertility, and other key parameters. Factors such as the genetic background of the colony, nutrition, apiary environment, and virgin queen rearing method may influence egg-laying, colony productivity, and the overall colony strength (Cobey 2007; Hasnat 2018; Lee *et al*. 2019; Dolasevic *et al*. 2020).

We referred to the artificial insemination method of honey bees proposed by Cobey *et al*. (2013) (Fig. 2) and observed that the quantity of spermatozoa affects the efficiency of queens in producing fertilized eggs. Providing (4.5 ± 1.2) × 10^6 spermatozoa resulted in approximately (59.6 ± 10.2%) fertilized eggs, while providing (2.4 ± 0.3) × 10^7 spermatozoa resulted in more than (95.2 ± 1.8%) fertilized eggs (Chen 2023). There was no significant difference in the efficiency of producing fertilized eggs between naturally mated queens and artificially inseminated queens with more than a million of spermatozoa. It is suggested that artificial insemination of honey bees using selected drones may facilitate the purification of honey bee strains, breeding, and genetic research. Harbo (1977) attempted to cryopreserve semen in liquid nitrogen for 48 h, resulting in the inseminated queens laying more drones than workers. Gül *et al*. (2017) cryopreserved honey bee spermatozoa for 2 wk, thawed the sperm using a suspension in glucose solution, ram semen plasma, and bee semen plasma, achieving a fertilized egg rate of 40–47% in inseminated queens. Hopkins *et al*. (2012) studied the rate of fertilized eggs in queens artificially inseminated with cryopreserved spermatozoa, which ranged from 17.9–100%, with an average of 49.5%, and found that the queens' lifespans were about 2 mo. Wegener *et al*. (2014) preserved spermatozoa in liquid nitrogen for 9 mo, and the percentage of fertilized eggs produced by queens in the insemination treatment was 59.4%. Overall, although cryopreserved spermatozoa have lower insemination efficacy compared to fresh sperm, they offer the potential to preserve honey bee genetic resources and provide opportunities for the transportation and exchange of germplasm.

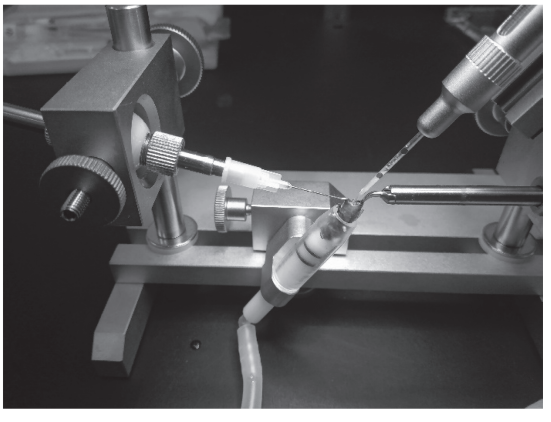

Fig. 2. Instrument used for artificial insemination of a queen bee.

CONCLUSION

In summary, breeding *Varroa* mite-resistant bee strains involves steps as follows: (1) collecting honey bee stocks, (2) assessing the diversity of CSD genes in the stock colonies, (3) evaluating the health status of the stock colonies, (4) assessing the social immune behavioral competencies of the stock colonies, (5) evaluating the expression of social immune behavioral genes, (6) comprehensively assessing the expression of social immune behavioral competencies and genes to select parental

colonies, and (7) evaluating the performance of social immune behavioral traits in offspring colonies. In Taiwan, honey production is an important source of profit for beekeepers. To breed *Varroa* mite-resistant strains of honey bees, we established a honey bee stock consisting of 16 local strains. We surveyed both honey production and hygienic behavior from the bee stock and reared virgin queens from colonies with high honey production and drones from colonies with high hygienic behavior, and then allowed the virgin queens and drones to mate naturally. This procedure was repeated over a period of four years, with one generation reared per year (Fig. 3), resulting in the preliminary establishment of a potentially hygienic bee line (T). The expression level of OBP16 in the T line was significantly higher than that in the control colonies (CK) (Fig. 4B). Although the dead pupa removal rate in the T line was 69.9 ± 10.9%, compared to 43.9–52.3% in the CK (Fig. 4A), the difference was not statistically significant. The resistance traits of honey bees against *Varroa* mites are polygenic and require long-term repeated breeding (Kaskinova *et al*. 2020). It is recommended to conduct comparisons of honey production, *Varroa* mite infestation rates and hygienic behavior to breed *Varroa*-resistant strains of honey bees, contributing to the development of IPM strategies and promoting bee health and sustainable beekeeping.

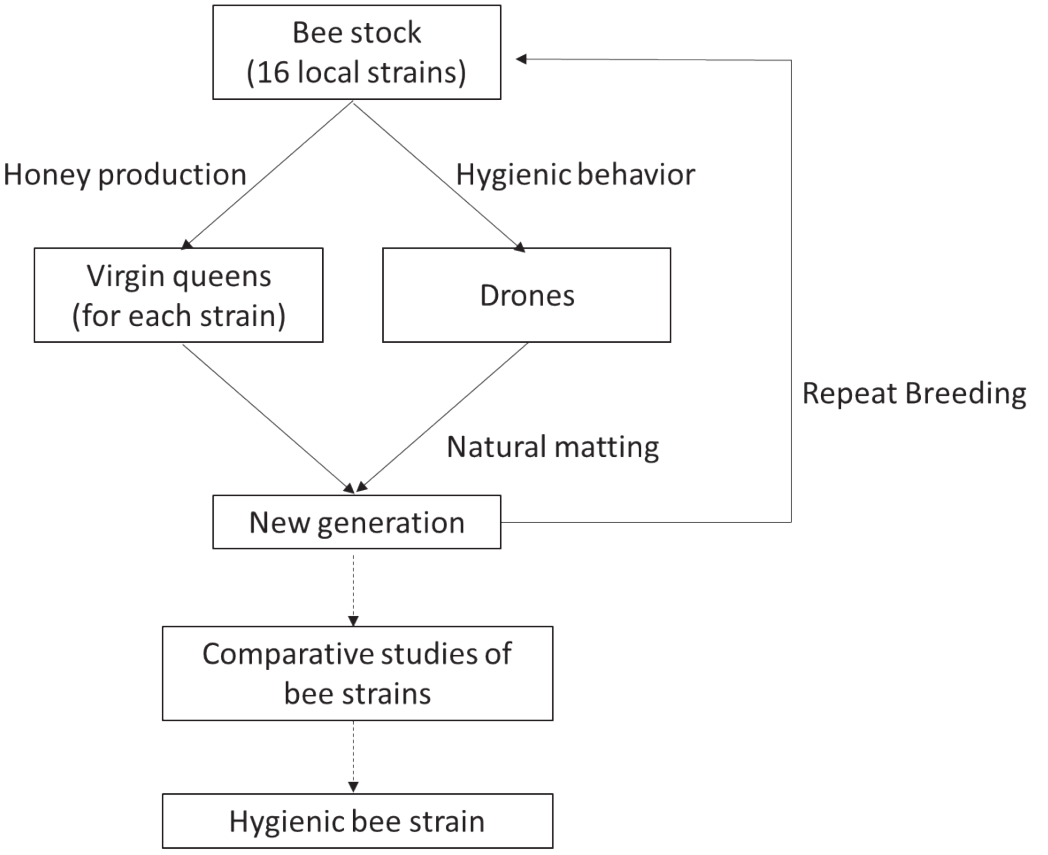

Fig. 3. The process of breeding hygienic strains of Western honey bees.

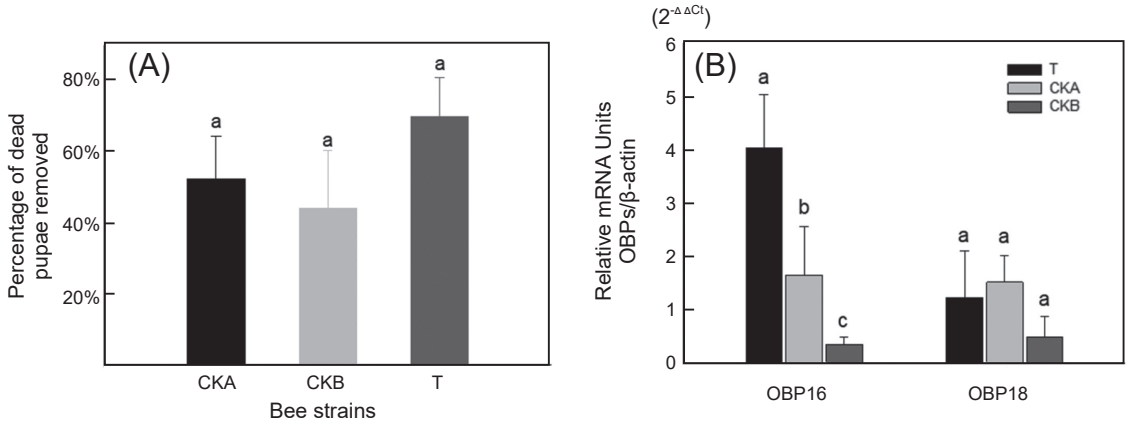

Fig. 4. Preliminary comparative studies of bee strains. (A) Percentage of dead pupae removed: the bee pupae were freeze-killed with liquid nitrogen, and the percentage of dead pupae removed was measured after 24 h. Bar graphs represent the mean (n = 3) ± *SD* (standard deviation). (B) Relative expression of odorant-binding proteins (OBPs): Different letters on the graph indicate significant differences (Fisher's protected LSD test, $P < 0.05$). CKA and CKB are control colonies provided by different beekeepers, whereas T represents the hygienic breeding strain.

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西方蜜蜂提高抗蜂蟹�螨能力之育種方法

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摘要

陳本翰、黃子豪、徐培修、潘其彥、吳姿嫻。2025。西方蜜蜂提高抗蜂蟹蟎能力之育種方法。台灣農業研究 74(3):237–248。

西方蜜蜂 (*Apis mellifera*) 是重要的授粉昆蟲，對蜂產業生產蜂產品亦具重大貢獻，蜜蜂的健康對糧食安全與農業盈利至關重要。蜜蜂的健康受到蜂蟹蟎 (*Varroa destructor*) 嚴重的威脅，蜂蟹蟎是一種體外寄生蟎，會傳播蜜蜂的疾病與影響蜜蜂的發育，最終影響農業經營收益。為了控制蜂蟹蟎，蜂農傳統上會在蜂巢中使用殺蟎劑，然而，長期使用殺蟎劑會增加蜂蟹蟎抗藥性與蜂產品藥物殘留的風險。除了化學防治，蜜蜂的社會性免疫行為也能提升對蜂蟹蟎的防治效果，這些行為包括工蜂移除死亡的蜜蜂或蜂蟹蟎，減少病原與害蟎在蜂巢內的孳生，而這些社會性免疫行為具有遺傳性。本篇小型綜述聚焦再討論提升蜜蜂抗蜂蟹蟎能力的育種方法，主要包括：(1) 評估種原蜂群的健康狀況；(2) 綜合性評估蜂群的社會性免疫行為能力與基因表現，以篩選親本；(3) 評估子代蜂群社會性免疫行為表現性狀，預期此育種方法將有助於發展更完善的綜合病蟲害管理 (Integrated Pest Management; IPM) 策略。

關鍵詞：西方蜜蜂、蜂蟹蟎、社會性免疫行為、綜合病蟲害管理。

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