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JOURNAL OF INSECTS AS FOOD AND FEED 11 (2025) 1357–1384

Journal of Insects as Food and Feed
brill.com/jiff

REVIEW ARTICLE

Genetic improvement of farmed insect species: programmes, progress, and prospects

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Received 5 September 2024 | Accepted 9 December 2024 | Published online 9 January 2025 |
Published in issue 30 May 2025

Abstract

Like other animal farming systems that aim for maximum productivity and economic sustainability, the cultivation of insects for food and feed sectors requires the use of high-performance genetic lines that are adapted to specific rearing conditions. Therefore, investing in genetics and breeding programmes to domesticate and develop insect strains suitable for commercial production is imperative: if implemented appropriately, breeding programmes can achieve significant returns on investment. Developing genetic improvement programmes for insects entails considering various factors, including biology, reproduction, production system, and identifying breeding goals optimal for available resources. This review summarises the various techniques available for implementing selective breeding programmes in insects, as well as their current applications and developments in four insect species: the honey bee, silkworm, black soldier fly and mealworm.

Keywords

black soldier fly – honey bee – mealworm – selective breeding – silkworm

1 Introduction

Insects are the most diverse and numerous animal group on earth and represent an under-exploited yet sustainable nutrient source with minimal environmental impact for incorporation in animal feed, or as a human food commodity (Gahukar, 2016; Makkar *et al.*, 2014; Van Huis, 2013). Currently, over two billion people worldwide are either directly or indirectly incorporating insects into their diets: directly by consuming insects, or insect products, and indirectly by consuming animal products that have been raised on feed containing insect meal (Imathiu, 2020). This trend is notable, with over 2,000 insect species recorded as now being utilised for these purposes (Ramos-Elorduy, 2009; Van Huis, 2013). Projections indicate that the insect farming industry, catering to human food and animal feed, is poised to reach a market potential of US $8 billion by 2030, boasting a compound annual growth rate of 24% (Verner *et al.*, 2021).

The cultivation of insects within systems of food production holds economic promise. For many insects, cultivation also aligns with the principles of the circular economy by transforming waste materials into

Published with license by Koninklijke Brill BV | DOI: 10.1163/23524588-00001387
| ISSN: 2352-4588 (online)

valuable protein sources (Dagevos and Taufik, 2023). This contribution to sustainable food production is crucial in enhancing global food security. Among the notable recorded edible insects are cicadas, moths, beetles, mealworms, grasshoppers, ants, and flies (Dickie *et al.*, 2019). Recognising the potential of insect-based proteins, the European Union has approved the use of processed animal proteins derived from insects in animal diets (EU Reg. 2017/893) (EU, 2017). This regulatory framework specifically lists seven approved species, including the black soldier fly (BSF) (*Hermetia illucens*), house fly (*Musca domestica*), mealworm (*Tenebrio molitor*), beetle (*Alphitobius diaperinus*), house cricket (*Acheta domesticus*), tropical house cricket (*Gryllodes sigillatus*), and Jamaican field cricket (*Gryllus assimilis*) (Madau *et al.*, 2020). In the USA, the regulatory body Association of American Feed Control Officials approved the use of dried BSF larvae (BSFL) in diets for canines and for aquaculture feeds. Likewise, in Canada, authorities have approved the use of BSFL in chicken and aquaculture feed. In Australia, feeds containing insect meal are also approved for use in aquaculture (Lähteenmäki-Uutela *et al.*, 2018; Larouche *et al.*, 2023). Apart from these feed-related species, honey bees and silkworms are well-known in the public sector and are the pioneer species in insect industrialisation (Chen *et al.*, 2022).

Genetic improvement through selective breeding in insects has historically received limited attention, with notable exceptions such as the honey bee and silkworm, both subject to domestication and genetic improvement through selection and hybridisation (Eriksson and Picard, 2021; Hoy, 1976). In contrast, numerous genetic improvement programmes exist for plants, livestock, and aquaculture species. Demonstrating their effectiveness, these programmes have contributed to increased farmer profit by maximising genetic gain and preserving the potential for future improvements (Camara and Symonds, 2014; Guinan *et al.*, 2023). Selective breeding improves desired commercial traits, such as growth rate, disease resistance, reproductive efficiency, and nutrient content, through the selection of advantageous allelic combinations in an organism (Janssen *et al.*, 2017). If done effectively, selective breeding increases overall productivity and reduces the cost per unit production at the same time (Gjedrem and Baranski, 2010). Thus, although rarely applied to date, selective breeding presents a viable avenue for optimising insects as an alternative protein source (Eriksson and Picard, 2021). This approach aligns with the goals of the circular economy and supports the achievement of the United Nations Sustainable Development Goals (SDGs). However, implementing selective breeding programmes for insects poses unique challenges compared to traditional programmes for plants, livestock, and aquaculture species.

Traditional genetic selection methodologies necessitate individual and family identification for estimating breeding values, which is crucial for selecting parents for the next generation (Gjedrem and Baranski, 2010). Usually, an animal's pedigree is obtained either through tagging with a physical tag or through DNA genotyping. However, applying these methods to insects proves challenging due to the difficulty of individually tagging and identifying family structures and obtaining the outputs of DNA genotyping quickly enough to make selection decisions due to short generation times. Additionally, breeding and domesticating insects in a controlled environment present further obstacles that require careful consideration and innovative solutions (Lecocq and Toomey, 2021). Addressing these challenges is essential for the successful implementation of selective breeding programmes for insect genetic improvement.

The burgeoning sector of insects for food and feed is driving researchers and industry to venture into new domains, such as insect breeding, aiming to enhance economically significant insect production and fitness traits (Adamaki-Sotiraki *et al.*, 2023). With ongoing advancements in insect production techniques and computational and genomic tools, insect farming industries are experiencing notable improvements (Eriksson and Picard, 2021). However, further research and development efforts are imperative to advance the industry. This review aims to consolidate previous research and development on insect genetic improvement programmes and elucidate future prospects for enhancement through the evolution of selection tools and methods.

2 Domestication and genetic improvement in insects

Domestication

The domestication of insects is defined as the process in which the insect populations are propagated in human-controlled environments, accompanied by a combination of genetic changes across successive generations and environmental events affecting these generations (Gjedrem and AKVAFORSK, 2005; Lecocq and Toomey, 2021). The history of insect domestication dates back approximately 10,000 years (Xia *et al.*, 2009). In China, the silkworm was first domesticated for silk production, while in pharaonic Egypt, the honey bee was domesticated for honey production, with additional benefits from pollination to increase crop production (Weber, 2013; Xiang *et al.*, 2018). Over the millennia of rearing these insects in captivity, they have adapted to environmental conditions, resulting in changes in their behaviour and a tendency to become docile. This transformation has played a pivotal role in the large-scale production of silk and honey for human use (Zhou *et al.*, 2020). The selection of desirable traits emerges as a key factor in the domestication process. Through natural selection, insects that are best adapted to a particular environment tend to propagate more progeny that can survive compared to those less adapted. Farmers consistently select animals with high growth rates and desirable behaviour, leading to directional selection. Domesticated lines of silkworms and honey bees thrive better in farming conditions compared to their wild counterparts (Mason and Mason, 1984; Xiang *et al.*, 2013; Zhou *et al.*, 2020). This highlights the substantial impact of human intervention on the evolution and behaviour of these insects, resulting in their enhanced suitability for agricultural practices.

Selective breeding

Selective breeding, also known as artificial selection, involves mating of individuals with desirable phenotypic traits to produce progeny with those traits (Song *et al.*, 2023). Over time, this process leads to the accumulation of favourable alleles in a population, leading to the development of populations with increased frequencies of the desired phenotype (e.g. typically those associated with production, such as yield, disease resistance, and stress tolerance) (Varshney *et al.*, 2021). However, a structured selective breeding program requires control over the reproduction, rearing, and welfare of individuals, and the core of a successful program lies in the strategic management of breeding stocks (Brito *et al.*, 2020). This involves routine phenotyping of targeted traits, pedigree recording, record-keeping of all activities, and the careful selection of individuals for the propagation of the next generation based on their estimated genetic merit.

In selective breeding, the enhancement of a population's performance over successive generations, resulting from a single generation of selection, is not a consistent process; it may take several generations for the genes of the selected individuals to become established throughout the population (Hill, 1974; Varshney *et al.*, 2021). During this process, factors such as differential family contribution, survival, selection intensity and mate choice play significant roles in genetic gain. It is important to note that the extent of differential family contribution may result in varied genetic diversity contributions to the next generation. Therefore, the successful propagation of improved individuals is essential to achieve genetic gain as it is a cumulative process (Domingos *et al.*, 2014).

In insect farming, the genetic management of commercial colonies is of paramount importance. This is particularly true because the majority of insects are *r*-selected species, characterised by high fecundity and specific mating behaviours (e.g. Lekking in BSF) that can lead to inbreeding-related consequences (Hoffmann *et al.*, 2021). Therefore, selective breeding serves not only to drive improvements in production but also to maintain adequate levels of genetic diversity. For example, genetic stock identification in closely bred Russian honey bees across three generations indicated that genetic diversity levels were comparable to the initial stock, and allelic richness and gene diversity were consistent over time (Bilodeau, 2022).

Genetic parameters

Understanding the sources of variation and covariation for production traits is essential for designing breeding programmes and predicting selection responses (Hansen *et al.*, 2024). To establish a genetic selection program for any species, it is necessary to grasp the magnitude of genetic parameters, such as the heritabilities of production traits and genetic correlations among them (Falconer and Mackay, 2009; Hansen *et al.*, 2024). These parameters quantify the relative magnitude of additive genetic variation and covariation and allow for the estimation of the breeding values for selected candidates within the population and the prediction of the potential response to selection (Gjedrem and Rye, 2018; Singh and Singh, 2018).

Genetic correlation is the proportion of resemblance between two traits that individuals share due to additive genetic variance (Falconer and Mackay, 2009; Lynch and Walsh, 1998; van Rheenen *et al.*, 2019). When selection pressure is applied to target traits, genetic correlation determines the correlated response, which explains how targeted and non-targeted traits change in multiple and single-trait selection (Falconer and Mackay, 2009). Overall, the knowledge on these parameters is crucial for making the breeding decisions, fine-tuning the selection strategy, and defining breeding goals.

Heritability values for body size in insects such as BSF, mealworm, drosophila, and silkworm range from moderate (0.2-0.5) to high (>0.5) (Akhund-Zade *et al.*, 2021; Bouwman *et al.*, 2022; Sellem *et al.*, 2024; Zambrano-Gonzalez *et al.*, 2022). These values indicate a substantial genetic component, making it feasible to select and breed for larger or smaller body sizes based on breeding objectives. Development time is moderate to high heritability, ranging from 0.3 to 0.6 (Bouwman *et al.*, 2022; Sellem *et al.*, 2024; Zambrano-Gonzalez *et al.*, 2022). This is critical for species like honey bee, where rapid development can impact colony productivity and resilience. Fecundity (egg production) can vary widely but is often moderately to highly heritable, ranging from 0.2 to 0.6 (Sellem *et al.*, 2024). For BSF and mealworms, higher fecundity is desirable for mass production in waste management and animal feed industries. Mating success and related behaviours are typically less heritable, often around 0.2 to 0.4, due to significant environmental influences (Bretman *et al.*, 2014). For instance, in fruit flies, understanding these values aids in studies of sexual selection and evolutionary biology. Disease resistance traits are low to moderately heritable, ranging from 0.02 to 0.44 (Guichard *et al.*, 2020b; Maucourt *et al.*, 2020). In the context of silkworm and honey bee breeding, selecting for disease-resistant strains can significantly reduce losses caused by Varroa mites in honey bees and Bombyx mori nucleopolyhedrovirus (BmNPV) infections in silkworms. The species-specific genetic parameter estimates for insect production traits are listed in the subsequent sections.

Genotype-environment interactions

The success of a genetic improvement programme depends on several biological factors. One of these factors is genotype-by-environment (G × E) interactions (Falconer and Mackay, 2009; Jerry *et al.*, 2022; Lynch and Walsh, 1998). In conventional selective breeding programmes, it is often assumed that G × E interactions are non-existent. However, it is important to recognise that these interactions carry a wide range of implications for phenotypic plasticity, profoundly influencing the selection objectives within breeding programmes (Saltz *et al.*, 2018). The presence of such interactions between genotype and environment can have detrimental implications for the performance of a breeding program, particularly when the selection process is executed in an environment that deviates from the primary production setting (Murani *et al.*, 2023). The evidence of genotype and interaction effect means "the best genotype in one environment is not the best genotype in another environment" (Falconer and Mackay, 2009). For example, the study conducted by Sandrock *et al.* (2022) revealed interactions between the diets and genetic strains of BSF. When four genetically distinct strains (F_{ST}: 0.11-0.35) were raised on three different diets (poultry feed, food waste, and poultry manure), the larval performance traits were significantly affected by the diet, but also by considerable genetic differentiation. Additionally, it was found that there is a trade-off between production traits, as there was no single superior strain among the four. Notably, two strains exhibited significantly higher mortality levels when fed nutrient-rich poultry feed and food waste, despite showing higher growth rates. Conversely, a reduction in growth rate was observed in association with increased survival on the low-nutrient poultry manure diet across different genetic strains.

Notably, attributes related to production and their genetic basis are subject to the influence of various environmental factors, including but not limited to the production system, dietary composition, and nutritional constituents (Murani *et al.*, 2023). Within the realm of animal breeding, it is well-established that disparate genotypes exhibit differential responses to distinct environmental variables (Jerry *et al.*, 2022; Le Boucher *et al.*, 2011; Mayne and Gordon, 1995; Pryce *et al.*, 1999). In the context of BSF, Mealworms and other insect production systems, insect larvae's growth rate and final composition hold critical economic significance. It is worth noting that the final composition of insect larvae primarily depends on the nutritional factors in their diet (Chia *et al.*, 2020; Danieli *et al.*, 2019; Sandrock *et al.*, 2022). They can be raised on different substrates, i.e. fruit and vegetable waste, soy processing waste, etc. Therefore, considering interactions between genotype and diet within the insect production paradigm is essential. This endeavour is indispensable for the development of a nutritionally balanced diet conducive to optimising insect production outcomes.

Selective breeding strategies

The techniques employed in selective breeding programmes in aquaculture are broadly classified into three categories, which can be combined in various ways if sufficient resources are available, rendering them non-mutually exclusive (Camara and Symonds, 2014). The most basic and common strategy is the selection of individuals (mass selection) or families (family selection). In this method, individuals or families are identified based on their genetic merit and bred to produce the next generation (Allier *et al.*, 2019). The goal is to achieve predicted and cumulative improvement over several generations, thereby accumulating desired alleles in the population. This approach primarily operates on the principle of selecting for additive genetic effects resulting from alleles' cumulative influence at different loci (Houston *et al.*, 2020). The second category is crossbreeding, which involves the crossing of two different breeds or populations to produce offspring with favourable traits from both parental lines. This method aims to exploit non-additive genetic effects, such as dominance effects or hybrid vigour, thereby facilitating improvement (Bartley *et al.*, 2000; Liu *et al.*, 2020). The third category involves incorporating statistical models and molecular genetics techniques and tools to identify genes or markers controlling or influencing traits of interest and quantify their effects, such as marker-assisted selection and genomic selection (Houston *et al.*, 2020). This information is then utilised to select parents for achieving improvement in the production traits. Moreover, these techniques can be equally applied in insect breeding programmes, as insects exhibit high fecundity, short generation intervals, and similar breeding goals to those found in aquaculture species.

Within category one insect breeding programmes, mass selection stands as a common strategy employed to improve stocks for better productivity. It is the simplest and most cost-effective approach to implement and potentially yields rapid genetic gains to selection (Facchini *et al.*, 2022). In mass selection, information is directly obtained or measured on the selection candidates without consideration of their pedigree. However, it possesses drawbacks. It can only be applied efficiently when the trait of interest can be measured non-lethally and exhibits high heritability (Fan *et al.*, 2022). Furthermore, it is difficult to separate the environmental and genetic influences on the trait of interest, and it cannot estimate G × E interactions. Given the high fecundity in insect species, mass selection can lead to inbreeding and its associated inbreeding depression phenotypic consequences (Hoffmann *et al.*, 2021). To reduce the risk of inbreeding, it is necessary to maintain an effective population size of 100 (50 mating pairs) in the breeding nucleus and obtain 30-50 progenies per mating pair (Bentsen and Olesen, 2002). Molecular techniques, such as genotyping, offer a means to avoid the crossing of related individuals by identifying their relationships through parentage analysis. However, applying these techniques in insect breeding presents challenges due to difficulties in obtaining sufficient DNA for genotyping without killing individuals. Additionally, timely decision-making is hindered by the short generation time of insects, with the exception of honey bee (Bubnič *et al.*, 2020).

In the family selection method applied in aquaculture, data is collected on groups of siblings along with their pedigrees to make selection decisions. Based on their genetic merit and relatedness, they are chosen as broodstock for production of the subsequent generation (Allier *et al.*, 2019). This method facilitates the assessment of traits from culled animals (i.e. carcass quality), allowing their relatives to be considered as potential selection candidates. Moreover, it aids in accounting for G × E interactions by rearing families in different environments. By combining both between and within family selection approaches, genetic gain can be maximised while simultaneously maintaining the genetic diversity within the breeding population (Gjedrem and Baranski, 2010). Adopting this method in insect breeding may reduce the efficiency of selection when common environmental effects affect the full sibling groups, leading to bias in the estimation of variance components, as evidenced in the case of BSF (Bouwman *et al.*, 2022) and House fly (Hansen *et al.*, 2024). To mitigate this, the environment can be standardised, or families can be distributed across multiple separate environments (Gjedrem and Baranski, 2010). The traditional selection strategies followed in livestock and aquaculture, which are most often family-based, pedigree-based and involve progeny testing, require routine phenotyping and the physical maintenance of pedigrees. However, these approaches are not practically feasible in the context of insect breeding due to the complexities associated with their biology, morphology, reproduction, and lifecycle, as well as the discrete generations that make progeny testing impossible. For example, insects shed their exoskeleton during their development, so breeders cannot rely on physical tagging to retain the pedigree record and implement selection. Identification of different life stages also poses a challenge. For example, identification of the instar stages is difficult in BSF and mealworms since they lack distinctive morphological features. Moreover, when it comes to reproduction, species often exhibit complex social structures (e.g. honey bees) or mating behaviours (e.g. lekking behaviour in BSF).

In recent decades, advancements in DNA sequencing/genotyping and statistical computation have made genomic selection (a method that utilises the markers across the genome to predict the genetic merit of individuals for specific traits) a reality (Goddard and Hayes, 2007). It has proven effective in selecting complex production traits across various domains, including livestock (Guinan *et al.*, 2023; Hayes *et al.*, 2009), aquaculture (Houston *et al.*, 2020; Yanez *et al.*, 2023), and plant breeding (Crossa *et al.*, 2017). Advanced prediction

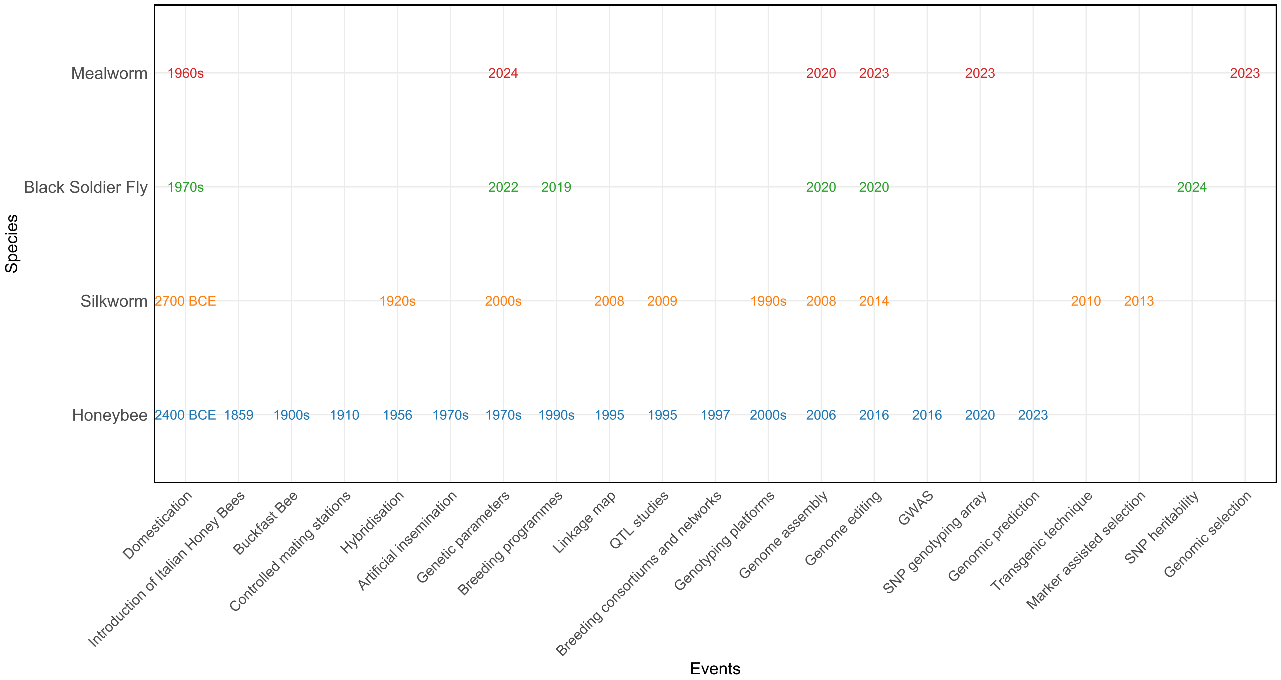

FIGURE 1 Evolution of key genetic and breeding events across insect species.

models are employed to predict phenotypes and breeding values based on genomic data in genetic improvement programmes. These prediction models may facilitate the process of introducing new external germplasm to the breeding nucleus in the event of reduced genetic diversity or inbreeding by assessing the genetic merit of external germplasm. Alternatively, these models can be used to predict the genetic merit of the breeding candidates within the production cycle. However, practically implementing these models in insect species with short life cycles and metamorphosis poses challenges. It is difficult to genotype individuals and return genotypes for analyses in a short time, and metamorphosis presents a unique challenge in identifying individuals. Nonetheless, accuracies of genomic prediction models have been proven in the context of livestock, honey bee, and aquaculture breeding programmes (Bernstein *et al.*, 2023; Kriaridou *et al.*, 2023; Lund *et al.*, 2016; Zenger *et al.*, 2019). However, a comprehensive evaluation of their effectiveness is required for their implementation in insect production. The models must be designed to improve genetic merit prediction accuracy, whether for on-farm use or for external replacement broodstock. This is necessary to enhance specific production traits and tailor breeding programmes to particular locations or regions. Additionally, a cost-benefit analysis should be conducted to determine which traits offer the most significant biological benefit based on increased accuracy in selection. This advancement will also enable the selection of the most appropriate breeding strategy based on a thorough understanding of biology for breeding.

By considering the present research and development activities in insect breeding, economic importance, and reproductive and biological intricacies, four species have been chosen, namely the honey bee, silkworm, black soldier fly and mealworm to comprehensively review the up-to-date progress in their genetic improvement programmes. This review is supported by a timeline of genetic and breeding events in these species, illustrated in Figure 1.

3 Honey bee

History

The Honey bee holds significant importance among insects due to its multifaceted utility for humans; the European honey bee, *Apis mellifera* L., is the world's most widely cultured bee (Papa *et al.*, 2022). Beekeeping or apiculture refers to the practice of rearing honey bees. These bees play a pivotal role in agriculture by facilitating pollination and producing honey. According to experts at the Food and Agriculture Organisation (FAO), approximately one-third of the world's food production relies on honey bee pollination. In 2018-19, global honey production reached 1.72 MMT (Puranik *et al.*, 2023).

Ancient Egyptians were pioneers in beekeeping, using rudimentary hives made from mud and straw to house their colonies (Weber, 2013). Over time, beekeepers began to understand and utilise traits such as docility, honey production, and disease resistance, selectively breeding colonies that exhibited these traits for propagation (Guichard *et al.*, 2020a). In China, historical evidence suggests that beekeeping has been practised since the Han Dynasty (206 BCE-220 CE) (Pattinson, 2019). In medieval Europe, monastic communities, where monks experimented with various beekeeping techniques, played a significant role (Postan, 1966). Brother Adam of Buckfast Abbey in England developed the Buckfast Bee. A hybrid known for its gentle temperament, high honey yield, and disease resistance, leading to a revolution in beekeeping in the early 20th century (Adam, 1987). During the late 19th and 20th centuries, researchers started applying the principles of quantitative genetics to bee breeding, developing selection criteria based on traits such as honey yield, overwintering survival, and resistance to pests and diseases. The introduction of artificial insemination in the mid-20th century further accelerated the breeding process, enabling beekeepers to control mating and selectively propagate desirable genetic traits (Bernstein *et al.*, 2023; Collins, 2004; Mackensen, 1964).

Alongside traditional breeding methods, molecular biology and genomics have played a prominent role in honey bee breeding in recent decades (Dogantzis and Zayed, 2019). Researchers have unravelled the genetic basis of traits such as hygienic behaviour (Patel, 2018), varroa mite resistance (Spotter *et al.*, 2016), and pollen collection efficiency, paving the way for marker-assisted selection and genomic selection programmes (Bernstein *et al.*, 2023; Sainsbury *et al.*, 2022). Nowadays, honey bee breeding is a collaborative endeavour, with researchers, beekeepers, and breeding associations working together to develop resilient and productive bee stocks (Uzunov *et al.*, 2017). Breeding programmes focus on enhancing traits that promote colony health and productivity while mitigating the impacts of environmental stressors such as habitat loss, pesticide exposure, and climate change.

Genetic improvement programmes for honey bee have been developed and implemented across the globe. However, the rate of genetic progress has not achieved the same level of success as compared to other animal production species. The main constraint in honey bee breeding lies in modelling them statistically to estimate the variance components during genetic analyses, owing to their complex genetic and reproductive characteristics (Andonov *et al.*, 2019; Bienefeld *et al.*, 2007). However, advancements in computation, informatics, and genomics have now made it possible to create statistical models consistent with the genetics of honey bees, thereby facilitating the efficient implementation of genetic selection in honey bee populations (Bernstein *et al.*, 2023).

Breeding objectives

The industry worldwide engaged in Apiculture primarily focuses on honey production. Therefore, the honey yield and behaviour of bees, such as defensiveness, calmness, and swarming, are crucial factors in production (Andonov *et al.*, 2019). The total honey yield per colony is of paramount importance due to its economic significance. This trait must be consistent, and the behaviour of bees is also important because aggressiveness can pose challenges to beekeepers during hive inspections and honey harvesting. Among behavioural traits, foraging determines their ability to collect nectar, while swarming, a natural reproductive process where a portion of the colony, including the queen, leaves to establish a new hive, can reduce honey yield if it occurs frequently. Additionally, the behaviour of the queen is important because it influences colony dynamics, which are closely associated with overall productivity. In recent times, traits related to resistance to parasites such as *Varroa destructor*, as well as fungal and bacterial diseases, have also gained interest among breeders (Boecking *et al.*, 2000; Büchler *et al.*, 2024; Guichard *et al.*, 2020a; Guichard *et al.*, 2021; Maucourt *et al.*, 2020). *V. destructor* is a parasitic mite that infests honey bee colonies, feeding on the bodily fluids of adult bees and their blood, leading to the complete destruction of colonies (Traynor *et al.*, 2020). The hygienic behaviour of the colony is also an important trait in mitigating infestation. Overall, both production and health-related traits are considered when designing breeding programmes for honey bees.

Honey bee breeding consortia and companies operate breeding programmes based on the selection of pedigreed queens and colonies with multiple desired traits. Additionally, for some farmers, there is an objective driven by agricultural crop production, focusing mainly on the pollination of agricultural crops by providing pollination services. Some beekeepers receive payment for providing this service by placing hives near farming sites, while others offer the service for free, ensuring bees have access to nectar (Khalifa *et al.*, 2021).

Breeding strategy

The breeding strategy in honey bees, particularly for managed colonies, involves various techniques. This includes selecting queens and drones based on their genetic merit for production traits, achieved by mating queens with drones from colonies exhibiting desired traits with known pedigrees (Hoppe *et al.*, 2020). In some cases, beekeepers opt for instrumental insemination, where they collect semen from drones with desirable traits and artificially inseminate selected queen bees (Collins, 2004). This technique offers precise control over mating and genetic diversity. Another approach is natural mating, where queens are allowed to mate freely with drones from surrounding colonies. While this method lacks precision, it helps maintain genetic diversity within the bee population.

Challenges and opportunities

Beekeepers are facing several challenges in maintaining their colonies for honey production. Honey bees are susceptible to various diseases and pest infection, with the major pest being *V. destructor* infestation, a parasitic mite that infests honey bee colonies, weakening bees and transmitting viruses; in the United States, a 43% colony loss between April 2019 and April 2020 was reported, largely due to varroa (Insolia *et al.*, 2022; Warner *et al.*, 2024). Various breeding programmes are already in place for selecting queens and drones for varroa resistance (Le Conte *et al.*, 2020). From a genetic standpoint, maintaining genetic diversity within populations is crucial for resilience against diseases and environmental stressors. Pedigree record-keeping and the development of genetic traceability tools (single nucleotide polymorphism (SNP) chips) to assess parentage can be used to maintain genetic diversity and reduce inbreeding.

In honey bee breeding programmes, estimating breeding value poses another challenge because the traits are generally observed at the colony level, and these measurements involve an interplay between workers and between workers and the queen (Bienefeld *et al.*, 2007); however, only the queen is selected for the reproduction of future generations. The overarching objective is to generate virgin queens from exceptional colonies, which are subsequently mated with drones also sourced from superior colonies. To accommodate the haplo-diploid reproductive system, it is recommended to utilise groups of sister queens (offspring of the superior colony) for drone production (Ruttner, 1988).

Progress to date

Various studies have been conducted to estimate the genetic parameters for production traits in *Apis mellifera* L. and other subspecies. The primary objective of honey bee breeding programmes is to enhance honey yield, improve workability, and boost disease resistance, traits that are typically observed at the colony level (Bernstein *et al.*, 2023) and for which routine data collection exists in many countries (Andonov *et al.*, 2019). The heritability estimates for these production traits, documented in the various studies, are summarised in Table 1. Heritability values for honey yield ranged from 0.02 to 0.70, while for the workability trait, swarming drive varied between 0.06 and 0.44. Varroa infection development (VID) exhibited significant variation, ranging from 0.02 to 0.44, reflecting differences in populations, estimation methods and sample sizes. In statistical modelling for variance component estimation, heritability was assessed using three distinct models: heritability associated with the worker effect of an individual (h^2_w), heritability linked to a group of workers ($h^2_{\overline{W}}$), and heritability attributed to the queen effect (h^2_Q). This complexity stems from the collaborative interactions between workers and the queen within a colony. Traits such as honey yield and behavioural attributes like aggressiveness and calmness are influenced by the genotypes of both workers and the queen (Bienefeld and Pirchner, 1990). This holds true for resistance to varroa mite infestation as well (Ehrhardt *et al.*, 2010). The studies have highlighted a strong negative correlation between the contributions of both queen and workers to economic traits, such as honey yield (Bienefeld and Pirchner, 1990).

In the current context, the most commonly used method for estimating breeding values in other animals, the Best Linear Unbiased Prediction (BLUP) – Animal model, has been adapted for genetic evaluation in honey bees (Bienefeld *et al.*, 2007). This methodology incorporates maternal effects (from the queen) by utilising all available records of relatives and adjusts for environmental effects, genetic merits of parents and tested colonies. It estimates breeding values for both queen and worker effects on colony traits for each queen. Estimating breeding values necessitates specific adjustments, and incorporating sires into the pedigree is only feasible when the mating of queens and drones is meticulously controlled. Mating control within breeding programmes can be achieved through the implementation of isolated mating stations, where colonies of known origin are exclusively present, usually within a radius of 3 to 10 km, or through instrumental insemination techniques.

The *Apis mellifera carnica* subspecies of honey bee is renowned for its gentle temperament and high honey yield. Systematic breeding initiatives commenced in

TABLE 1 Published heritability estimates for various production, workability and disease resistance traits in honey bees

Trait	Heritability			Reference
Honey production (kg)	0.20 (0.13)			Maucourt *et al.* (2020)
Hygienic behaviour (%)	0.18 (0.13)			
Varroa destructor infestation	0.44 (0.56)			
Spring development	0.30 (0.14)			
Winter weight loss (kg)	0.11 (0.09)			
Honey production	0.27 (0.32)			Zakour *et al.* (2012)
Gentleness	0.08 (0.28)			
Honey production	0.16 (0.02)			Padilha *et al.* (2013)
Syrup collection rate	0.23 (0.03)			
Propolis production	0.66 (0.24)			
Hygienic behaviour	0.52 (0.12)			
Mites on adult bees (%)	0.13 (0.01)			
Honey production	0.22 (0.018)			Tahmasbi *et al.* (2015)
Defence behaviour	0.44 (0.027)			
Swarming behaviour	0.34 (0.028)			
Hygienic behaviour towards infested brood cells	0.18 (0.27)			Boecking *et al.* (2000)
Hygienic behaviour towards dead brood cells	0.36 (0.30)			
Honey yield	0.25 (0.04)			Andonov *et al.* (2019)
Defensive behaviour	0.43 (0.05)			
Swarming behaviour	0.42 (0.05)			
Hygienic behaviour	0.37 (0.25)			Facchini *et al.* (2019)
Honey (kg)	0.34 (0.20)			Kistler *et al.* (2024)
Varroa destructor load	0.14 (0.11)			
Hygienic behaviour	0.25 (0.19)			
	h^2_w	$h^2_{\overline{W}}$	h^2_Q	
Honey yield	0.06 (0.09)	0.02 (0.04)	0.10 (0.06)	Guichard *et al.* (2020b)
Defensive behaviour	0.85 (0.21)	0.34 (0.09)	0.32 (0.08)	
Calmness during inspection	0.39 (0.17)	0.16 (0.07)	0.12 (0.06)	
Swarming drive	0.16 (0.12)	0.06 (0.05)	0.07 (0.05)	
Varroa destructor infestation	0.04 (0.07)	0.02 (0.03)		
Hygienic behaviour	0.47 (0.19)	0.19 (0.07)	0.18 (0.08)	
Colony size growth rate	0.06 (0.09)	0.02 (0.04)	0.08 (0.08)	
Honey yield	0.13 (0.02)	0.14 (0.01)	0.17 (0.03)	Bernstein *et al.* (2023)
Gentleness	0.43 (0.05)	0.39 (0.03)	0.22 (0.04)	
Calmness	0.38 (0.04)	0.36 (0.03)	0.18 (0.04)	
Swarming drive	0.12 (0.02)	0.15 (0.02)	0.11 (0.03)	
Hygienic behaviour	0.18 (0.03)	0.21 (0.02)	0.10 (0.03)	
Varroa Infestation development	0.08 (0.02)	0.09 (0.01)	0.09 (0.03)	
Honey yield	0.70 (0.07)		0.36 (0.06)	Brascamp *et al.* (2016)
Gentleness	0.41 (0.07)		0.14 (0.06)	
Calmness	0.43 (0.07)		0.07 (0.05)	
Swarming behaviour	0.36 (0.07)		0.25 (0.05)	

TABLE 1 (Continued)

Trait	Heritability		Reference
Varroa population growth	0.32 (0.03)	0.17 (0.02)	Ehrhardt *et al.* (2010)
Hygienic behaviour	0.47 (0.02)	0.15 (0.03)	
Honey	0.40 (0.28)	0.24 (0.26)	Guichard *et al.* (2021)
Calmness	0.62 (0.28)	0.54 (0.31)	
Swarming	0.32 (0.34)	0.17 (0.25)	
Varroa spring	0.25 (0.20)	0.05 (0.18)	
Honey yield	0.42 (0.05)	0.23 (0.03)	Hoppe *et al.* (2020)
Gentleness	0.90 (0.07)	0.20 (0.03)	
Calmness	0.85 (0.06)	0.17 (0.02)	
Swarming	0.44 (0.06)	0.22 (0.03)	
Hygiene	0.50 (0.06)	0.12 (0.03)	
Varroa Infestation development	0.04 (0.02)	0.06 (0.02)	

[1] h_w^2 = heritability associated with the worker effect of an individual.

[2] $h_{\overline{W}}^2$ = heritability linked to a group of workers.

[3] h_Q^2 = heritability attributed to the queen effect.

the early 20th century, although progress remained sluggish until the advent of modern genetic evaluation techniques in the mid-1990s. Subsequent analysis of the official breeding value estimation data in BeeBreed.eu reveals a notable acceleration in breeding progress from around the year 2000 onwards. This acceleration has led to significant improvements in honey yield and desirable traits, all achieved without a corresponding increase in inbreeding coefficients. The success of breeding efforts focused on *A. m. carnica* underscores the potential efficacy of genetic evaluation methodologies (Hoppe *et al.*, 2020). The same study also revealed that significant breeding advancements within the registered *A. m. carnica* population, including an approximate increase of 5 kg in honey yield per colony, enhancement of manageability properties by around 0.3-mark points, a 9% improvement in clearance rate, and a reduction of approximately 0.2 mites per 10 g bee sample, have predominantly occurred post-2000, coinciding with the implementation of breeding value estimation methodologies.

The establishment of a central registry of breeders and queens in BeeBreed likely facilitated the exchange of breeding materials within the beekeeping community (Hoppe, 2020). Moreover, heightened public awareness regarding the importance of beekeeping has spurred both national and international funding initiatives for honey bee breeding, exemplified by programmes such as EurBeST of the European Union, which partially supports breeding endeavours (EurBeST). This increased funding has motivated beekeepers to engage in breeding activities, consequently expanding the breeding population. European initiatives like SmartBees have played a pivotal role in educating beekeepers to transition into breeders (Uzunov *et al.*, 2018).

Emerging breeding frameworks are becoming apparent within European honey bee populations. Despite the increasing understanding of genetic evaluations in honey bees, there remains a lack of comprehension regarding the impact of selection decisions on the genetic compositions of these populations (Plate *et al.*, 2019). Simulation studies have investigated the effectiveness of genomic breeding value estimation in honey bees, with single-step Genomic BLUP (ssGBLUP) emerging as a promising method (Bernstein *et al.*, 2021; Gupta *et al.*, 2013). Recent developments include the creation of a 100K high-density SNP chip, enabling the genotyping of phenotyped queens and facilitating the validation of genomic prediction methods (Jones *et al.*, 2020). With the advancement of these tools, a large-scale genomic prediction was conducted on data from BeeBreed, involving 36,503 phenotyped queens and 2,389 genotyped queens. This resulted in an improvement in prediction accuracy from the traditional pedigree BLUP approach to the genomic approach, with an increase from 0.12 to 0.23 for honey yield, while the accuracy for workability traits increased from a range of 0.42 to 0.61 to a range of 0.44 to 0.65. However, the inclusion of genomic marker data did not enhance the prediction accuracy of disease-related traits. This may be attributed to the size of the reference population and the relationship between the training and test candidates, which could be improved by either increasing the reference population size or identifying the causative SNPs associated with these traits (Bernstein *et al.*, 2023).

Future prospects

The future prospects for the apiculture industry are promising, with international organisations collaborating to enhance productivity while maintaining genetic diversity. The establishment of the BeeBreed consortium is a positive step towards further developing genomic resources and advanced statistical models for investigating genetic architecture and conducting genetic evaluations. This initiative will provide insights into the effectiveness of breeding programmes and pave the way for further improvements in honey bee population production, workability and disease resistance traits. Additionally, resilient breeding programmes should be designed to address challenges posed by climate change and emerging diseases.

4 Silkworm

History

The silkworm (*Bombyx mori* L.) is a domesticated, economically significant insect native to Northern Asia, predominantly bred in both seasonal and tropical regions (Goldsmith *et al.*, 2005; Yang *et al.*, 2014; Zambrano-Gonzalez *et al.*, 2022). Serving as the primary source of silk, often referred to as "the queen of natural fibres," *B. mori* contributes approximately 90% to global production (ISC, 2014). Sericulture, the practice of cultivating silkworms to produce silk, dating back over 5,000 years, originated in China, spreading to other regions such as India and Japan (Kurin and Borden, 2002). According to statistics from the International Sericultural Commission, silk production reached 91,221 metric tonnes in 2022. The major contributor to this is China, followed by India, with approximately 90% originating from Asian countries. The total value of the silk transaction was about US $1.91 billion in 2022 (OEC, 2024).

The species *B. mori* possesses over 3,000 improved genetic lines and around 400 heritable mutants (Buhroo *et al.*, 2018). This amounts to an estimated total of 4,310 distinct geographical races, lines, and mutants, which are dispersed across various gene banks worldwide (Goldsmith *et al.*, 2005). The process of selective breeding in silkworms began with the domestication of wild silkworms, likely the species *B. mandarina*, which naturally fed on the leaves of mulberry trees (Zhu *et al.*, 2019). Ancient Chinese farmers observed and eventually controlled the breeding of these silkworms to enhance silk production (Xiang *et al.*, 2018).

Selective breeding techniques were employed to cultivate silkworms with desirable traits such as larger cocoon weight/size (CW), cocoon shell weight (CSW), and cocoon shell percentage (CSP) (Zamani *et al.*, 2019). Over generations, these efforts led to the development of the domestic silkworm, *B. mori*, which became entirely dependent on humans for its survival (Zhu *et al.*, 2019). The domestication of silkworms revolutionised silk production and became a closely guarded secret in ancient China. The silk trade played a crucial role in the economy and cultural exchange along the Silk Road, connecting China with the rest of the world (McLaughlin, 2016). Intensive domestication has led to the absence of wild *B. mori* populations (Yukuhiro *et al.*, 2002), resulting in limited adaptability to adverse climatic conditions, particularly prevalent in tropical countries (Kumari *et al.*, 2011).

Breeding objectives

The main objective of silkworm breeding is to boost the profitability of silk producers (Hussain *et al.*, 2010; Mavvajpour and Seidavi, 2010; Talebi and Subramanya, 2009) and different sectors within the sericulture industry by enhancing economic traits such as CW, CSW, and CSP (Hosseini *et al.*, 2005). Various traits are pivotal in sericulture, and their importance varies among different sectors of the industry. Silkworm egg producers aim to acquire lines with high breeding potency, while cocoon producers focus on improving production, cocoon shell percentage, and resistance against diseases (Neshagaran Hemmatabadi *et al.*, 2016; Singh and Samson, 1998). Cocoon weight is closely associated with the quantity of silk that can be extracted from each cocoon. Increased cocoon weights generally lead to higher silk yield per unit of raw material, thereby enhancing overall productivity in silk production. Additionally, the quality of silk is influenced by factors such as cocoon size and silk density. Larger cocoons tend to yield silk with superior uniformity, strength, and texture, all of which are desirable attributes for various silk products, including textiles, garments, and industrial materials.

While assessing silk yield, it's crucial to consider the total weight of the cocoon, encompassing both shell and silk. The weight of the cocoon shell specifically impacts the amount of usable silk obtained. Higher cocoon shell weights often signify a greater volume of silk fibroin, contributing to a higher silk yield per cocoon. Likewise, cocoon shell percentage plays a vital role in determining the amount of usable silk derived from each cocoon. A higher cocoon shell percentage indicates a larger proportion of silk fibroin, thereby increasing silk yield per cocoon. In addition to focusing on production traits, breeding objectives should encompass aspects such as disease resistance, environmental adaptability, and enhanced feed efficiency to ensure sustainable production practices. These factors are essential for maintaining the health and productivity of silkworm populations while promoting long-term sustainability in the sericulture industry.

Breeding strategy

The domesticated silkworm, *B. mori* L., comprises a large number of geographical breeds and hybrid lines (Furdui *et al.*, 2014). There are over 3,000 silkworm strains that can be distinguished (Nagaraju *et al.*, 2001). Four major geographical breeds can be identified as Chinese, Japanese, European, and Tropical (Liu *et al.*, 2010). Silkworm breeders follow line breeding, where they cross different lines to obtain hybrid vigour in order to improve the lines for the trait or traits of interest. The pure lines developed are carefully and occasionally crossed with other lines to maintain genetic diversity.

Challenges and opportunities

The majority of silkworm varieties exhibit susceptibility to various pathogens, encompassing viruses, bacteria, and fungi, with viral infections posing the most significant challenge, contributing to approximately 80% of the annual cocoon production losses (Hu *et al.*, 2024). Notable viral pathogens encompass *B. mori* nucleopolyhedrovirus (BmNPV), *B. mori* densovirus (BmDNV), and *B. mori* cytoplasmic polyhedrosis virus (BmCPV) (Jiang, 2021; Lü *et al.*, 2018). Particularly, BmNPV emerges as a pervasive threat to sericulture globally, presenting challenges in effective containment measures (Jiang and Xia, 2014).

To tackle the challenge of disease resistance, in 2017, a *piggyBac* transgenic vector was designed to specifically disrupt early replication factors, *ie0* and *me*53, within the BmNPV genome. This strategic knockout strategy resulted in a significant suppression of BmNPV proliferation and replication (Chen *et al.*, 2017). Consequently, this pioneering accomplishment signified the initial success in producing transgenic silkworms resistant to BmNPV through the integration of gene editing and transposition techniques (Li *et al.*, 2023).

With the advancement of genomic resources and technology, efforts must be made to comprehend the genetic architecture of *B. mori* concerning disease resistance against the aforementioned diseases and production traits. This understanding will enable the implementation of suitable selection strategies, such as marker-assisted selection and genomic selection, to develop improved strains.

Progress to date

The genetic improvement of *B. mori* is intertwined with social and economic factors that influence the outcomes of breeding programmes tailored to each country (Ruiz and Almanza, 2018). As highlighted by (Jalali *et al.*, 2011), the primary factors contributing to success in *B. mori* breeding include (1) the implementation of robust breeding methodologies grounded in quantitative genetic principles, (2) the ongoing and consistent augmentation of heterosis for economically significant traits, and (3) the establishment of information processing systems to support breeding efforts.

The research on *B. mori* in the 20th century was primarily focused on investigating G × E interactions across different climatic seasons (Asadpour Ardehjani *et al.*, 2023) and geographical locations, with a particular emphasis on harnessing the potential of hybrid vigour to address the requirements of raw silk production for the textile industry (Asadpour Ardehjani *et al.*, 2023; Tzenov, 2003). This approach entailed examining various aspects, including the expression of heterosis in F1, positive transgressions in F2, combinatorial ability, genetic correlations and regressions, heritability of key qualitative and quantitative traits, utilisation of improved inbred lines, exploration of parthenogenesis and androgenesis, and enhancement of seasonal hybrids and lines (specifically, those for summer-autumn) (Asadpour Ardehjani *et al.*, 2023). These efforts aimed to achieve enhanced yields in egg production, larval rearing, cocoon quality and production, as well as raw silk production, while also facilitating adaptation to diverse environmental conditions, such as temperature, humidity, climatic seasons, and rearing density (Darmand *et al.*, 2011; Hosseini *et al.*, 2005; Lea, 1993; Mirhosseini *et al.*, 2005; Moghaddam *et al.*, 2000; Neshagaran Hemmatabadi *et al.*, 2016; Zambrano-Gonzalez *et al.*, 2022).

In the 21st century, genetic improvement in *B. mori* was focused on attaining high-yielding hybrids, optimising silk production constrained by sex (larvae), and selecting parental breeds with diverse cocoon colours for hybrid production (Tzenov, 2003). In countries like India, efforts are directed towards harnessing the productive potentials of bi- and polyvoltine parental breeds. Bi-voltine breeds aim to enhance silk quality and establish a presence in international markets (Satish *et al.*, 2023). Polyvoltine breeds, on the other hand, are evaluated for their resilience to fluctuating environmental conditions prevalent in tropical regions, particularly under high temperatures. This underscores the necessity of developing *B. mori* genotypes with genetic adaptability, including thermotolerance and stability, to mitigate the adverse climatic impacts on silk production (Chandrakanth *et al.*, 2015; Premalatha *et al.*, 2013).

Numerous studies have demonstrated that CW, CSW, and CSP are influenced by quantitative trait loci (QTLs) (Zhan *et al.*, 2009) and additive genetic effects with moderate to high heritability's (Darmand *et al.*, 2011; Hosseini *et al.*, 2005; Zambrano-Gonzalez *et al.*, 2022). The heritability estimates for these production traits, as documented in the studies, are summarised in Table 2. Consequently, these traits exhibit substantial responsiveness to genetic selection and are thus suitable for inclusion in breeding programmes. Given the high economic significance and heritability of these traits, it is crucial to determine the optimal selection strategy to achieve the greatest enhancement in silk production within the shortest timeframe.

B. mori bidensovirus (BmBDV) induces "Flacherie" disease, resulting in significant economic losses for the sericulture industry (Ito *et al.*, 2021). Resistance to BmBDV is governed by the recessive gene nsd-2 (non-susceptible to DNV-2). Consequently, the screening and development of silkworm breeds for BmBDV resistance via artificial inoculation may prove ineffective, as the nsd-2 resistant allele is in a heterozygous state. Deletion within the nsd-2 gene correlates with BmBDV resistance, thereby serving as a potential molecular marker. Silkworm breeds harbouring the nsd-2 resistant allele in a heterozygous state can be identified and selectively bred using marker-assisted breeding techniques (Gundi *et al.*, 2023; Ito *et al.*, 2021).

As of now, the integration of gene-editing technology into silkworm disease resistance and silk production has advanced steadily (Chen *et al.*, 2024; Liu *et al.*, 2024; Wang *et al.*, 2023; Xu *et al.*, 2024; Yu *et al.*, 2024). Simultaneous editing of multiple pathogen genes has been accomplished, alongside the knockout of host genes essential for pathogen proliferation (Baci *et al.*, 2021). Multiple knockout sites have been employed for single target genes to bolster editing efficiency, while the utilisation of inducible promoters aims to enhance editing efficiency and minimise host damage. Notably, the creation of several resistant strains has been realised. Hence, in conjunction with existing clustered regularly interspaced short palindromic repeats (CRISPR) gene-editing technology, the utilisation of inducible promoters alongside multiple genes and targets holds promise for achieving efficient resistance breeding (Li *et al.*, 2023).

Future prospects

Incorporation of genomic selection into silkworm breeding can accelerate genetic improvement by providing precise and rapid trait predictions using DNA markers. It also reduces inbreeding and can be more cost-effective in the long run compared to current crossbreeding techniques that rely on slower phenotypic evaluations. Simultaneously, utilising gene editing techniques to develop strains resistant to evolving diseases will enhance the industry's resilience. Moreover, expanding the utilisation of silk protein in biomedicine, cosmetics, and the feed industry warrants further attention.

5 Black soldier fly

History

The history of black soldier fly (BSF) breeding is a relatively recent phenomenon compared to insects like the honey bee and silkworm. While BSF have been present for millennia, their deliberate breeding for specific purposes is a more recent development (Hoffmann *et al.*, 2021). Interest in the species has increased due to BSF's high protein (36-65%), crude fat (4.6-38.6%), and vital minerals and amino acids (Mohan *et al.*, 2022). The biomass conversion ratio varies between 23% to 55.8% (Hua *et al.*, 2019), providing a sustainable alternative to traditional feed sources like soybean meal and fish meal. The market valuation of BSF amounted to US $180 million in 2021 and is projected to increase from US $240.66 million in 2022 to US $3,285.39 million by 2030, with a compound annual growth rate (CAGR) of 33.7% during the forecast period spanning from 2023 to 2030 (Skyquest, 2024).

Information regarding the early breeding and farming practices of the BSF is limited; however, historical records suggest that Indigenous populations in the Americas may have observed the breeding habits of BSF in decomposing organic material prior to the 1900s (Marshall *et al.*, 2015). Formalised breeding and farming of BSF began to gain attention and recognition in the late 20th and early 21st centuries. The extensive

TABLE 2 Published heritability estimates for various production traits in silkworm

Species	Trait	Heritability	Reference
Bombyx mori L. (Chinese)	Cocoon length	0.48 (0.03)	Zambrano-Gonzalez *et al.* (2022)
	Cocoon weight	0.54 (0.03)	
	Shell weight	0.50 (0.03)	
Bombyx mori L. (Japanese)	Cocoon length	0.71 (0.05)	
	Cocoon weight	0.89 (0.08)	
	Shell weight	0.93 (0.08)	
Bombyx mori L. (Indian)	Cocoon length	0.36 (0.03)	
	Cocoon weight	0.43 (0.03)	
	Shell weight	0.40 (0.03)	
Bombyx mori L. (31)	Cocoon weight	0.05	Darmand *et al.* (2011)
	Cocoon shell weight	0.06	
	Cocoon shell percentage	0.48	
Bombyx mori L. (103)	Cocoon weight	0.03	
	Cocoon shell weight	0.01	
	Cocoon shell percentage	0.08	
Bombyx mori L. (107)	Cocoon weight	0.06	
	Cocoon shell weight	0.70	
	Cocoon shell percentage	0.19	
Bombyx mori L. (101)	Cocoon shell weight	0.27 (0.06)	Hosseini *et al.* (2005)
Bombyx mori L. (102)	Cocoon shell weight	0.46 (0.08)	
Bombyx mori L. (103)	Cocoon shell weight	0.39 (0.07)	
Bombyx mori L. (104)	Cocoon shell weight	0.36 (0.07)	
Bombyx mori L. (101)	Single shell cocoon weight	0.27 (0.05)	Moghaddam *et al.* (2000)
	Single cocoon weight	0.39 (0.07)	
	Cocoon shell percentage	0.16 (0.04)	
Bombyx mori L. (102)	Single shell cocoon weight	0.48 (0.08)	
	Single cocoon weight	0.34 (0.08)	
	Cocoon shell percentage	0.37 (0.06)	
Bombyx mori L. (103)	Single shell cocoon weight	0.39 (0.07)	
	Single cocoon weight	0.50 (0.08)	
	Cocoon shell percentage	0.26 (0.05)	
Bombyx mori L. (104)	Single shell cocoon weight	0.36 (0.06)	
	Single cocoon weight	0.38 (0.06)	
	Cocoon shell percentage	0.25 (0.05)	
Bombyx mori L. (110)	Cocoon weight	0.64 (0.03)	
	Shell weight	0.60 (0.03)	
	Shell percentage	0.32 (0.01)	

research conducted on the BSF as a bioremediation agent, which transforms organic waste into valuable resources such as animal protein for conventional livestock and human consumption, lipids for various applications including feeds, foods, biofuels, and industrial uses, as well as agricultural fertilisers, has led to the proliferation of numerous BSF production enterprises worldwide (Siddiqui *et al.*, 2022). These ventures span from small-scale 'subsistence' or hobbyist operations to large-scale industrial facilities (Banks *et al.*, 2014; Diener *et al.*, 2009; Lalander *et al.*, 2015; Mohan *et al.*, 2022).

Based on the current literature, there are only two recorded genetic improvement programmes in BSF. One, in 2019, a genetic improvement program was

TABLE 2 (Continued)

Species	Trait	Heritability	Reference
Bombyx mori L. (107)	Cocoon weight	0.52 (0.03)	Mirhosseini *et al.* (2005)
	Shell weight	0.34 (0.02)	
	Shell percentage	0.22 (0.01)	
Bombyx mori L. (101433)	Cocoon weight	0.73 (0.03)	
	Shell weight	0.73 (0.03)	
	Shell percentage	0.26 (0.02)	
Bombyx mori L. (Xinhong1)	Cocoon weight	0.66 (0.02)	
	Shell weight	0.71 (0.02)	
	Shell percentage	0.33 (0.02)	
Bombyx mori L. (Koming1)	Cocoon weight	0.55 (0.03)	
	Shell weight	0.61 (0.02)	
	Shell percentage	0.61 (0.01)	
Bombyx mori L. (Y)	Cocoon weight	0.60 (0.03)	
	Shell weight	0.59 (0.03)	
	Shell percentage	0.34 (0.02)	

jointly conducted by Hendrix Genetics and Protix Biosystems Netherlands to enhance the larval weight in BSFL (Facchini *et al.*, 2022). The other is a selective breeding program implemented by South China Agricultural University, China, aimed at developing a cold-tolerant strain to expand BSF production to temperate regions (Ma *et al.*, 2024). In addition to these programmes, Beta Bugs Ltd is actively involved in the genetic improvement of BSF production traits to enhance productivity.

Breeding objectives

The farmers and industries associated with BSFL farming aim to improve productivity by increasing larval yield. Larval yield is measured in terms of larval weight, the number of larvae produced per breeding cycle, and the time taken to reach harvest size, all of which contribute to faster growth rates and enhance resource utilisation and productivity. In terms of quality, larval composition, including protein and fat content, is crucial. Regarding reproduction, increased egg production and mating efficiency are important as they directly contribute to larval input into the production system. Additionally, the adaptability of BSFL to different feedstocks enables farmers to introduce new substrates into the production cycle.

Breeding strategy

In BSF breeding, mass breeding is widely employed, wherein breeding adults are selected primarily based on desirable traits, notably fast-growth (Facchini *et al.*, 2022). These individuals undergo mating in a mass breeding event, after which females lay egg masses. While this approach is straightforward, it is less precise compared to family and pedigree selection methods (Eriksson and Picard, 2021). In terms of management, optimising egg collection involves providing suitable oviposition media. Additionally, improving larval rearing conditions is essential, achieved by maintaining ideal temperature, humidity, and ventilation in the rearing containers. Improved lines are maintained alongside production lines, with occasional introductions of wild stocks to maintain genetic diversity in the breeding population (Hoffmann *et al.*, 2021).

Challenges and opportunities

BSF breeding holds immense potential but also faces unique challenges and limitations. The industry, still relatively young compared to other livestock and aquaculture sectors, lacks standardised breeding practices and regulations across regions (Raman *et al.*, 2022). Overcoming negative perceptions about insects as food or waste processors remains a challenge, necessitating crucial public education and awareness campaigns for wider adoption of BSF products (Higa *et al.*, 2021).

Traditional selective breeding programmes typically rely on phenotyping, pedigree recording, and selecting individuals based on their genetic merit (Falconer and Mackay, 2009). However, with BSF, difficulties arise in tracking mating pairs, recording pedigrees, and monitoring individuals through different life cycle stages due to their complex biology and short life cycle of 38-42 days under artificial mass rearing depending on factors like temperature and humidity (Gobbi *et al.*, 2013; Nguyen *et al.*, 2013).

Recent advances in Near-Infrared Spectroscopy (NIRS) based phenotyping offer promise for accurate phenotyping of individual larvae, essential for genetic evaluation, representing a significant development in insect phenotyping (Alagappan *et al.*, 2024; Cruz-Tirado *et al.*, 2023). These tools enable precise estimation of crude protein and fat content, critical traits in the BSFL production cycle. Maintaining genetic diversity in commercial farms is also a concern, as mass breeding techniques in production lines, coupled with BSF's lekking behaviour, contribute to inbreeding, with colonies collapsing after 10-15 generations (Rhode *et al.*, 2020). To address this issue, it is necessary to develop genomic resources and utilise genetic merit prediction tools, such as genomic prediction, to assess the merit of external germplasm for introduction into the breeding nucleus. This approach should be employed alongside traditional methods to maintain genetic diversity within breeding programmes.

Progress to date

The structured breeding program for BSF is currently limited. To implement a selective breeding program, it is essential to evaluate genetic parameters such as heritability, genetic correlations, and breeding values of the trait of interest for the specific population. One study estimated these parameters using a full-sib design in European BSF. In this study, heritability estimates for body weight at prepupa, body weight at pupa, and development time to prepupa were reported as 0.25, 0.45, and 0.38, respectively. However, these estimates may be confounded as they were unable to separate additive genetic effects from non-additive genetic effects, and the high standard error impacts the reliability of the estimates (Bouwman *et al.*, 2022). Additionally, a recent study revealed the genetic architecture of the BSF production trait, individual larval mass, identifying 69 SNPs with small effects. This study highlighted the polygenic inheritance of the trait and estimated SNP heritability for individual larval mass to be 0.179, with a low standard error of 0.031 (n = 146). This finding implies there is additive genetic variance present in the BSF population, indicating the potential for improvement through traditional or genomic selection (Hull *et al.*, 2024).

Artificial selection for improving larval weight in BSFL was undertaken jointly by Hendrix Genetics and Protix Biosystems Netherlands in 2019. Over two years and 16 generations, each generation of the improved line was selected for increased larval body weight while minimising the increase in inbreeding. Both the selected line and the control line were maintained entirely indoors under controlled environmental conditions. Significant improvements were achieved in the selected line compared to the control line, with an average increase of 39% in larval weight, 34% in wet crate yield, 26% in dry matter crate yield, 32% in crude protein per crate, and 21% crude fat per crate, demonstrating substantial genetic improvement in BSF through selection is possible (Facchini *et al.*, 2022).

Another selective breeding program, implemented by South China Agricultural University, aimed to develop cold-tolerant strains to expand BSFL production to temperate regions. They conducted nine generations of selective breeding at 12 and 16 degrees Celsius. Successful development of cold-tolerant BSF lines at both temperatures was achieved. Selection was based on the size of the pupae, with pupae unable to pass through a 3.35 mm mesh selected for the next generation. The line developed at 12 degrees Celsius achieved a 75.4% increase in larval weight compared to the control line, with 50% of larvae reaching the prepupal stage in 44.3 days compared to 41.3 days in the control group due to lower temperatures, while survival rates also increased. In the case of the 16-degree Celsius selected line, larval weight improved by around 161% compared to the control group. The time necessary for half of the larvae to reach the prepupal stage increased slightly from 39 to 40 days in the 16 °C bred group due to temperature. Notably, the bred group exhibited a significantly higher survival rate (68%) compared to the control group (59%), indicating the potential of selective breeding to develop cold-tolerant strains for high productivity and expanding BSFL production to colder regions (Ma *et al.*, 2024). A study used CRISPR-Cas9 gene editing technology to knock out the *Ptth* (prothoracicotropic hormone) gene, contributing to moulting and metamorphosis in BSF. This intervention delayed the pupation process, extending the larval stage duration and allowing for more feeding on the waste substrate, which is beneficial for effective waste management on an industrial scale (Zhan *et al.*, 2020). Another study highlighted the genetic engineering of BSF to produce provitamin carotenoids by manipulating the carotenoid biosynthetic genes, CarRA and CarB (Gunther *et al.*, 2024).

Future prospects

The outlook for the BSFL industry appears promising. Expansion strategies in the foreseeable future aim to foster industry growth with a sustained focus on delivering products. Breeding programmes must adapt to address evolving environmental conditions and substrate variations effectively. Moreover, the development and application of genomic techniques and tools in BSF breeding are imperative to realise optimal genetic advancements and meet the anticipated demand for insect protein from the animal and aqua feed sector in the future.

6 Mealworm

History

The larvae of *Tenebrio molitor*, commonly known as mealworm or yellow mealworm, are distributed worldwide and are a pest of flour, grain, and food (Ramos-Elorduy *et al.*, 2002). They exhibit a favourable nutritional profile, including high protein content, digestibility, and palatability (Benzertiha *et al.*, 2019). Additionally, they possess functional properties and are straightforward to breed and maintain. Notably, their protein content remains consistent irrespective of their diet. Consequently, *T. molitor* larvae have become a prevalent food source for pets, zoo animals, and even livestock production (Hong *et al.*, 2020).

The history of mealworm breeding and domestication lacks extensive documentation. However, archaeological findings provide some insight, with the earliest evidence of mealworms traced back to Bronze Age Turkey, indicating human familiarity with them at least 3,000 years ago. Additionally, there is evidence suggesting that mealworms likely originated in the Mediterranean region, where the climate provided an ideal habitat for their natural development (Panagiotakopulu, 2001). It is believed that human trade and colonisation facilitated the spread of mealworms to various parts of the world (Moruzzo *et al.*, 2021).

In recent decades, mealworms have gained importance as a feed source, leading to increased research and development efforts. These activities focus on improving mass-rearing techniques (Kröncke *et al.*, 2020), refining breeding strategies (Mlček *et al.*, 2021), enhancing the nutritional profile (Bordiean *et al.*, 2022), and employing selective breeding approaches to enhance production efficiency (Song *et al.*, 2022).

Breeding objectives

Selective breeding of mealworms is still in its infancy despite the establishment of various breeding programmes in insects. Mealworm breeders are pursuing different objectives and approaches to optimise their production processes. Central to their efforts is the enhancement of yield and efficiency. Breeders prioritise the cultivation of mealworms with accelerated growth rates and expedited maturation, enabling more frequent harvesting intervals (Özsoy and Gündoğdu, 2017). Moreover, they aim to cultivate strains capable of withstanding higher population densities within confined spaces, thereby maximising production output. Efficiency gains are further realised through the selection of mealworms that exhibit enhanced feed conversion efficiency, potentially by thriving on more economical, alternative substrates (Song *et al.*, 2022).

In addition to considerations of yield, breeders wanted to address the nutritional composition of mealworms. Given the already favourable protein content of mealworms, augmenting protein content stands out as a primary objective. Furthermore, manipulating the fatty acid composition enables breeders to customise mealworms for specific applications. For instance, elevating omega-3 fatty acid levels could render them more suitable for certain livestock or even human consumption (Hong *et al.*, 2020). Breeding programmes may also target the enrichment of mealworms with specific vitamins or minerals to bolster their overall nutritional profile.

Breeding strategy

In general, farmers employ mass breeding techniques, wherein colonies are established and maintained throughout the production cycle. Improved lines are cultivated through the selection of individuals with desirable phenotypes, primarily focusing on growth traits, to serve as broodstock for producing the next generation (Sellem *et al.*, 2024). Based on current literature, there is no information available on how these mass breeding practices are realising genetic gain or affecting genetic diversity.

Challenges and opportunities

Mealworm breeding presents unique challenges compared to other insects. Structured breeding programmes for mealworms are uncommon, with most farmers and industries relying on mass-rearing techniques. Identifying the various life stages of mealworms proves to be difficult. However, recent studies indicate that Artificial Intelligence (AI) and NIRS offer promising solutions for monitoring rearing systems and recording essential phenotypic data of mealworm larvae (Kröncke *et al.*, 2020; Kroncke and Benning, 2022; Kroncke *et al.*, 2023a, b; Ni *et al.*, 2024), facilitating selective breeding or artificial selection.

Similar to conventional livestock, mealworms are susceptible to diseases such as viral and fungal infections or parasitic mites (Armién *et al.*, 2023). Therefore, maintaining a clean environment and adhering to proper breeding practices are imperative. While small-scale breeding operations are manageable, expanding production necessitates efficient methods for egg collection, life stage separation, and harvest. Automation emerges as a crucial consideration for scaling up operations effectively.

Progress to date

The mealworm farming industry is currently directing investment towards automating mass production systems, including temperature and humidity control, as well as automated feeding and harvesting of the larvae (Grau *et al.*, 2017). Separation of mealworm larvae from the substrate during harvesting can be achieved using a zig-zag air separator (Kröncke *et al.*, 2020). Efficient control of temperature and humidity ensures optimal breeding conditions (Majewski *et al.*, 2022), enhancing larval growth rates and facilitating precise feeding schedules.

Recent studies have focused on developing methods for measuring protein, fat, and moisture content in live mealworms using NIRS (Kroncke and Benning, 2022; Kroncke *et al.*, 2023a). This technology enables accurate phenotyping of production traits in mealworm breeding systems. Additionally, the application of artificial intelligence and image analysis facilitates the identification of various larval stages, aiding decision-making in breeding practices.

Research has also explored the optimisation of diet and feeding for mealworms, investigating the influence of different diets on growth and nutritional composition (Bordiean *et al.*, 2022; Ruschioni *et al.*, 2020). Continuous refinement of diet formulation and feeding strategies remains an investigation focus. Genetic parameter estimation for production traits in mealworms has been limited to two studies. The first study reported heritability estimates for larval weight, pupa weight, adult weight, duration of pupa, duration of pupal stay, and duration of adulthood as 0.45, 0.65, 0.43, 0.27, 0.91, and 0.32, respectively (Özsoy and Gündoğdu, 2017). The second, more recent study employed a multi-trait approach to estimate genetic parameters for production traits, revealing moderate to substantial heritability values ranging from 0.17 to 0.54 for reproduction phenotypes, 0.10 to 0.44 for growth parameters, 0.06 to 0.22 for developmental time, and 0.10 to 0.17 for larval survival rates (Sellem *et al.*, 2024). Recently, the insect production company ŸNSECT in France announced the development of the SNP genotyping chip Axiom® YNS_Mol1 for mealworms, aimed at implementing genomic selection in mealworm breeding (ŸNSECT, 2023).

Future prospects

The mealworm production industry should prioritise establishing comprehensive selective breeding programmes targeting key production traits such as growth rate, disease resistance, feed conversion efficiency, and reproductive performance. This can be achieved by developing phenotyping tools for accurate assessment and implementing a robust selection index to identify individuals with high genetic merit for the next generation. The creation of genomic resources will aid the breeding programmes in accelerating genetic gains. Additionally, emphasis should be placed on researching and implementing automation for monitoring growth, health, and environmental conditions to improve scalability and efficiency. These efforts should be coupled with farming techniques that optimise diet formulation, housing, and environmental management to maximise yield. Collaboration between industry, academia, and technology developers will be essential for advancing these initiatives and integrating them into mealworm farming operations.

7 Conclusions and future recommendations

Insect production for food and feed represents a rapidly growing sector within animal production worldwide. The farming of honey bees and silkworms has already demonstrated significant economic and social benefits for farmers. Selective breeding programmes for these species have been established globally, resulting in substantial genetic gains and improvements in production traits. It is imperative that other insect species also have their own selective breeding programmes tailored to enhance their commercial production traits, thereby improving animal welfare by enhancing their overall health and resilience. Breeding insects for disease resistance can reduce mortality, leading to healthier populations. By standardising diet, environment, and space, better management practices can be implemented, ultimately meeting the increasing demand for insect-derived products.

Currently, mass selection is the predominant approach in most insect species, with the exception of honey bees, where pedigreed selection is employed. To further advance selective breeding efforts, genetic parameters, genetic architecture, and G × E interactions for the production traits in insect species need to be estimated accurately and studied. This will enable the establishment of population and species-specific breeding programmes. Additionally, the creation of genomic resources and the adoption of cost-effective technologies are necessary.

Gene editing techniques have shown promise in creating disease-resistant lines in silkworms, highlighting the potential for genetic improvement in insect species. From this review, it is evident that among insects, there is no one ideal selective breeding technique that can be universally implemented. Instead, these techniques must be tailored carefully, considering all aspects of production, reproduction, and biology. Continued genetic improvement programmes in insect species will play a crucial role in supplying superior products to the growing global population.

With this in mind, suggested areas of research focus include the development of rapid phenotyping tools, such as NIR, image processing, and X-ray, to precisely identify and quantify traits, thereby enhancing the efficiency of selection processes. Additionally, creating rapid genotyping tools or on-farm genotyping solutions would facilitate timely and accurate assessment of genetic merit, enabling prompt selection decisions that aligned with the abbreviated life cycles of insects. Advanced prediction models should be developed to estimate and compare the genetic value of external germplasm, supporting its incorporation into the breeding nucleus for effective management of genetic diversity. Breeding models and strategies need to be formulated to maintain genetic diversity while enhancing productivity for food and feed applications. Establishing live gene banks will aid in the preservation and maintenance of germplasm. Furthermore, developing breeding data consortiums is crucial for managing and disseminating data among breeders, thereby promoting collaborative efforts and information sharing among insect breeders across multiple species and geographical locations.

Future research should also focus on incorporating value-added traits into breeding objectives, such as antimicrobial peptides (AMPs) from BSF and silk protein from silkworms, which are valuable for biomedicine, cosmetics, and other applications. Additionally, improving the insects' ability to thrive on alternative diets (e.g. seaweed) as part of decarbonisation strategies could add significant value to the insect production industry.

Author contributions

K.B. Gowda: methodology, writing – original draft, data curation, conceptualization. D.R. Jerry: writing – review and editing, conceptualization, validation, project administration. K.R. Zenger: writing – review and editing, conceptualization, validation, project administration.

Conflicts of interest

The authors have no conflicts of interest to declare.

Funding

Funding for this work was provided by the Australian Research Council Linkage project (LP210301250).

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