

Genetic and genomic selection in insects as food and feed

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Abstract

This review will summarise existing tools and resources and highlight areas of focus for the insects as food and feed industry for the production of insects as alternative protein sources. By applying knowledge gained from other agricultural organisms coupled with the ease of insect population growth and rearing capabilities, and the increase in biotechnological advances, strains optimised for various economic and biological traits should be one of the most attainable goals for researchers and insect farmers alike. We have reviewed strengths (and weaknesses) of various genetic and genomic approaches, and consider the future of insect farming in the context of genetic and genomic selection of insects.

Keywords: yellow mealworm, black soldier fly, BSF, honey bee, silkworm, crickets, genetic selection, genomics

1. Introduction

The first animal genome belongs to the fruit fly, *Drosophila melanogaster*, published in 2000 (Adams *et al.*, 2000), and human genome drafts followed suite in 2001 after nearly 2 decades of sequencing (Lander *et al.*, 2001; Venter *et al.*, 2001). Sequencing technologies have advanced rapidly since, significantly lowering cost and increasing coverage. Indeed, here we are in 2020 and one can generate an animal genome of sufficient quality that fits on a USB flash drive plugged into a standard laptop in less than a week (Fologea *et al.*, 2005). Furthermore, along with the progress in sequencing technology, advances in software for the biologists have enabled those without an informatics background to assemble, annotate and analyse genomes to answer basic biological questions (www.digitalinsights.qiagen.com). Together these innovations have revealed new avenues for industries whose business models benefit substantially from optimising traits of organisms (such as those in the agri- and aquacultural spaces), by increasing the speed and precision of optimisation. In some cases this means creating transgenic organisms by introducing the DNA sequence of one species into another to confer, for example, insect resistance on *Bt* corn (EPA, 1995). A more common, tried-and-true method of trait enhancement relies on selectively breeding conspecific individuals carrying desirable genetic and phenotypic profiles to produce offspring with desirable

traits. This practice has been carried out for a very long time using traditional breeding strategies (e.g. breed males to multiple females and observe phenotypes, and reciprocal crossing), but can be time-consuming, labour-intensive, and sometimes unsuccessful without knowledge of the underlying traits' genetics. With next-generation biotechnologies, the process can be accelerated and more efficient, since genotype-phenotype relationships can be more readily identified and can be used to formulate more optimal artificial selection and crossing schemes, reducing false leads and the number of generations required to increase the frequency of optimal phenotypes.

Selective breeding is not only useful to traditional crops, livestock and other agricultural products, but will also be an important tool used for the optimisation of insects as alternative protein sources (Van Huis, 2013; Van Huis *et al.*, 2015). In this context, the main differences between traditional agri- and aquacultural animals, most of which are vertebrates, and insects, lie in the mode of reproduction. Most insects evolved to produce many offspring quickly but each with little chance of survival (i.e. the r-selected strategy) whereas many vertebrates produce small numbers of more expensive offspring with typically some parental care ensuring their increased survival (i.e. the K-selected strategy) (Pianka, 1970). Therefore, artificial selection and selective breeding efforts can be done more efficiently in

insects. However, it should be noted that the diversity of insect sex determination mechanisms is far more diverse than across vertebrate systems (Bachtrog *et al.*, 2014), and may have an influence on insect management.

The modern trait-optimisation workflow may involve genome-wide association studies (GWAS) in which loci are identified as being linked to economically important traits (e.g. fecundity, stress resiliency, or growth rates), followed by genetic modifications that introduce existing DNA sequences from conspecifics (or heterospecifics) into a controlled baseline genetic background, with the overall goal of reducing the number of undesirable effects (e.g. reduced fitness) while optimising the desirable ones (Box 1). This review will examine known cases of artificial selection and selective breeding in insects, outline strengths (and weaknesses) surrounding these methods, and discuss what we see as the future for insects as food and feed.

2. Optimisation via artificial selection and selective breeding

Similar to its natural counterpart, artificial selection operates on standing heritable genotypic variation in a population in favour of individuals with phenotypes deemed desirable by the human selector. Once identified,

the selected individuals are allowed to mate, over successive generations fixing the associated alleles and resulting in strains with particular phenotypes (Box 2). In free-ranging insects such as the honey bee *Apis mellifera*, natural populations serve as reservoirs for variation. Regional variability is well described in many subspecies (also called races or ecotypes) native to different parts of the world (Alqarni *et al.*, 2011; Engel, 1999) which exhibit distinct characteristics including coloration, morphometry (Alpatov, 1929; Alqarni *et al.*, 2011), venom biochemistry (Palma and Brochetto-Braga, 1993), and behaviour (Alqarni *et al.*, 2011; Winston and Katz, 1982), with new variation still being discovered (Sheppard and Meixner, 2003). Managed colonies require open ranges to forage and therefore can interact and intermix with feral hives, and may lead to a reduction in the genetic diversity of wild populations (Meixner *et al.*, 2010).

On the other hand, mating of parasitoids, the black soldier fly *Hermetia illucens*, and the house cricket *Acheta domesticus* can be done in closed spaces, thus preventing outcrossing with wild populations. This capability minimises pathogen exposure and enables controlled breeding, but promotes mating among close kin which can lead to inbreeding depression. Nonetheless, genetic depauperation may be ameliorated by starting a colony with

Box 1. Genetically modified organisms.

It is important to note some important differences in some terms used when discussing genetic selection. Genetically modified organisms (GMOs) is a broad term that describes an organism that has been genetically modified using technology in which would not have happened naturally. This broad term represents a wide variety of modifications, some of which are related to genetic selection. More specific are the terms transgenesis and cisgenesis. Transgenesis refers to the practice of using genes or other genetic loci from another organism, and this could not happen naturally as the organisms being considered are heterospecific with divergent evolutionary histories and therefore not sexually compatible. An example of transgenesis is the engineering of foods we eat such as corn (maize). The classic example is *Bt* corn, a strain of corn that contains a bacterial gene that confers insecticide resistance, or corn with increased nutritional value by expressing a common bacterial gene that produces methionine, an essential amino acid.

The alternative to this is cisgenesis, in which a gene is introduced using genetic engineering methods into

an organism, but that gene comes from a sexually compatible organism (for example, the same species or a closely-related species). In this situation, the gene, in theory, could be introduced via mating and introgression, but it is unlikely to happen naturally perhaps due to geographical barriers preventing reproductively compatible populations from intermixing. Examples of this include taking a gene or a non-coding regulatory element (e.g. promoter and enhancer) from the same organism by using genetic engineering to introduce it by itself into a background which contains a variety of desirable traits. Currently, a lot of controversy surrounds the use of genetically modified organisms, mostly related to transgenetics, and many of the regulations are based on the process (how genes are engineered) rather than the type of gene used (gene function and species of origin).

In each and every case, careful considerations of local regulations, the potential for environmental spread through the sale of live insects, and consumer acceptance will play a role in the selection of technologies and strategies outlined in this review. In many cases, genetic modifications can play an useful role in functional characterisations important for an overall understanding of the insects' biology.

Box 2. Strains.

Historically in entomology, a strain generally refers to populations, wild or captive, that possess some stable, consistent characteristic over multiple generations that enable distinguishing one population from another (Carpenter and Bloem, 2002; Russo *et al.*, 2001; Tabashnik *et al.*, 2009; Zatssepina *et al.*, 2001), such as susceptibility to insecticides (Huang *et al.*, 2004), stress resistance (Force *et al.*, 1995), aggression (Alaux *et al.*, 2009) and sex-specific sterility (Heinrich and Scott, 2000). This usage is common, for example, in the literature of insect pests (Argentine *et al.*, 1992; Kuno, 2010; Liao *et al.*, 2019; Liu *et al.*, 2004; Mertz,

1975; Pashley, 1988), *Drosophila* fruit flies (Arking *et al.*, 2002; Cingolani *et al.*, 2012; Seong *et al.*, 2019; Zatssepina *et al.*, 2001), and the silkworm *Bombyx mori* (Murakami and Ohtsuki, 1989; Ruiz and Almanza, 2018; Zhou *et al.*, 2008). Often strain, line, and breed are interchangeably used (Furdui *et al.*, 2014; Seong *et al.*, 2019) but occasionally distinctions are made. Another commonly used convention relates to colony, which can be a strain, line or breed, but is typically formed as an off-shoot from a wild or field-collected sample or from other colonies already established. For the purposes of this review, we will use strain as the dominant term referring to unique population, naturally or artificially selected for.

sufficiently high effective population size, and occasional outcrossing with wildtypes or stocks from different sources. For instance in *H. illucens*, human-assisted dispersal has broadened the natural distribution significantly (Marshall *et al.*, 2015), with cultivated populations reared in factories and laboratories worldwide (Dzepe *et al.*, 2020; Kenis *et al.*, 2018; Sheppard *et al.*, 2002; Zhou *et al.*, 2013). Phenotypic divergence has been observed between laboratory strains (Zhou *et al.*, 2013), likely driven by unintentional selection and local adaptation. Although challenging, it is critical to strike a balance between minimising the genetic load and preserving selected phenotypes in established strains, while also preventing modified organisms from escaping into the local ecosystem. The latter point is an obvious concern with small, mobile, and highly fecund insects such as those mentioned above.

The domesticated silkworm *Bombyx mori*, arguably the only truly domesticated insect, originated from the wild silkworm *Bombyx mandarina* through to a single domestication event in China with little subsequent gene flow between wild ancestors and the domesticated stock (Arunkumar *et al.*, 2006; Cheng *et al.*, 2015; Xia *et al.*, 2009). Therefore, wild *B. mori* does not exist, and consequently standing genetic variation exists solely among commercial and laboratory strains. Interestingly, the initial domestication bottleneck did not significantly reduce standing genetic variation in *B. mori* (Xia *et al.*, 2009), enabling subsequent successful artificial selection. Today, existing strains number in the thousands (Jingade *et al.*, 2011). A similar situation exists for the yellow mealworm *Tenebrio molitor*. A known pest of cereal stores, this mealworm species has evolved in close association with humans and presumably no truly wild population currently exists. It has been a popular feed species mostly for exotic pets and therefore produced in large number by the pet feed industry. *T. molitor* is also widely reared with populations maintained by hobbyists and at many laboratories (Morales-Ramos *et al.*, 2019).

3. Improving traits for the production of insects: the old way

Principles of natural selection can be applied to artificially change phenotypic frequencies in insect populations. In the context of insect production, first, we may wish to make a distinction between phenotypes associated with economic and fitness traits. Economic traits are defined as those directly linked to the intrinsic commercial value of the insect (e.g. production rate of silk and honey). Fitness traits such as fecundity, immunity, and environmental tolerance affect how robust an insect is at surviving and reproducing under artificial conditions. Optimising an economic trait may be at the expense of a fitness trait, and vice versa.

Even without knowledge of the underlying genetic landscape, desirable traits can be intentionally propagated by selective breeding of individuals with desirable traits, such as what was done in early agricultural systems with livestock, poultry and crops. Most traits under selection are continuous (e.g. weight, number of eggs produced, offspring size) with a range of possible phenotypes expressed in a population. Hybridisation, the mating of individuals from distinct genetic backgrounds, is often used to bring together naturally arisen variation from reproductively isolated populations, to create novel genetic landscapes and interactions that may extend the range of selectable phenotypic variation. As above, this method (introducing genetically variable individuals to induce hybrid vigour) is also at the mercy of the unintended consequences for the possibility of the introduction of potentially positive, but also, detrimental phenotypes.

The typical aim of selection programs is to increase the prevalence of phenotypes that would increase the quantity or quality of the commercial product (e.g. amount of silk per cocoon or honey per hive, neatness and reelability of silk threads, etc.), decrease in the amount time to harvest

(e.g. growth rate, development time, voltinism), or promote the stability and health in artificial rearing environments (e.g. disease and parasite resistance, temperature tolerance, cannibalism reduction). In other words, it is desirable to optimise economic traits as much as possible without sacrificing fitness. Principles of genetic improvements and domestication of cultivated insects have been reviewed elsewhere (Gregory, 2009; Hoy, 1976). Below we highlight outstanding examples in insect-rearing history.

For millennia, humans have cultivated insects in large numbers for a wide range of valuable products and services they provide. The best documented and most widespread practices are the sericulture of *B. mori* for silk threads and the apiculture of *A. mellifera* for honey and crop pollination, both of which date back to about 5,000 years ago (Alqarni *et al.*, 2011; Ruiz and Almanza, 2018). Also significant is the century-old biological pest-control industry (Mackauer, 1972; McGugan and Coppel, 1962; Turnbull and Chant, 1961; Van Den Bosch and Messenger, 1973) which grow natural enemies (e.g. the parasitoid wasps *Trichogramma* sp.) to control populations of pest insects (Greany *et al.*, 1984). More recently, the insect as feed and food industry has emerged and is rapidly growing, producing insects for livestock, poultry, aquaculture and pets, and to some extent, human food (Makkar *et al.*, 2014; Van Huis, 2013). The three insects most widely produced and commercialised for these purposes are *H. illucens*, *T. molitor*, and *A. domesticus*.

Sericulture

In *B. mori*, the economic value of silk threads, spun as cocoons by larvae in preparation for pupation, has long directed artificial selection efforts. As previously mentioned, the balance between economic and fitness traits is important, and both were optimised. For example, while economic traits important for silk productions were under extensive selection (weight of cocoons, cocoon's raw silk content, reelability, and length, size, and neatness of silk filament (Datta *et al.*, 2001; Kumar *et al.*, 1995; Shekar and Basavaraja, 2008)), traits related to domestication and fitness were also in focus (e.g. flightlessness, synchronous hatching, number of annual generations, larval duration, survival and hardiness, pupation rate, egg production (Cheng *et al.*, 2015; Moorthy *et al.*, 2007; Murakami and Ohtsuki, 1989; Pradeep *et al.*, 2005; Shekar and Basavaraja, 2008)). Because many of these traits are polygenic, quantitative and interact via epistasis, completely disentangling one from the others is often challenging. Furthermore, the environment can impact the economics of cultivating silkworm. Environmental tolerance is an emerging need to expand the reach of this valuable insect to communities in climatically diverse localities and to cope with global climate change, possibly resulting in improved hybrids (Datta *et al.*, 2001; Shekar and Basavaraja, 2008). In modern sericulture, selective breeding and assessment of outcomes are highly quantitative, informed

by both molecular and phenotypic data combined with multivariate statistical analyses and indices (Datta *et al.*, 2001; Hasan *et al.*, 2011; Mano, 1993; Mirhosseini *et al.*, 2005; Moorthy *et al.*, 2007; Shekar and Basavaraja, 2008). In fact, many reviews have been published related to modern methods for optimising silkworm breeding and production including artificial selection history (Nagaraju *et al.*, 1996; Neshagaran Hemmatabadi *et al.*, 2016), genetics (Jingade *et al.*, 2011; Mizoguchi and Okamoto, 2013; Tanaka, 1953), silk properties (Mondal *et al.*, 2007), diseases and immunity (Bhat *et al.*, 2009; Jing *et al.*, 2013), trait heritability (Singh *et al.*, 2011; Tanaka, 1953), rearing conditions (Rahmathulla, 2012), diet (Kanafi *et al.*, 2007), and molecular resources (Goldsmith *et al.*, 2005; Zhou *et al.*, 2008).

Apiculture

In addition to generating valuable hive products including honey and wax, *A. mellifera* plays a critical role in crop pollination and food security (Carreck and Williams, 1988; Klein *et al.*, 2007; Southwick and Southwick Jr, 1992). The honey bee's economic importance and unusual genetic sex determination system have spurred basic research on many traits, many of which have been shown to be variable and heritable including parasite defence (Moritz, 1985), queen mating frequency (Kraus *et al.*, 2005), foraging behaviour (Page Jr *et al.*, 2000), honey production and alarm response (Collins *et al.*, 1984), body size (Oldroyd *et al.*, 1991), and pollen preference (Basualdo *et al.*, 2007). A variety of genes and their functions and correlations to traits are characterised (Alaux *et al.*, 2009; Kerr *et al.*, 2010; Scott Schneider *et al.*, 2004), including those associated with pollen hoarding (Hunt *et al.*, 1995), hygiene (Lapidge *et al.*, 2002), parasite defence (Spötter *et al.*, 2016), and alarm behaviour (Moritz and Southwick, 1987). To improve their colonies, apiculturists and breeders have imposed selection on both economic traits including honey production (Guzmán-Novoa and Page Jr, 1999) and pollen preference (Basualdo *et al.*, 2007; Nye and Mackensen, 1968; 1970) as well as vitality traits including climate tolerance (Alqarni *et al.*, 2011), hygiene behaviours (Perez-Sato *et al.*, 2009), parasite tolerance (Huang *et al.*, 2014), pollen hoarding (Page and Fondrk, 1995). Comprehensive, standardised protocols for queen care, trait selection, and selective breeding are well established (Büchler *et al.*, 2013; Uzunov *et al.*, 2017).

Biological pest control

Populations of pest insects can be controlled with systematic releases of their natural enemies or via the release of sterile individuals (Greany *et al.*, 1984; Sørensen *et al.*, 2012; Van Lenteren and Nicoli, 2004). Examples of natural enemies include the chalcid wasps *Dahlbominus fuscipennis* (Wilkes, 1942), *Aphytis lingnanensis* (White *et al.*, 1970), and *Trichogramma* sp. (Sorati *et al.*, 1996), all of which are parasitoids. Insects reared for sterile release include

the melon fly *Bactrocera cucurbitae* (Miyatake, 2006) and the New World screwworm *Cochliomyia hominivorax* (Krafsur, 1998). The economic value of these insects is tied with quantity which is strongly influenced by their ability to survive and reproduce in artificial rearing environment. Therefore, artificial selection has focused on improving life-history traits including development rate (Miyatake, 2006), sex ratio (Simmonds, 1947; Wilkes, 1947), and female fecundity (Wilkes, 1947). For example, a laboratory selection for productive females resulted in a 40% increase in female productivity, and thus ensuing in a much greater number of offspring generated without having to invest more on materials and labour, just by removing less productive females (Wilkes, 1947). Similar to the silkworm, environmental tolerance is important for pest-control insects, resulted in selection for temperature tolerance (White *et al.*, 1970; Wilkes, 1942; 1947) and insecticide resistance (Wilkes *et al.*, 1952). Cultivated strains were also under selection to maintain normal foraging behaviours and vitality upon field release (Boller, 1972; Van Lenteren and Nicoli, 2004).

Entomoculture

Unlike the aforementioned established industries, growing insects as feed and food alternatives is still in its infancy. Recent focused reviews have evaluated the nutritional content and suitability for animal feed (Makkar *et al.*, 2014) as well as challenges to mass-rearing, genetic improvements and management practices (Jensen *et al.*, 2017). Though many insects are reared worldwide for these purposes, the more promising species include the black soldier fly *H. illucens*, the yellow mealworm *T. molitor*, and the house cricket *A. domesticus* have been attracting the most attention and interest. Other noteworthy species include the oak moth *Antheraea pernyi* (Li *et al.*, 2017, 2020), the house fly *Musca domestica* (Elahi *et al.*, 2020; Hall *et al.*, 2018), and the palm weevil *Rhynchophorus ferrugineus* (Chinarak *et al.*, 2020).

In the last few decades, the black soldier fly's potential as a feed alternative for livestock and aquaculture, and a processor of organic waste has been recognised and promoted (Newton *et al.*, 1977; Sheppard, 1983; Sheppard *et al.*, 1994; Wang and Shelomi, 2017). The latter is being actively explored for manure management (Rehman *et al.*, 2017) and biofuel conversion (Elsayed *et al.*, 2020). Life history (Booth and Sheppard, 1984; Cammack and Tomberlin, 2017; Furman *et al.*, 1959; Zhou *et al.*, 2013), distribution and diversity (Park *et al.*, 2017; Stahls *et al.*, 2020), mating behaviours (Giunti *et al.*, 2018), and response to variable rearing conditions (Dzepe *et al.*, 2020; Hoc *et al.*, 2019; Lalander *et al.*, 2019; Meneguz *et al.*, 2018; Rhode *et al.*, 2020; Tschirner and Simon, 2015; Zhou *et al.*, 2013), gut endosymbiont (Bruno *et al.*, 2019; Cifuentes *et al.*, 2020; Varotto Boccazzi *et al.*, 2017), nutritional values (Makkar *et al.*, 2014) and livestock feeding on these flies (Newton

et al., 1977; Rimoldi *et al.*, 2019; Schiavone *et al.*, 2017) have all been investigated. Innovations enabling scaling up and industrialising *H. illucens* rearing are being rapidly developed (Liu *et al.*, 2020; Marien *et al.*, 2018; Zhan *et al.*, 2020). Although wild founders can start captive colonies, rapid collapse occurred within several generations, an outcome attributed to inbreeding (Rhode *et al.*, 2020). Rapid inbreeding depression can greatly hinder selective mating following artificial selection, and consequently genetic improvement of traits, and although improvement efforts are undoubted underway, so far none has been published.

Another species being mass produced as feed is the yellow mealworm *T. molitor*. Its usage began with the pet feed industry as early as late 1900's (Martin *et al.*, 1976), and more recently being seriously considered as a viable alternative source of protein and lipid for livestock and aquaculture (Choi *et al.*, 2018; Henry *et al.*, 2018; Oonincx and De Boer, 2012; Veldkamp and Bosch, 2015) and for food as it is currently a part of the human diet in Africa, Asia, Australia and the Americas. In addition, yellow mealworms can also degrade mycotoxins present in crops (Van Broekhoven *et al.*, 2017) and plastics (Yang *et al.*, 2018a,b), and produce nitrogen-rich frass (Poveda *et al.*, 2019), greatly increasing their versatility and commercial value. Life cycle, effects of environmental conditions and diet on development and fitness traits including reproduction and immunity (McConnell and Judge, 2018; Ribeiro *et al.*, 2018; Vigneron *et al.*, 2019), and mating behaviours (Worden and Parker, 2001) have been studied. Experimental evolution experiments successfully used artificial selection and selective breeding to improve important economic and vitality traits including body size, body weight, growth rate (Leclercq, 1963; Morales-Ramos *et al.*, 2019), fecundity and food conversion efficiency (Morales-Ramos *et al.*, 2019), and improved immunity (Armitage and Siva-Jothy, 2005). Hybridisation technique was successfully used to study segmentation patterns (Hein, 1924).

Like the yellow mealworm, the house cricket *A. domesticus* has been sold commercially as pet feed (Nakagaki *et al.*, 1987). *A. domesticus* is also produced for human consumption in some parts of the world (Nakagaki and DeFoliart, 1991), and maintained in laboratories as a research model (Wilson *et al.*, 2010). Along with other edible crickets, this species is being produced by tens of thousands of growers around the world (Halloran *et al.*, 2016; Wilkie, 2018). Risk profile has been investigated (Fernandez-Cassi *et al.*, 2019). Mass rearing protocols are developed, some capable of producing 6,000 individuals daily (Parajulee *et al.*, 1993). Some cooperatives can produce upward of 700-800 kg daily (Halloran *et al.*, 2016). Studies have explored the effects of diet and abiotic conditions on the efficiency of farming *A. domesticus* at different scales (Clifford and Woodring, 1990; Collavo *et al.*, 2005; Orinda *et al.*, 2017). Experimental selection has produced crickets

with larger body sizes, a heritable trait positively correlated with immune function (Ryder and Siva-Jothy, 2001), by manipulating size of food parcels for 10 generations (Tennis, 1985). Body size was studied in great detail in the context of mate choice and sexual selection (Castillo, 2005). Strains with increased longevity can also be selectively bred, resulting in long-living individuals more resilient to oxidative stresses induced by environmental toxins (Flasz *et al.*, 2020). Natural trade-offs between immunity and fitness traits have been characterised in *A. domesticus* (Bascunan-Garcia *et al.*, 2010) and other members of the subfamily Gryllinae (Kerr *et al.*, 2010). However, we found no published record of trait improvements in the context of mass production.

Trait trade-offs

Generations of selection can lead to negative correlations between traits, or trade-offs, such as among life history characteristics (Stearns, 2000), and between immunity and reproduction (Schwenke *et al.*, 2016). Evolutionary trade-offs in natural populations may be viewed as a complex interplay of reproductive success optimisation, lineage-specific constraints, density and frequency dependent selection, and short-term population-specific dynamics (Stearns, 2000). These forces are also present in production populations of cultivated insects. Selective sweeps may be a possible mechanism that generate negative trait correlations, where strong directional selection on a desirable trait brings along linked, deleterious alleles (Berry *et al.*, 1991; Smith and Haigh, 1974) that in a closed, inbreeding populations manifest as undesirable phenotypes in other traits.

In mass-produced insects, trade-offs have been observed between economic traits and fitness traits, as well as among them (Neumann and Blacquiere, 2017). In *B. mori*, strains with better survival tend to be less productive (Datta *et al.*, 2001; Shekar and Basavaraja, 2008) and there is a negative correlation between cocoon weight and shell percentage (Mirhosseini *et al.*, 2005). In *A. mellifera*, selection for increased pollen hoarding resulted in workers with smaller bodies (Page and Fondrk, 1995) and larvae with increased sensitivity to the nutritional environment during development (Linksvayer *et al.*, 2011). Furthermore, there is evidence that hybrid bees are less fit than their pure-bred parents, afflicted with reduced foraging efficiency (Quezada-Euán *et al.*, 1996), lower metabolic rates, and increased wing shape asymmetry (Scott Schneider *et al.*, 2004). The importance of considering traits influencing bee colony fitness and population stability, and not just those immediately linked to economic values, has been advocated (Meixner *et al.*, 2010). In fact, commercial values are very much dependent on long term stability of managed populations. For parasites reared for biological control, trade-offs can occur between longevity and fecundity (Miyatake, 2006; Nagarkatti and Nagaraja,

1978). Mass-rearing conditions may lead to degradation of host acceptance (Van Bergeijk *et al.*, 1989) perhaps due to inadvertent adaptation to rearing diets and conditions. However, host acceptance can be rescued by means of artificial selection (Kölliker-Ott *et al.*, 2003). In *T. molitor*, selection for increased pupal weight unintentionally resulted in reduced larval survival in one example, ultimately impacting total biomass production (Leclercq, 1963; Morales-Ramos *et al.*, 2019). In the absence of directed artificial selection, local adaptation by natural selection can maintain life history variation and phenotypic plasticity between strains (Urs and Hopkins, 1973).

Inbreeding

Inbreeding depression is a longstanding problem for many closed populations of insects, a consequence of mating among close relatives that is exacerbated in captive populations founded from a small effective population of founders. Prolonged inbreeding in just about any species quickly results in decreased genetic variation among the progeny (Jingade *et al.*, 2011; Rhode *et al.*, 2020).

In the honey bee, the negative impacts of management on colony fitness are of top concerns among apiculturists, and the positive effect of genetic diversity on colony wellbeing is well documented (Seeley and Tarpy, 2007). In some cases, loss of genetic variation is exacerbated by commercial queen-breeding practices that produce large number of offspring from relatively few matriline, and the persistent non-random mating to maintain pure lines (Meixner *et al.*, 2010), however, in this particular case, it may not be due entirely to management but rather natural bottlenecks caused by out-of-Africa expansions (Harpur *et al.*, 2012). Therefore, protocols for queen selection and mating techniques have been refined to minimise depletion of genetic variation (Büchler *et al.*, 2013).

A similar situation is observed among biological control insects. Inbred lines of a chalcid parasite were less long-lived, likely due to inbreeding depression, but survival in females could be improved with selection on field stock (Wilkes, 1947). Inbreeding depression can take time to manifest, for instance, no negative changes in female fecundity, male mating success, and morphometry (Sorati *et al.*, 1996) were observed over four generations of sibling mating in a *Trichogramma* parasitic wasp.

4. Improving traits for the production of insects: the new way

Genetic selection

Selection has long been used in the agriculture space. In the early days, this was based on the inference of heritability based on pedigrees and breeding programs (for example,

Mendel's peas; Mendel, 1865), in which the actual genes responsible for the phenotypes were not known. This process works well, albeit, it is very slow to optimise, especially when the traits can only be measured after several months or years, especially true in domesticated agricultural animals. Furthermore, due to the possible presence of other genes which may not be entirely desirable to transmit, the animal may optimise in one phenotype to the detriment of another.

To complicate matters further for selection methods, many traits are not monogenetic, expressed as the result of more than one gene. Monogenetic traits are probably uncommon in nature, but some have been discovered. A clear example is hairlessness in certain dog breeds, attributed to the transcription factor *FOXI3* which is involved in the expression of hair and teeth (Drogemuller *et al.*, 2008). More commonly are quantitative or complex traits, in which many genes are involved, and each individual gene has a small effect on the phenotype. For example, milk protein yield in a breed of cattle is associated with 144 single nucleotide polymorphisms (SNPs) (Daetwyler *et al.*, 2008), and multiple quantitative trait loci (QTL) affecting cocoon traits and ectoparasite defence have been identified in the silkworm and honey bee, respectively (Behrens *et al.*, 2011; Lu *et al.*, 2004). Additionally, the environment can have an impact, with a continuum of phenotypic responses across individuals.

Genetic selection is using genetic tools to identify genes or genetic loci that are associated with traits, then selectively cross those individuals with the appropriate genetics to produce subsequent generations. However, most traits are quantitative or complex traits, meaning multiple genes/genetic loci are responsible for producing the continuous variability we see (e.g. milk yield in dairy cows or clutch size in birds). The ability to identify/characterise the genes that produce phenotypic changes and that are heritable forms the basis of genetic selection. Unfortunately, there are many challenges to identifying these genes that would allow us to make inferences about the heritability of a particular trait (i.e. how much of the variation is attributable to the genes being studied), in part, many of the effects that are seen in phenotypes due to a single gene is a small effect, it is only the additive genetic effect that produces a large effect.

Tools and resources

Next-generation sequencing technologies have been leveraged for many cultivated insects to assemble nuclear genomes (The Honeybee Genome Sequencing Consortium, 2006; The International Silkworm Genome Consortium, 2008; Ferguson *et al.*, 2020; Xia *et al.*, 2009; Zhan *et al.*, 2020), transcriptomes (Cheng *et al.*, 2015; Liu *et al.*, 2015; Oppert *et al.*, 2020; Zhan *et al.*, 2020; Zhu *et al.*, 2019), and microbiomes (Jung *et al.*, 2014; Zhan *et al.*, 2020).

In addition, an increasing number of individual genomic loci have been characterised, including genetic markers (Kumar *et al.*, 2009; Solignac *et al.*, 2003), coding genes and proteins (Gao *et al.*, 2019; Giannetto *et al.*, 2017; Lee *et al.*, 2016; Park *et al.*, 2015). As an example, for *T. molitor*, much research has been done in characterising antimicrobial peptides, immunity-related genes, and their regulation (Jo *et al.*, 2017; Johnston *et al.*, 2014; Keshavarz *et al.*, 2020; Kim *et al.*, 1998; Lee *et al.*, 1996; Moon *et al.*, 1994). Other subjects of investigations include peptidases (Oppert *et al.*, 2012; Prabhakar *et al.*, 2007), insulin (Sevala *et al.*, 1993), and microsatellites (Petitpierre *et al.*, 1988).

Multiple strategies exist for applying next-generation sequencing technologies in different contexts. For example, a GWAS as discussed above is typically done using pre-designed arrays that allow for the quick and efficient genotyping of millions of SNPs, but this only works if there is an existing array. An alternative to discovering genome-wide SNPs across the genome is to genotyping by sequencing, wherein the genomic DNA is typically fragmented using a restriction enzyme, and then sequenced using massively parallel sequencing technologies (Elshire *et al.*, 2011). Where genome-wide expression patterns are of interest, transcriptomes are a valuable resource. Transcriptomics refers to the generation and assembly of transcriptomes, or the coding part of the genome, that allow for the analysis of variation in expression across cell types and tissues or among organisms and strains (e.g. see if multiple genes are changing in response to a stimulus, how gene expression varies between selected strains, etc.). Transcriptomes tend to be less expensive and easier to assemble relative to genomes, as they are typically less complex, are less repetitive, and reference genes typically exist. In some situations, metagenomics, a growing field that studies the environments' genetic material most often attributed to microbial and other microbiological material, is also relevant.

These resources are modernising genetic improvements, where genomic DNA can be modified precisely to bring together desirable genetic variances while preventing hitchhiking of deleterious alleles, or to design transgenic organisms more efficiently (Heinrich and Scott, 2000; Wen *et al.*, 2010). Editing methods relying on the CRISPR/Cas nuclease technology (Ran *et al.*, 2013) are being successfully developed for many arthropods (Sun *et al.*, 2017) including *A. mellifera* (Hu *et al.*, 2019; Kohno *et al.*, 2016), *B. mori* (Ma *et al.*, 2014; Wei *et al.*, 2014; Xu *et al.*, 2019), *H. illucens* (Zhan *et al.*, 2020), and *Tribolium castaneum*, a close relative of *T. molitor* (Adrianos *et al.*, 2018; Gilles *et al.*, 2015). Some examples of traits manipulated successfully in CRISPR/Cas in experiments include silk proteins (Kojima *et al.*, 2007; Xu *et al.*, 2018), sensory systems and behaviours (Liu *et al.*, 2017), and expression of recombinant proteins (Acharya *et al.*, 2002; Wen *et al.*, 2010) in *B. mori*, and larval duration, body size, and flightlessness in *H. illucens* (Zhan *et al.*, 2020).

5. Methods for genetic selection and engineering

There are generally two approaches to identifying genomic loci for genetic engineering and subsequent selection. They may be labelled inside-out and outside-in. In the former, you look at a targeted list of loci that may have some functional association already established in other, often model, species. For example, in the insect world, the *D. melanogaster* database (www.flybase.org) has a wealth of information on well-characterised genes that have been experimentally associated with a wide range of biological and molecular processes with homology in other insects. Researchers can leverage such a database as a starting point to identify loci that affect a trait of interest in their focal organisms. While relevant genes may actually be identified from knowledge of other organisms, the amount of phenotypic variation observed in the focal species that can be attributed to those identified genes may be small, because traits of interest are often polygenic and may have divergent underlying genetics between different species, therefore the accounting of effector loci is often incomplete.

Instead of focusing on a handful of genes with known functions, the alternative outside-in approach takes a bird-eye view of genomic variation to establish genotype-phenotype correlations in a large number of individuals displaying a range of phenotypes. Without a reference genome, researchers may choose to carry out a GWAS (see Figure 1 for a schematic diagram) to pinpoint alleles associate with desirable phenotypes. For example, there may be a variable position that is located in or near an effector locus, be it a gene or a non-coding regulatory element, and due to its close proximity and the lack of recombination it is an informative marker of an uncharacterised chromosomal location that contains a significant allele. Currently for the common insects reared as feed and food, nuclear genome assemblies are only available for the black soldier fly (Zhan *et al.*, 2020) and the yellow mealworm (Eriksson *et al.*, 2020). While this resource has yet to exist for the other important feed and food insects such as crickets and the palm weevil, basic research goals can still be accomplished using published genomes of closely related species. For example, prior to the completion of a *T. molitor* reference genome assembly in 2020, the *Tribolium castenum* genome (*Tribolium* Genome Sequencing Consortium *et al.*, 2008) was used to study the yellow mealworm in our laboratory.

Re-sequencing experiments become possible with a reference genome, where it can be used to map whole genome reads sequenced from multiple individuals exhibiting different phenotypes. Variances can then be called from the mappings, and their significance to traits can be statistically established from known phenotypic scores. Albeit more prone to false positives, the outside-in strategy enables the discovery of non-coding loci

with regulatory functions (e.g. transcription start sites, enhancers, promoters, silencers) and novel taxon-specific genes (i.e. genes only found in a single species or group). This method would instead allow you to discover new genetic loci, especially those that strongly affect phenotypes, and gain a better understanding of the underlying genetic variation attributed to a given phenotype, and allow you to screen a large number of individuals for these specific alleles, and allowing for selective mating to occur.

A genome-editing project may benefit from a combination of both of the approaches discussed above. Armed with an understanding of individual genes' molecular functions and genotype-phenotype correlations among multiple strains, one can more accurately predict candidate loci linked to important traits that would cause appreciable phenotypic changes following genome editing.

Challenges and drawbacks

As with nearly all scientific innovation, there is a balance needed between the cost and the value. Spending money upfront to generate a large dataset could be advantageous in the long run, as there would likely be little need to run additional samples if your existing dataset contains a lot of data. For re-sequencing and GWAS, the number of samples is highly important. Although more costly, the greater the number of unrelated individuals across the phenotypes of interest, the more power the method has to detect actual associated genotypes. Advances in sequencing technology have made running larger number of samples more affordable, but the DNA library preparation for sequencing is still currently costly.

The basic design of a GWAS is to sample animals with a range of phenotypes of interest, and then genotype those animals using SNP arrays or panels. Then, complex statistical analyses are performed to identify SNPs linked to the trait while reducing the false positive rate. Admixture is a source of bias in many GWAS, thus it is important to account for in your statistical model and to select appropriate samples. In correlational analyses, including individuals sharing recent ancestry (i.e. non-independent samples, such as siblings, parents and offspring) risks statistically biasing an association between a trait and a marker. For insect populations, sampling a group of sufficiently unrelated individuals can be challenging given managed insects' high reproductive outputs and lack of outcrossing opportunities, with some insects more challenging than others. For example, all extant yellow mealworm populations are in captivity, and to avoid sampling closely related individuals a GWAS would need to obtain specimens from different source populations (e.g. commercial suppliers, laboratories). This challenge also highlights the necessity of keeping detailed pedigrees and estimating relatedness within and among strains. Other insects such as the black soldier fly

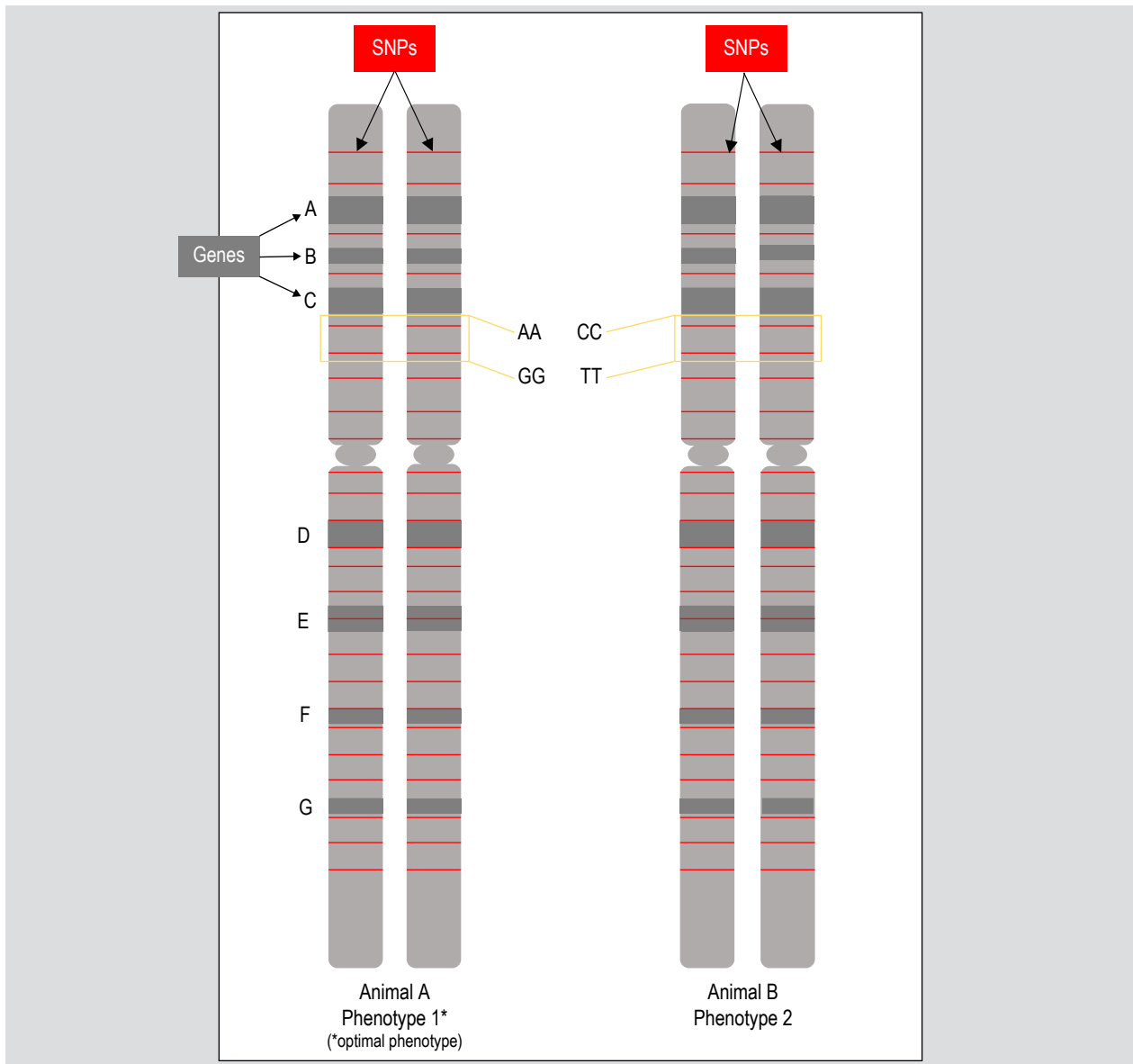


Figure 1. Simplified design of a genome association study, in which multiple locations (red lines: single nucleotide polymorphisms (SNPs), represented here as a single chromosome) randomly span the length of the chromosome. A genome-wide association study would include multiple individuals of varying phenotypic levels, and then the association of the genotypes per phenotype can be assigned. Often the SNPs are not located in genes, but are physically close to genes, and inferences are possible.

have robust wild, geographical populations with different evolutionary histories, and therefore less likely to suffer from sampling bias. Another drawback of large-scale association studies is that they are often labour intensive and time consuming. In each case, researchers would need to establish separate laboratory populations using founders from different sources, and maintain them in conditions that would not skew the expression of the traits in question, measure a suite of phenotypes for several generations, and then genotype.

When designing an experiment, SNP density (i.e. how close the SNPs are to one another?) and location should be

considered. If a SNP is too far away from the quantitative-trait locus of interest, then it would not be detected as 'linked' by the analysis. A dense SNP array usually improves the precision in detecting a linked SNP. This feature is sensitive to linkage disequilibrium (LD), the magnitude of which varies between species and even across regions based on genomic features as seen in the honey bee (Wallberg *et al.*, 2015). The sample size of a GWAS is determined in part by the effect size or, the proportion of the phenotype that can be explained by the genotype. A single gene with large, obvious effects on phenotypes is easily detectable in a small number of animals, but those with smaller effects require a larger sample to detect. This in turn is all dependent on

heritability of the trait, the proportion of the variation explained by the QTL, and LD. In the end, if you have many markers, and many unrelated samples, then the discovery of informative SNPs is likely. Since the false discovery rate when using a large number of SNPs is very high and that the SNP showed up as significant is expected by chance, it is often recommended to validate the detected variants in additional, independent sets of samples.

Relative to vertebrates, there are inherent advantages to using r-selected insects for selection experiments, namely short generation time and high fecundity. Indeed, within a few years of artificial selection and selective breeding, a population with phenotypic improvements could be generated. These conventional means work but are vulnerable to the hitch-hiking of deleterious or undesirable alleles in LD with desirable ones.

And finally, there are copy number and structural variants (large insertions or deletions, or inversions) to consider. These variants are much more difficult to detect using traditional massively parallel sequencing platforms. However, technology has improved to be able to address this. Long-read sequencing technology, offers by company such as PacBio, can be used to bridge these gaps, but suffers from higher error rates relative to short-read Illumina sequencing and requires computationally expensive error corrections. Other companies like 10x Genomics takes advantage of less error prone short reads and proprietary partitioning methods to assemble longer scaffolds, albeit

they have discontinued this technology. And Hi-C makes use of library preparation protocols that link long-range chromosomal segments together to understand spatial organisation of a chromosome. Generally, 10X outperforms (Srikanth *et al.*, 2020; Srivastava *et al.*, 2020) other currently available long read sequencing platforms. The first insect to be sequenced exclusively using this platform includes the mealworm (Eriksson *et al.*, 2020).

Future directions

There is little doubt alternatives to conventional ranching and farming will soon be needed to meet growing global demand for protein. Climate change, increased human population and antibiotic resistance are shifting the economics of raising traditional livestock and poultry with large carbon footprints. In response, the emerging insect as feed and food industry is rapidly scaling up capacity, taking advantage of insects' natural abilities to mature rapidly, produce large number of offspring, tolerate crowded rearing conditions, and consume a wide range of feed, including waste. We predict that many innovations will be fuelled by next-generation molecular technologies, particularly with the CRISPR/Cas genome editing toolkit (Ran *et al.*, 2013). This trend is already in motion in many of the insects discussed, and has yielded promising results.

With generally two approaches available for the isolation and characterisation of genetic variants linked to particular (desirable or not) phenotypes, one method holds promise

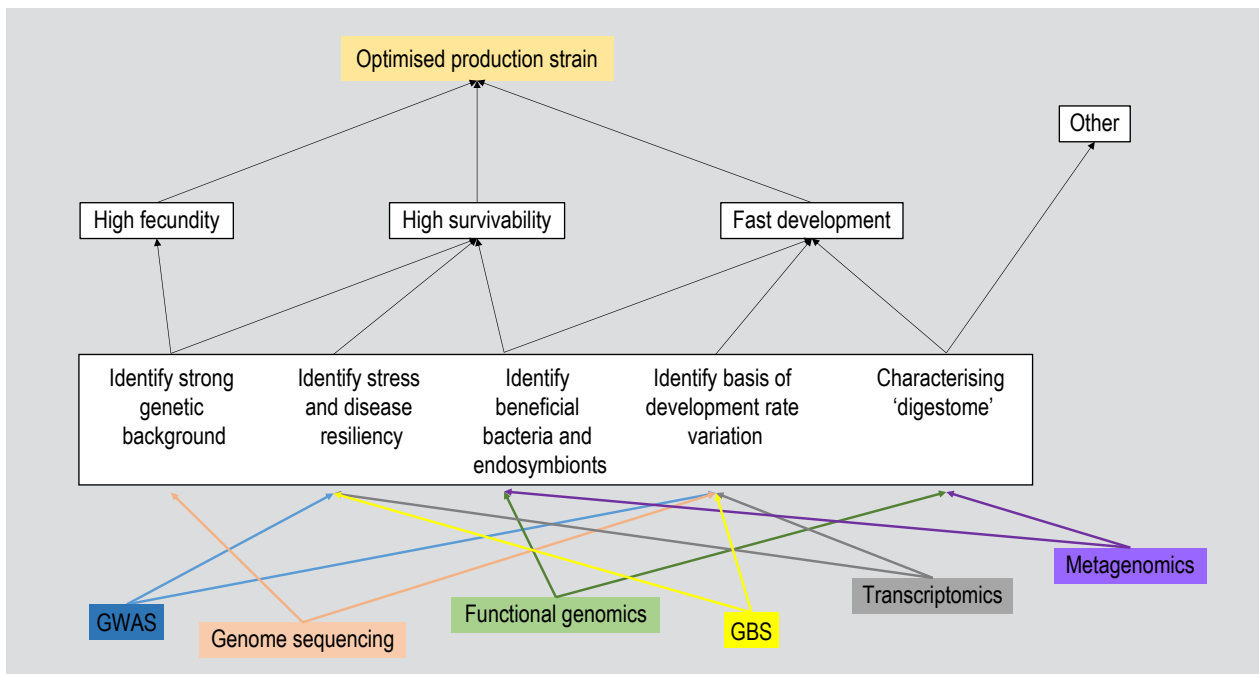


Figure 2. In this simplified and non-exhaustive example, the production of optimised strains can encompass multiple areas (including some not included here), and can be determined using many different genetic and genomic tools (GBS = genotype by sequencing; GWAS = genome wide association study).

https://www.wageningenacademic.com/doi/pdf/10.3920/JIFF2020.0097 - Friday, October 29, 2021 12:55:07 PM - IP Address: 72.106.61.223

over the other. In selective breeding strategies that focus on improving specific phenotypes, linked genotypes may be quickly identified in subsequent genomic analyses. The main issue with this method is that many genomic changes could have taken place during selection, and it may be not able to isolate the causative genotypes (lots of genetic hitchhiking). An alternative approach is to use population genetics to identify adaptive genes that can then be correlated to the phenotypes. This requires large samples sizes across many phenotypes, and requires native or wild populations to be variable across the phenotypic landscape, but it is more likely to yield successful outcomes (Ross-Ibarra *et al.*, 2007).

Another aspect for consideration when assessing the functional characterisation of any significant variants correlated to a phenotype would include an understanding of the impacts of the microbial communities associated with these insects. Endosymbionts, such as *Wolbachia*, are well-known to manipulate biological processes from cytoplasmic incompatibilities (Werren and Windsor, 2000; Werren *et al.*, 2008), contributions to degradation of waste (e.g. (Przemieniecki *et al.*, 2020), to the potential nutritional mutualism (Nikoh *et al.*, 2014). There is very little research of *Wolbachia* and other endosymbionts on the majority of the proposed insects discussed here (crickets, mealworms and back soldier flies), albeit well-known in other insects used for biocontrol, possibly an indication of its inexistence, or more likely, this is an area of needed research for the continuation of an understanding of the biology of the insects, from wild to farmed populations.

As an example of what insect farmers and researchers can look forward to, the first reference cattle genome was available in 2009 (The Bovine Genome Sequencing and Analysis Consortium *et al.*, 2009), launching the practice of linking traits to genotypes with SNPs identified that were unique to different breeds of cattle. The 1000 bull genome project (Hayes and Daetwyler, 2019) began as a means to quantify the variation present in various cattle breeds ($n=121$), and to date, there are 2,703 cattle genomes. With each subsequent analyses the group does by adding new individuals, the number of SNPs increases, and for species with a lot of variability that number increases with each subsequent analysis. As opposed to species with little variation, that number plateaus despite the addition of new genomes. Most SNPs are intergenic variants (i.e. not in a gene) with intronic SNPs the second most common (Hayes and Daetwyler, 2019). This particular dataset demonstrates the need for additional genetic and genomic data to better understand the insects we wish to commercialise, while highlighting limitations with current agricultural processes. Genome editing may be able to address this problem, by selectively changing the genomic DNA sequence at single-nucleotide level, but without the basic research and knowledge to start from, it will remain to be seen. However,

academic and the industry are armed with the best tools and resources to disrupt traditional agricultural processes in producing sustainable alternative protein sources.

Conflicts of interest

The authors declare no conflicts of interest.

References

- Acharya, A., Sriram, S., Sehrawat, S., Rahman, M., Sehgal, D. and Gopinathan, K., 2002. *Bombyx mori* nucleopolyhedrovirus: molecular biology and biotechnological applications for large-scale synthesis of recombinant proteins. *Current Science* 83: 455-465.
- Adams, M.D., Celniker, S.E., Holt, R.A., Evans, C.A., Gocayne, J.D., Amanatides, P.G., Scherer, S.E., Li, P.W., Hoskins, R.A., Galle, R.F., George, R.A., Lewis, S.E., Richards, S., Ashburner, M., Henderson, S.N., Sutton, G.G., Wortman, J.R., Yandell, M.D., Zhang, Q., Chen, L.X., Brandon, R.C., Rogers, Y.H., Blazej, R.G., Champe, M., Pfeiffer, B.D., Wan, K.H., Doyle, C., Baxter, E.G., Helt, G., Nelson, C.R., Gabor, G.L., Abril, J.F., Agbayani, A., An, H.J., Andrews-Pfannkoch, C., Baldwin, D., Ballew, R.M., Basu, A., Baxendale, J., Bayraktaroglu, L., Beasley, E.M., Beeson, K.Y., Benos, P.V., Berman, B.P., Bhandari, D., Bolshakov, S., Borkova, D., Botchan, M.R., Bouck, J., Brokstein, P., Brottier, P., Burtis, K.C., Busam, D.A., Butler, H., Cadieu, E., Center, A., Chandra, I., Cherry, J.M., Cawley, S., Dahlke, C., Davenport, L.B., Davies, P., de Pablos, B., Delcher, A., Deng, Z., Mays, A.D., Dew, I., Dietz, S.M., Dodson, K., Doup, L.E., Downes, M., Dugan-Rocha, S., Dunkov, B.C., Dunn, P., Durbin, K.J., Evangelista, C.C., Ferraz, C., Ferreira, S., Fleischmann, W., Fosler, C., Gabrielian, A.E., Garg, N.S., Gelbart, W.M., Glasser, K., Glodek, A., Gong, F., Gorrell, J.H., Gu, Z., Guan, P., Harris, M., Harris, N.L., Harvey, D., Heiman, T.J., Hernandez, J.R., Houck, J., Hostin, D., Houston, K.A., Howland, T.J., Wei, M.H., Ibegwam, C., Jalali, M., Kalush, F., Karpen, G.H., Ke, Z., Kennison, J.A., Ketchum, K.A., Kimmel, B.E., Kodira, C.D., Kraft, C., Kravitz, S., Kulp, D., Lai, Z., Lasko, P., Lei, Y., Levitsky, A.A., Li, J., Li, Z., Liang, Y., Lin, X., Liu, X., Mattei, B., McIntosh, T.C., McLeod, M.P., McPherson, D., Merkulov, G., Milshina, N.V., Mobarry, C., Morris, J., Moshrefi, A., Mount, S.M., Moy, M., Murphy, B., Murphy, L., Muzny, D.M., Nelson, D.L., Nelson, D.R., Nelson, K.A., Nixon, K., Nusskern, D.R., Pacleb, J.M., Palazzolo, M., Pittman, G.S., Pan, S., Pollard, J., Puri, V., Reese, M.G., Reinert, K., Remington, K., Saunders, R.D., Scheeler, F., Shen, H., Shue, B.C., Siden-Kiamos, I., Simpson, M., Skupski, M.P., Smith, T., Spier, E., Spradling, A.C., Stapleton, M., Strong, R., Sun, E., Svirskas, R., Tector, C., Turner, R., Venter, E., Wang, A.H., Wang, X., Wang, Z.Y., Wassarman, D.A., Weinstock, G.M., Weissenbach, J., Williams, S.M., Woodage, T., Worley, K.C., Wu, D., Yang, S., Yao, Q.A., Ye, J., Yeh, R.F., Zaveri, J.S., Zhan, M., Zhang, G., Zhao, Q., Zheng, L., Zheng, X.H., Zhong, F.N., Zhong, W., Zhou, X., Zhu, S., Zhu, X., Smith, H.O., Gibbs, R.A., Myers, E.W., Rubin, G.M. and Venter, J.C., 2000. The genome sequence of *Drosophila melanogaster*. *Science* 287: 2185-2195.
- Adrianos, S., Lorenzen, M. and Oppert, B., 2018. Metabolic pathway interruption: CRISPR/Cas9-mediated knockout of tryptophan 2, 3-dioxygenase in *Tribolium castaneum*. *Journal of Insect Physiology* 107: 104-109.

- Alaux, C., Sinha, S., Hasadsri, L., Hunt, G.J., Guzmán-Novoa, E., DeGrandi-Hoffman, G., Uribe-Rubio, J.L., Southey, B.R., Rodriguez-Zas, S. and Robinson, G.E., 2009. Honey bee aggression supports a link between gene regulation and behavioral evolution. *Proceedings of the National Academy of Sciences* 106: 15400-15405.
- Alpatov, W., 1929. Biometrical studies on variation and races of the honey bee (*Apis mellifera* L.). *The Quarterly Review of Biology* 4: 1-58.
- Alqarni, A.S., Hannan, M.A., Owayss, A.A. and Engel, M.S., 2011. The indigenous honey bees of Saudi Arabia (Hymenoptera, Apidae, *Apis mellifera jemenitica* Ruttner): their natural history and role in beekeeping. *Zookeys* 134: 83-98. <https://doi.org/10.3897/zookeys.134.1677>
- Argentine, J.A., Clark, J.M. and Lin, H., 1992. Genetics and biochemical mechanisms of abamectin resistance in two isogenic strains of Colorado potato beetle. *Pesticide biochemistry and physiology* 44: 191-207.
- Arking, R., Novoseltseva, J., Hwangbo, D.-S., Novoseltsev, V. and Lane, M., 2002. Different age-specific demographic profiles are generated in the same normal-lived *Drosophila* strain by different longevity stimuli. *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences* 57: B390-B398.
- Armitage, S.A. and Siva-Jothy, M.T., 2005. Immune function responds to selection for cuticular colour in *Tenebrio molitor*. *Heredity* 94: 650-656. <https://doi.org/10.1038/sj.hdy.6800675>
- Arunkumar, K.P., Metta, M. and Nagaraju, J., 2006. Molecular phylogeny of silkmoths reveals the origin of domesticated silkmoth, *Bombyx mori* from Chinese *Bombyx mandarina* and paternal inheritance of *Antheraea proylei* mitochondrial DNA. *Molecular Phylogenetics and Evolution* 40: 419-427. <https://doi.org/10.1016/j.ympev.2006.02.023>
- Bachtrog, D., Mank, J.E., Peichel, C.L., Kirkpatrick, M., Otto, S.P., Ashman, T.L., Hahn, M.W., Kitano, J., Mayrose, I., Ming, R., Perrin, N., Ross, L., Valenzuela, N. and Vamosi, J.C., 2014. Sex determination: why so many ways of doing it? *PLoS Biology* 12: e1001899. <https://doi.org/10.1371/journal.pbio.1001899>
- Bascunan-Garcia, A.P., Lara, C. and Cordoba-Aguilar, A., 2010. Immune investment impairs growth, female reproduction and survival in the house cricket, *Acheta domesticus*. *Journal of Insect Physiology* 56: 204-211. <https://doi.org/10.1016/j.jinsphys.2009.10.005>
- Basualdo, M., Rodríguez, E., Bedascarrasbure, E. and De Jong, D., 2007. Selection and estimation of the heritability of sunflower (*Helianthus annuus*) pollen collection behavior in *Apis mellifera* colonies. *Genetics and Molecular Research* 6: 374-381.
- Behrens, D., Huang, Q., Gessner, C., Rosenkranz, P., Frey, E., Locke, B., Moritz, R.F. and Kraus, F.B., 2011. Three QTL in the honey bee *Apis mellifera* L. suppress reproduction of the parasitic mite *Varroa destructor*. *Ecology and Evolution* 1: 451-458. <https://doi.org/10.1002/ece3.17>
- Berry, A.J., Ajioka, J. and Kreitman, M., 1991. Lack of polymorphism on the *Drosophila* fourth chromosome resulting from selection. *Genetics* 129: 1111-1117.
- Bhat, S.A., Bashir, I. and Kamili, A.S., 2009. Microsporidiosis of silkworm, *Bombyx mori* L. (Lepidoptera-Bombycidae): a review. *African Journal of Agricultural Research* 4: 1519-1523.
- Boller, E., 1972. Behavioral aspects of mass-rearing of insects. *Entomophaga* 17: 9-25.
- Booth, D.C. and Sheppard, C., 1984. Oviposition of the black soldier fly, *Hermetia illucens* (Diptera: Stratiomyidae): eggs, masses, timing, and site characteristics. *Environmental entomology* 13: 421-423.
- Bruno, D., Bonelli, M., De Filippis, F., Di Lelio, I., Tettamanti, G., Casartelli, M., Ercolini, D. and Caccia, S., 2019. The intestinal microbiota of *Hermetia illucens* larvae is affected by diet and shows a diverse composition in the different midgut regions. *Applied and environmental microbiology* 85: e01864-18. <https://doi.org/10.1128/AEM.01864-18>
- Büchler, R., Andonov, S., Bienefeld, K., Costa, C., Hatjina, F., Kezic, N., Kryger, P., Spivak, M., Uzunov, A. and Wilde, J., 2013. Standard methods for rearing and selection of *Apis mellifera* queens. *Journal of Apicultural Research* 52: 1-30. <https://doi.org/10.3896/ibra.1.52.1.07>
- Cammack, J.A. and Tomberlin, J.K., 2017. The impact of diet protein and carbohydrate on select life-history traits of the black soldier fly *Hermetia illucens* (L.) (Diptera: Stratiomyidae). *Insects* 8: 56. <https://doi.org/10.3390/insects8020056>
- Carpenter, J.E. and Bloem, S., 2002. Interaction between insect strain and artificial diet in diamondback moth development and reproduction. *Entomologia Experimentalis et Applicata* 102: 283-294.
- Carreck, N. and Williams, I., 1988. The economic value of bees in the UK. *Bee World* 79: 115-123. <https://doi.org/10.1080/0005772x.1998.11099393>
- Castillo, R.C.d., 2005. The quantitative genetic basis of female and male body size and their implications on the evolution of body size dimorphism in the house cricket *Acheta domesticus* (Gryllidae). *Genetics and Molecular Biology* 28: 843-848.
- Cheng, T., Fu, B., Wu, Y., Long, R., Liu, C. and Xia, Q., 2015. Transcriptome sequencing and positive selected genes analysis of *Bombyx mandarina*. *PLoS ONE* 10: e0122837. <https://doi.org/10.1371/journal.pone.0122837>
- Chinarak, K., Chaijan, M. and Panpipat, W., 2020. Farm-raised sago palm weevil (*Rhynchophorus ferrugineus*) larvae: Potential and challenges for promising source of nutrients. *Journal of Food Composition and Analysis* 92: 103542.
- Choi, I.-H., Kim, J.-M., Kim, N.-J., Kim, J.-D., Park, C., Park, J.-H. and Chung, T.-h., 2018. Replacing fish meal by mealworm (*Tenebrio molitor*) on the growth performance and immunologic responses of white shrimp (*Litopenaeus vannamei*). *Acta Scientiarum. Animal Sciences* 40: e39077. <https://doi.org/10.4025/actascianimsci.v40i1.39077>.
- Cifuentes, Y., Glaeser, S.P., Mvie, J., Bartz, J.-O., Müller, A., Gutzeit, H.O., Vilcinkas, A. and Kämpfer, P., 2020. The gut and feed residue microbiota changing during the rearing of *Hermetia illucens* larvae. *Antonie van Leeuwenhoek* 113: 1323-1344. <https://doi.org/10.1007/s10482-020-01443-0>
- Cingolani, P., Platts, A., Wang le, L., Coon, M., Nguyen, T., Wang, L., Land, S.J., Lu, X. and Ruden, D.M., 2012. A program for annotating and predicting the effects of single nucleotide polymorphisms, SnpEff: SNPs in the genome of *Drosophila melanogaster* strain w1118; iso-2; iso-3. *Fly (Austin)* 6: 80-92. <https://doi.org/10.4161/fly.19695>

- Clifford, C.W. and Woodring, J., 1990. Methods for rearing the house cricket, *Acheta domesticus* (L.), along with baseline values for feeding rates, growth rates, development times, and blood composition. *Journal of Applied Entomology* 109: 1-14.
- Collavo, A., Glew, R.H., Huang, Y.-S., Chuang, L.-T., Bosse, R. and Paoletti, M.G., 2005. House cricket small-scale farming. *Ecological implications of minilivestock: potential of insects, rodents, frogs and snails* 27: 515-540.
- Collins, A.M., Rinderer, T.E., Harbo, J.R. and Brown, M.A., 1984. Heritabilities and correlations for several characters in the honey bee. *Journal of Heredity* 75: 135-140. <https://doi.org/10.1093/oxfordjournals.jhered.a109888>
- Daetwyler, H.D., Schenkel, F.S., Sargolzaei, M. and Robinson, J.A., 2008. A genome scan to detect quantitative trait loci for economically important traits in Holstein cattle using two methods and a dense single nucleotide polymorphism map. *Journal of Dairy Science* 91: 3225-3236. <https://doi.org/10.3168/jds.2007-0333>
- Datta, R., Basavaraja, H., Reddy, N.M., Kumar, S.N., Kumar, N.S., Babu, M.R., Ahsan, M. and Jayaswal, K., 2001. Breeding of new productive bivoltine hybrid, CSR12×CSR6 of silkworm *Bombyx mori* L. *International Journal of Industrial Entomology* 3: 127-133.
- Drogemuller, C., Karlsson, E.K., Hytonen, M.K., Perloski, M., Dolf, G., Sainio, K., Lohi, H., Lindblad-Toh, K. and Leeb, T., 2008. A mutation in hairless dogs implicates *FOXP3* in ectodermal development. *Science* 321: 1462. <https://doi.org/10.1126/science.1162525>
- Dzepe, D., Nana, P., Kuietche, H.M., Kuate, A.F., Tchuinkam, T. and Djouaka, R., 2020. Role of pupation substrate on post-feeding development of black soldier fly larvae, *Hermetia illucens* (Diptera: Stratiomyidae). 8: 760-764.
- Elahi, U., Ma, Y.B., Wu, S.G., Wang, J., Zhang, H.J. and Qi, G.H., 2020. Growth performance, carcass characteristics, meat quality and serum profile of broiler chicks fed on housefly maggot meal as a replacement of soybean meal. *Journal of Animal Physiology and Animal Nutrition* 104: 1075-1084. <https://doi.org/10.1111/jpn.13265>
- Elsayed, M., Ran, Y., Ai, P., Azab, M., Mansour, A., Jin, K., Zhang, Y. and Abomohra, A.E.-F., 2020. Innovative integrated approach of biofuel production from agricultural wastes by anaerobic digestion and black soldier fly larvae. *Journal of Cleaner Production* 263: 121495. <https://doi.org/10.1016/j.jclepro.2020.121495>
- Elshire, R.J., Glaubitz, J.C., Sun, Q., Poland, J.A., Kawamoto, K., Buckler, E.S. and Mitchell, S.E., 2011. A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. *PLoS ONE* 6: e19379. <https://doi.org/10.1371/journal.pone.0019379>
- Engel, M.S., 1999. The taxonomy of recent and fossil honey bees (Hymenoptera: Apidae: *Apis*). *Journal of Hymenoptera Research* 8: 165-196.
- Environmental Protection Agency (EPA), 1995. Pesticide fact sheet. Name of chemical(s): *Bacillus thuringiensis* CryIA9(b) d-endotoxin and the genetic material necessary for its production (plasmid vector pCIB4431) in corn. Environmental Protection Agency, Washington, DC, USA.
- Eriksson, T., Andere, A.A., Kelstrup, H., Emery, V.J. and Picard, C.J., 2020. The yellow mealworm (*Tenebrio molitor*) genome: a resource for the emerging insect as food and feed industry. *Journal of Insects as Food and Feed* 6: 445-455. <https://doi.org/10.3920/jiff2019.0057>
- Ferguson, K.B., Kursch-Metz, T., Verhulst, E.C. and Pannebakker, B.A., 2020. Hybrid genome assembly and evidence-based annotation of the egg parasitoid and biological control agent *Trichogramma brassicae*. *G3: Genes, Genomes, Genetics* 10: 3533-3540. <https://doi.org/10.1534/g3.120.401344>
- Fernandez-Cassi, X., Supeanu, A., Vaga, M., Jansson, A., Boqvist, S. and Vagsholm, I., 2019. The house cricket (*Acheta domesticus*) as a novel food: a risk profile. *Journal of Insects as Food and Feed* 5: 137-157. <https://doi.org/10.3920/jiff2018.0021>
- Flasz, B., Dzięwiecka, M., Kędzierski, A., Tarnawska, M. and Augustyniak, M., 2020. Vitellogenin expression, DNA damage, health status of cells and catalase activity in *Acheta domesticus* selected according to their longevity after graphene oxide treatment. *Science of The Total Environment* 737. <https://doi.org/10.1016/j.scitotenv.2020.140274>
- Fologea, D., Gershow, M., Ledden, B., McNabb, D.S., Golovchenko, J.A. and Li, J., 2005. Detecting single stranded DNA with a solid state nanopore. *Nano Letters* 5: 1905-1909. <https://doi.org/10.1021/nl051199m>
- Force, A.G., Staples, T., Soliman, S. and Arking, R., 1995. Comparative biochemical and stress analysis of genetically selected *Drosophila* strains with different longevities. *Developmental genetics* 17: 340-351.
- Furdui, E.M., Marghitas, L.A., Dezmirean, D.S., Pasca, I., Pop, I.F., Erler, S. and Schluns, E.A., 2014. Genetic characterization of *Bombyx mori* (Lepidoptera: Bombycidae) breeding and hybrid lines with different geographic origins. *Journal of Insect Science* 14: 211. <https://doi.org/10.1093/jisesa/ieu073>
- Furman, D.P., Young, R.D. and Catts, P.E., 1959. *Hermetia illucens*(Linnaeus) as a factor in the natural control of *Musca domestica* Linnaeus. *Journal of economic entomology* 52: 917-921.
- Gao, Z., Deng, W. and Zhu, F., 2019. Reference gene selection for quantitative gene expression analysis in black soldier fly (*Hermetia illucens*). *PLoS ONE* 14: e0221420. <https://doi.org/10.1371/journal.pone.0221420>
- Giannetto, A., Oliva, S., Mazza, L., Mondello, G., Savastano, D., Mauceri, A. and Fasulo, S., 2017. Molecular characterization and expression analysis of heat shock protein 70 and 90 from *Hermetia illucens*reared in a food waste bioconversion pilot plant. *Gene* 627: 15-25. <https://doi.org/10.1016/j.gene.2017.06.006>
- Gilles, A.F., Schinko, J.B. and Averof, M., 2015. Efficient CRISPR-mediated gene targeting and transgene replacement in the beetle *Tribolium castaneum*. *Development* 142: 2832-2839.
- Giunti, G., Campolo, O., Laudani, F. and Palmeri, V., 2018. Male courtship behaviour and potential for female mate choice in the black soldier fly *Hermetia illucens* L. (Diptera: Stratiomyidae). *Entomologia Generalis* 38: 29-46. <https://doi.org/10.1127/entomologia/2018/0657>
- Goldsmith, M.R., Shimada, T. and Abe, H., 2005. The genetics and genomics of the silkworm, *Bombyx mori*. *Annual Review of Entomology* 50: 71-100. <https://doi.org/10.1146/annurev.ento.50.071803.130456>
- Greany, P., Vinson, S. and Lewis, W., 1984. Insect parasitoids: finding new opportunities for biological control. *American Institute of Biological Sciences Circulation*, McLean, VA, USA.

- Gregory, T.R., 2009. Artificial selection and domestication: modern lessons from Darwin's enduring analogy. *Evolution: Education and Outreach* 2: 5-27. <https://doi.org/10.1007/s12052-008-0114-z>
- Guzmán-Novoa, E. and Page Jr, R.E., 1999. Selective breeding of honey bees (Hymenoptera: Apidae) in Africanized areas. *Journal of economic entomology* 92: 521-525.
- Hall, H.N., Masey O'Neill, H.V., Scholey, D., Burton, E., Dickinson, M. and Fitches, E.C., 2018. Amino acid digestibility of larval meal (*Musca domestica*) for broiler chickens. *Poultry Science* 97: 1290-1297. <https://doi.org/10.3382/ps/pex433>
- Halloran, A., Roos, N., Flore, R. and Hanboonsong, Y., 2016. The development of the edible cricket industry in Thailand. *Journal of Insects as Food and Feed* 2: 91-100. <https://doi.org/10.3920/jiff2015.0091>
- Harpur, B.A., Minaei, S., Kent, C.F. and Zayed, A., 2012. Management increases genetic diversity of honey bees via admixture. *Molecular Ecology* 21: 4414-4421. <https://doi.org/10.1111/j.1365-294X.2012.05614.x>
- Hasan, M.A., Rahman, S.M. and Ahsan, M.K., 2011. Genetic variability, correlation, path analysis and construction of selection index in mulberry silkworm, *Bombyx mori* L. I Genetic variability. *University Journal of Zoology, Rajshahi University* 30: 33-36.
- Hayes, B.J. and Daetwyler, H.D., 2019. 1000 bull genomes project to map simple and complex genetic traits in cattle: applications and outcomes. *Annual Review of Animal Biosciences* 7: 89-102. <https://doi.org/10.1146/annurev-animal-020518-115024>
- Hein, S.A., 1924. Studies on variation in the mealworm, *Tenebrio molitor*. *Journal of Genetics* 14: 1-38.
- Heinrich, J.C. and Scott, M.J., 2000. A repressible female-specific lethal genetic system for making transgenic insect strains suitable for a sterile-release program. *Proceedings of the National Academy of Sciences* 97: 8229-8232.
- Henry, M., Gasco, L., Chatzifotis, S. and Piccolo, G., 2018. Does dietary insect meal affect the fish immune system? The case of mealworm, *Tenebrio molitor* on European sea bass, *Dicentrarchus labrax*. *Developmental & Comparative Immunology* 81: 204-209.
- Hoc, B., Noel, G., Carpentier, J., Francis, F. and Caparros Megido, R., 2019. Optimization of black soldier fly (*Hermetia illucens*) artificial reproduction. *PLoS ONE* 14: e0216160. <https://doi.org/10.1371/journal.pone.0216160>
- Hoy, M.A., 1976. Genetic improvement of insects: fact or fantasy. *Environmental entomology* 5: 833-839.
- Hu, X.F., Zhang, B., Liao, C.H. and Zeng, Z.J., 2019. High-Efficiency CRISPR/Cas9-Mediated Gene Editing in Honeybee (*Apis mellifera*) Embryos. *G3: Genes, Genomes, Genetics* 9: 1759-1766. <https://doi.org/10.1534/g3.119.400130>
- Huang, F., Subramanyam, B. and Toews, M.D., 2004. Susceptibility of laboratory and field strains of four stored-product insect species to spinosad. *Journal of Economic Entomology* 97: 2154-2159.
- Huang, Q., Lattorff, H.M., Kryger, P., Le Conte, Y. and Moritz, R.F., 2014. A selective sweep in a microsporidian parasite Nosema-tolerant honeybee population, *Apis mellifera*. *Animal Genetics* 45: 267-273. <https://doi.org/10.1111/age.12114>
- Hunt, G.J., Page, R., Fondrk, M.K. and Dullum, C.J., 1995. Major quantitative trait loci affecting honey bee foraging behavior. *Genetics* 141: 1537-1545.
- Jensen, K., Kristensen, T.N., Heckmann, L.-H. and Sørensen, J.G., 2017. Breeding and maintaining high-quality insects. In: Van Huis, A. and Tomberlin, J.K. (eds) *Insects as food and feed: from production to consumption*. Wageningen Academic Publishers, Wageningen, the Netherlands, pp. 174-198. <https://doi.org/10.3920/978-90-8686-849-0>
- Jing, W., Xiangyang, Z. and Xiujin, Z., 2013. A review of innate immunity of silkworm, *Bombyx mori*. *African Journal of Agricultural Research* 8: 2319-2325. <https://doi.org/10.5897/AJARx11.079>
- Jingade, A., Vijayan, K., Somasundaram, P., Srinivasababu, G. and Kamble, C., 2011. A review of the implications of heterozygosity and inbreeding on germplasm biodiversity and its conservation in the silkworm, *Bombyx mori*. *Journal of Insect Science* 11(1): 8. <https://doi.org/10.1673/031.011.0108>
- Jo, Y.H., Kim, Y.J., Park, K.B., Seong, J.H., Kim, S.G., Park, S., Noh, M.Y., Lee, Y.S. and Han, Y.S., 2017. TmCactin plays an important role in Gram-negative and -positive bacterial infection by regulating expression of 7 AMP genes in *Tenebrio molitor*. *Scientific reports* 7: 46459.
- Johnston, P.R., Makarova, O. and Rolff, J., 2014. Inducible defenses stay up late: temporal patterns of immune gene expression in *Tenebrio molitor*. *G3: Genes, Genomes, Genetics* 4: 947-955.
- Jung, J., Heo, A., Park, Y.W., Kim, Y.J., Koh, H. and Park, W., 2014. Gut microbiota of *Tenebrio molitor* and their response to environmental change. *Journal of Microbiology and Biotechnology* 24: 888-897.
- Kanafi, R.R., Ebadi, R., Mirhosseini, S., Seidavi, A., Zolfaghari, M. and Etebari, K., 2007. A review on nutritive effect of mulberry leaves enrichment with vitamins on economic traits and biological parameters of silkworm *Bombyx mori* L. *Invertebrate Survival Journal* 4: 86-91.
- Kenis, M., Bouwassi, B., Boafu, H., Devic, E., Han, R., Koko, G., Koné, N.G., Maciel-Vergara, G., Nacambo, S., Pomalegni, S.C.B., Roffeis, M., Wakefield, M., Zhu, F. and Fitches, E., 2018. Small-scale fly larvae production for animal feed. In: Halloran, A., Flore, R., Vantomme, P. and Roos, N. (eds) *Edible insects in sustainable food systems*. Springer, Cham, Switzerland, pp. 239-261. https://doi.org/10.1007/978-3-319-74011-9_15
- Kerr, A.M., Gershman, S.N. and Sakaluk, S.K., 2010. Experimentally induced spermatophore production and immune responses reveal a trade-off in crickets. *Behavioral Ecology* 21: 647-654. <https://doi.org/10.1093/beheco/arq035>
- Keshavarz, M., Jo, Y.H., Edosa, T.T., Bae, Y.M. and Han, Y.S., 2020. TmPGRP-SA regulates antimicrobial response to bacteria and fungi in the fat body and gut of *Tenebrio molitor*. *International Journal of Molecular Sciences* 21: 2113.
- Kim, D.-H., Lee, Y.T., Lee, Y.J., Chung, J.H., Lee, B.L., Choi, B.S. and Lee, Y., 1998. Bacterial expression of tenecin 3, an insect antifungal protein isolated from *Tenebrio molitor*, and its efficient purification. *Molecules & Cells* 8: 786-789.
- Klein, A.M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. and Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences* 274: 303-313. <https://doi.org/10.1098/rspb.2006.3721>

- Kohno, H., Suenami, S., Takeuchi, H., Sasaki, T. and Kubo, T., 2016. Production of knockout mutants by CRISPR/Cas9 in the European honeybee, *Apis mellifera* L. *Zoological Science* 33: 505-512. <https://doi.org/10.2108/zs160043>
- Kojima, K., Kuwana, Y., Sezutsu, H., Kobayashi, I., Uchino, K., Tamura, T. and Tamada, Y., 2007. A new method for the modification of fibroin heavy chain protein in the transgenic silkworm. *Bioscience, Biotechnology, and Biochemistry* 71: 2943-2951. <https://doi.org/10.1271/bbb.70353>
- Kölliker-Ott, U.M., Bigler, F. and Hoffmann, A.A., 2003. Does mass rearing of field collected *Trichogramma brassicae* wasps influence acceptance of European corn borer eggs? *Entomologia Experimentalis et Applicata* 109: 197-203.
- Krafsur, E.S., 1998. Sterile insect technique for suppressing and eradicating insect populations: 55 years and counting. *Journal of Agricultural Entomology* 15: 303-317.
- Kraus, F.B., Neumann, P. and Moritz, R.F.A., 2005. Genetic variance of mating frequency in the honeybee (*Apis mellifera* L.). *Insectes Sociaux* 52: 1-5. <https://doi.org/10.1007/s00040-004-0766-9>
- Kumar, G.A., Jalali, S., Nagesh, M., Venkatesan, T. and Niranjana, P., 2009. Genetic variation in artificially selected strains of the egg parasitoid, *Trichogramma chilonis* Ishii (Hymenoptera: Trichogrammatidae) using RAPD analysis. *Journal of Biological Control* 23: 353-359.
- Kumar, P., Bhutia, R. and Ahsan, M., 1995. Estimates of genetic variability for commercial quantitative traits and selection indices in bivoltine races of mulberry silkworm (*Bombyx mori* L.). *Indian Journal of Genetics and Plant Breeding* 55: 109-116.
- Kuno, G., 2010. Early history of laboratory breeding of *Aedes aegypti* (Diptera: Culicidae) focusing on the origins and use of selected strains. *Journal of Medical Entomology* 47: 957-971. [10.1603/me10152](https://doi.org/10.1603/me10152)
- Lalander, C., Diener, S., Zurbrügg, C. and Vinnerås, B., 2019. Effects of feedstock on larval development and process efficiency in waste treatment with black soldier fly (*Hermetia illucens*). *Journal of Cleaner Production* 208: 211-219. <https://doi.org/10.1016/j.jclepro.2018.10.017>
- Lander, E.S., Linton, L.M., Birren, B., Nusbaum, C., Zody, M.C., Baldwin, J., Devon, K., Dewar, K., Doyle, M., FitzHugh, W., Funke, R., Gage, D., Harris, K., Heaford, A., Howland, J., Kann, L., Lehoczky, J., LeVine, R., McEwan, P., McKernan, K., Meldrim, J., Mesirov, J.P., Miranda, C., Morris, W., Naylor, J., Raymond, C., Rosetti, M., Santos, R., Sheridan, A., Sougnez, C., Stange-Thomann, Y., Stojanovic, N., Subramanian, A., Wyman, D., Rogers, J., Sulston, J., Ainscough, R., Beck, S., Bentley, D., Burton, J., Clee, C., Carter, N., Coulson, A., Deadman, R., Deloukas, P., Dunham, A., Dunham, I., Durbin, R., French, L., Grafham, D., Gregory, S., Hubbard, T., Humphray, S., Hunt, A., Jones, M., Lloyd, C., McMurray, A., Matthews, L., Mercer, S., Milne, S., Mullikin, J.C., Mungall, A., Plumb, R., Ross, M., Shownkeen, R., Sims, S., Waterston, R.H., Wilson, R.K., Hillier, L.W., McPherson, J.D., Marra, M.A., Mardis, E.R., Fulton, L.A., Chinwalla, A.T., Pepin, K.H., Gish, W.R., Chissoe, S.L., Wendl, M.C., Delehaanty, K.D., Miner, T.L., Delehaanty, A., Kramer, J.B., Cook, L.L., Fulton, R.S., Johnson, D.L., Minx, P.J., Clifton, S.W., Hawkins, T., Branscomb, E., Predki, P., Richardson, P., Wenning, S., Slezak, T., Doggett, N., Cheng, J.F., Olsen, A., Lucas, S., Elkin, C., Uberbacher, E., Frazier, M., Gibbs, R.A., Muzny, D.M., Scherer, S.E., Bouck, J.B., Sodergren, E.J., Worley, K.C., Rives, C.M., Gorrell, J.H., Metzker, M.L., Naylor, S.L., Kucherlapati, R.S., Nelson, D.L., Weinstock, G.M., Sakaki, Y., Fujiyama, A., Hattori, M., Yada, T., Toyoda, A., Itoh, T., Kawagoe, C., Watanabe, H., Totoki, Y., Taylor, T., Weissenbach, J., Heilig, R., Saurin, W., Artiguenave, F., Brottier, P., Bruls, T., Pelletier, E., Robert, C., Wincker, P., Smith, D.R., Doucette-Stamm, L., Rubenfield, M., Weinstock, K., Lee, H.M., Dubois, J., Rosenthal, A., Platzer, M., Nyakatura, G., Taudien, S., Rump, A., Yang, H., Yu, J., Wang, J., Huang, G., Gu, J., Hood, L., Rowen, L., Madan, A., Qin, S., Davis, R.W., Federspiel, N.A., Abola, A.P., Proctor, M.J., Myers, R.M., Schmutz, J., Dickson, M., Grimwood, J., Cox, D.R., Olson, M.V., Kaul, R., Raymond, C., Shimizu, N., Kawasaki, K., Minoshima, S., Evans, G.A., Athanasiou, M., Schultz, R., Roe, B.A., Chen, F., Pan, H., Ramsay, J., Lehrach, H., Reinhardt, R., McCombie, W.R., de la Bastide, M., Dedhia, N., Blocker, H., Hornischer, K., Nordsiek, G., Agarwala, R., Aravind, L., Bailey, J.A., Bateman, A., Batzoglu, S., Birney, E., Bork, P., Brown, D.G., Burge, C.B., Cerutti, L., Chen, H.C., Church, D., Clamp, M., Copley, R.R., Doerks, T., Eddy, S.R., Eichler, E.E., Furey, T.S., Galagan, J., Gilbert, J.G., Harmon, C., Hayashizaki, Y., Haussler, D., Hermjakob, H., Hokamp, K., Jang, W., Johnson, L.S., Jones, T.A., Kasif, S., Kasprzyk, A., Kennedy, S., Kent, W.J., Kitts, P., Koonin, E.V., Korf, I., Kulp, D., Lancet, D., Lowe, T.M., McLysaght, A., Mikkelsen, T., Moran, J.V., Mulder, N., Pollara, V.J., Ponting, C.P., Schuler, G., Schultz, J., Slater, G., Smit, A.F., Stupka, E., Szustakowski, J., Thierry-Mieg, D., Thierry-Mieg, J., Wagner, L., Wallis, J., Wheeler, R., Williams, A., Wolf, Y.I., Wolfe, K.H., Yang, S.P., Yeh, R.F., Collins, F., Guyer, M.S., Peterson, J., Felsenfeld, A., Wetterstrand, K.A., Patrino, A., Morgan, M.J., de Jong, P., Catanese, J.J., Osoegawa, K., Shizuya, H., Choi, S., Chen, Y.J., Szustakowski, J. and International Human Genome Sequencing Consortium, 2001. Initial sequencing and analysis of the human genome. *Nature* 409: 860-921. <https://doi.org/10.1038/35057062>
- Lapidge, K.L., Oldroyd, B.P. and Spivak, M., 2002. Seven suggestive quantitative trait loci influence hygienic behavior of honey bees. *Naturwissenschaften* 89: 565-568.
- Leclercq, J., 1963. Artificial selection for weight and its consequences in *Tenebrio molitor* L. *Nature* 198: 106-107.
- Lee, Y.-S., Seo, S.-H., Yoon, S.-H., Kim, S.-Y., Hahn, B.-S., Sim, J.-S., Koo, B.-S. and Lee, C.-M., 2016. Identification of a novel alkaline amylopullulanase from a gut metagenome of *Hermetia illucens*. *International journal of biological macromolecules* 82: 514-521.
- Lee, Y.J., Chung, T.J., Park, C.W., Hahn, Y., Chung, J.H., Lee, B.L., Han, D.M., Jung, Y.H., Kim, S. and Lee, Y., 1996. Structure and expression of the tenecin 3 gene in *Tenebrio molitor*. *Biochemical and Biophysical Research Communications* 218: 6-11.
- Li, Q., Li, Y.-P., Ambuhl, D., Liu, Y.-P., Li, M.-W. and Qin, L., 2020. Nutrient composition of Chinese oak silkworm, *Antheraea pernyi*, a traditional edible insect in China: a review. *Journal of Insects as Food and Feed* 6: 355-369. <https://doi.org/10.3920/JIFF2019.0059>
- Li, W., Zhang, Z., Lin, L. and Terenius, O., 2017. *Antheraea pernyi* (Lepidoptera: Saturniidae) and its importance in sericulture, food consumption, and traditional Chinese medicine. *Journal of Economic Entomology* 110: 1404-1411. <https://doi.org/10.1093/jee/tox140>

- Liao, J., Xue, Y., Xiao, G., Xie, M., Huang, S., You, S., Wyckhuys, K.A.G. and You, M., 2019. Inheritance and fitness costs of resistance to *Bacillus thuringiensis* toxin Cry2Ad in laboratory strains of the diamondback moth, *Plutella xylostella* (L.). *Scientific Reports* 9: 6113. <https://doi.org/10.1038/s41598-019-42559-2>
- Linksvayer, T.A., Kaftanoglu, O., Akyol, E., Blatch, S., Amdam, G.V. and Page, R.E., Jr., 2011. Larval and nurse worker control of developmental plasticity and the evolution of honey bee queen-worker dimorphism. *Journal of Evolutionary Biology* 24: 1939-1948. <https://doi.org/10.1111/j.1420-9101.2011.02331.x>
- Liu, H., Cupp, E.W., Guo, A. and Liu, N., 2004. Insecticide resistance in Alabama and Florida mosquito strains of *Aedes albopictus*. *Journal of Medical Entomology* 41: 946-952.
- Liu, Q., Liu, W., Zeng, B., Wang, G., Hao, D. and Huang, Y., 2017. Deletion of the *Bombyx mori* odorant receptor co-receptor (BmOrco) impairs olfactory sensitivity in silkworms. *Insect Biochemistry and Molecular Biology* 86: 58-67. <https://doi.org/10.1016/j.ibmb.2017.05.007>
- Liu, S., Shi, X.-X., Jiang, Y.-D., Zhu, Z.-J., Qian, P., Zhang, M.-J., Yu, H., Zhu, Q.-Z., Gong, Z.-J. and Zhu, Z.-R., 2015. *De novo* analysis of the *Tenebrio molitor* (Coleoptera: Tenebrionidae) transcriptome and identification of putative glutathione S-transferase genes. *Applied entomology and zoology* 50: 63-71.
- Liu, Z., Najar-Rodriguez, A.J., Minor, M.A., Hedderley, D.I. and Morel, P.C.H., 2020. Mating success of the black soldier fly, *Hermetia illucens* (Diptera: Stratiomyidae), under four artificial light sources. *Journal of Photochemistry and Photobiology B* 205: 111815. <https://doi.org/10.1016/j.jphotobiol.2020.111815>
- Lu, C., Li, B., Zhao, A. and Xiang, Z., 2004. QTL mapping of economically important traits in silkworm (*Bombyx mori*). *Science in China Series C: Life Sciences* 47: 477-484.
- Ma, S., Chang, J., Wang, X., Liu, Y., Zhang, J., Lu, W., Gao, J., Shi, R., Zhao, P. and Xia, Q., 2014. CRISPR/Cas9 mediated multiplex genome editing and heritable mutagenesis of BmKu70 in *Bombyx mori*. *Scientific Reports* 4: 4489. <https://doi.org/10.1038/srep04489>
- Mackauer, M., 1972. Genetic aspects of insect production. *Entomophaga* 17: 27-48.
- Makkar, H.P., Tran, G., Heuzé, V. and Ankers, P., 2014. State-of-the-art on use of insects as animal feed. *Animal Feed Science and Technology* 197: 1-33.
- Mano, Y., 1993. A new method to select promising silkworm breeds/combinations. *Indian Silk* 31: 53.
- Marien, A., Debode, F., Aerts, C., Ancion, C., Francis, F. and Berben, G., 2018. Detection of *Hermetia illucens* by real-time PCR. *Journal of Insects as Food and Feed* 4: 115-122. <https://doi.org/10.3920/jiff2017.0069>
- Marshall, S., Woodley, N. and Hauser, M., 2015. The historical spread of the Black Soldier Fly, *Hermetia illucens*(L.)(Diptera, Stratiomyidae, Hermetiinae), and its establishment in Canada. *The Journal of the Entomological Society of Ontario* 146: 51-54.
- Martin, R., Rivers, J. and Cowgill, U., 1976. Culturing mealworms as food for animals in captivity. *International Zoo Yearbook* 16: 63-70.
- McConnell, M.W. and Judge, K.A., 2018. Body size and lifespan are condition dependent in the mealworm beetle, *Tenebrio molitor*, but not sexually selected traits. *Behavioral Ecology and Sociobiology* 72: 32. <https://doi.org/10.1007/s00265-018-2444-3>
- McGugan, B. and Coppel, H., 1962. Part II. Biological control of forest insects, 1910-1958. In: McLeod, J.H., Coppel, H.C. and McGugan, B.M. A review of the biological control attempts against insects and weeds in Canada. Commonwealth Agricultural Bureau, Franham Royal, UK, pp. 35-127.
- Meixner, M.D., Costa, C., Kryger, P., Hatjina, F., Bouga, M., Ivanova, E. and Büchler, R., 2010. Conserving diversity and vitality for honey bee breeding. *Journal of Apicultural Research* 49: 85-92. <https://doi.org/10.3896/ibra.1.49.1.12>
- Mendel, G., 1865. Versuche uber Pflanzen-Hybriden. *Abhandl. d. Naturf. Vereins in Brunn* 4: 3-47.
- Meneguz, M., Gasco, L. and Tomberlin, J.K., 2018. Impact of pH and feeding system on black soldier fly (*Hermetia illucens*, L.; Diptera: Stratiomyidae) larval development. *PLoS ONE* 13: e0202591. <https://doi.org/10.1371/journal.pone.0202591>
- Mertz, D.B., 1975. Senescent decline in flour beetle strains selected for early adult fitness. *Physiological Zoology* 48: 1-23.
- Mirhosseini, S., Ghanipoor, M., Shadparvar, A. and Etebari, K., 2005. Selection indices for cocoon traits in six commercial silkworm (*Bombyx mori* L.) lines. *The Philippine Agricultural Scientist* 88: 328-336.
- Miyatake, T., 2006. Quantitative genetic aspects of the quality control of mass-reared insects: the case of the melon fly (*Bactrocera cucurbitae*). *Formosan Entomologist* 26: 307-318.
- Mizoguchi, A. and Okamoto, N., 2013. Insulin-like and IGF-like peptides in the silkworm *Bombyx mori*: discovery, structure, secretion, and function. *Frontiers in Physiology* 4: 217. <https://doi.org/10.3389/fphys.2013.00217>
- Mondal, M., Trivedy, K. and Nirmal Kumar, S., 2007. The silk proteins, sericin and fibroin in silkworm, *Bombyx mori* Linn. – a review. *Caspian Journal of Environmental Sciences* 5: 63-76.
- Moon, H.J., Lee, S.Y., Kurata, S., Natori, S. and Lee, B.L., 1994. Purification and molecular cloning of cDNA for an inducible antibacterial protein from larvae of the coleopteran, *Tenebrio molitor*. *The Journal of Biochemistry* 116: 53-58.
- Moorthy, S., Das, S., Kar, N. and Urs, S.R., 2007. Breeding of bivoltine breeds of *Bombyx mori* suitable for variable climatic conditions of tropics. *International Journal of Industrial Entomology* 14: 99-105.
- Morales-Ramos, J.A., Kelstrup, H.C., Rojas, M.G. and Emery, V., 2019. Body mass increase induced by eight years of artificial selection in the yellow mealworm (Coleoptera: Tenebrionidae) and life history trade-offs. *Journal of Insect Science* 19: 4. <https://doi.org/10.1093/jisesa/iey110>
- Moritz, R.F., 1985. Heritability of the postcapping stage in *Apis mellifera* and its relation to varroaosis resistance. *Journal of Heredity* 76: 267-270.
- Moritz, R.F. and Southwick, E.E., 1987. Phenotype interactions in group behavior of honey bee workers (*Apis mellifera* L.). *Behavioral Ecology and Sociobiology* 21: 53-57.
- Murakami, A. and Ohtsuki, Y., 1989. Genetic studies on tropical races of silkworm (*Bombyx mori*), with special reference to cross breeding strategy between tropical and temperate races. 2. Multivoltine silkworms in Japan and their origin. *Journal of the Association for Research in Otolaryngology* 23: 123-127.
- Nagaraju, J., Raje, U. and Datta, R., 1996. Crossbreeding and heterosis in the silkworm, *Bombyx mori*: a review. *Sericologia* 36: 1-20.

- Nagarkatti, S. and Nagaraja, H., 1978. Experimental comparison of laboratory reared vs. wild-type *Trichogramma confusum* [Hym.: Trichogrammatidae] I. Fertility, fecundity and longevity. *Entomophaga* 23: 129-136.
- Nakagaki, B. and DeFoliart, G., 1991. Comparison of diets for mass-rearing *Acheta domesticus* (Orthoptera: Gryllidae) as of food conversion efficiency with values reported for livestock. *Journal of Economic Entomology* 84: 891-896.
- Nakagaki, B.J., Sunde, M.L. and Defoliart, G.R., 1987. Protein quality of the house cricket, *Acheta domesticus*, when fed to broiler chicks. *Poultry Science* 66: 1367-1371. <https://doi.org/10.3382/ps.0661367>
- Neshagaran Hemmatbadi, R., Seidavi, A. and Gharahveysi, S., 2016. A review on correlation, heritability and selection in silkworm breeding. *Journal of Applied Animal Research* 44: 9-23. <https://doi.org/10.1080/09712119.2014.987289>
- Neumann, P. and Blacquiere, T., 2017. The Darwin cure for apiculture? Natural selection and managed honeybee health. *Evolutionary Applications* 10: 226-230. <https://doi.org/10.1111/eva.12448>
- Newton, G., Booram, C., Barker, R. and Hale, O., 1977. Dried *Hermetia illucens* larvae meal as a supplement for swine. *Journal of Animal Science* 44: 395-400.
- Nikoh, N., Hosokawa, T., Moriyama, M., Oshima, K., Hattori, M. and Fukatsu, T., 2014. Evolutionary origin of insect-*Wolbachia* nutritional mutualism. *Proceedings of the National Academy of Sciences* 111: 10257-10262. <https://doi.org/10.1073/pnas.1409284111>
- Nye, W.P. and Mackensen, O., 1968. Selective breeding of honeybees for alfalfa pollen: fifth generation and backcrosses. *Journal of Apicultural Research* 7: 21-27.
- Nye, W.P. and Mackensen, O., 1970. Selective breeding of honeybees for alfalfa pollen collection: with tests in high and low alfalfa pollen collection regions. *Journal of Apicultural Research* 9: 61-64.
- Oldroyd, B., Rinderer, T. and Buco, S., 1991. Heritability of morphological characters used to distinguish European and Africanized honeybees. *Theoretical and Applied Genetics* 82: 499-504.
- Oonincx, D.G. and De Boer, I.J., 2012. Environmental impact of the production of mealworms as a protein source for humans – a life cycle assessment. *PLoS ONE* 7: e51145. <https://doi.org/10.1371/journal.pone.0051145>
- Oppert, B., Martynov, A.G. and Elpidina, E.N., 2012. *Bacillus thuringiensis* Cry3Aa protoxin intoxication of *Tenebrio molitor* induces widespread changes in the expression of serine peptidase transcripts. *Comparative Biochemistry and Physiology Part D: Genomics and Proteomics* 7: 233-242.
- Oppert, B., Perkin, L.C., Lorenzen, M. and Dossey, A.T., 2020. Transcriptome analysis of life stages of the house cricket, *Acheta domesticus*, to improve insect crop production. *Scientific Reports* 10: 3471. <https://doi.org/10.1038/s41598-020-59087-z>
- Orinda, M.A., Mosi, R.O., Ayieko, M.A. and Amimo, F.A., 2017. Growth performance of Common house cricket (*Acheta domesticus*) and field cricket (*Gryllus bimaculatus*) crickets fed on agro-byproducts. *Journal of Entomology and Zoology Studies* 5: 1664-1668.
- Page Jr, R., Fondrk, M., Hunt, G., Guzman-Novoa, E., Humphries, M., Nguyen, K. and Greene, A., 2000. Genetic dissection of honeybee (*Apis mellifera* L.) foraging behavior. *Journal of Heredity* 91: 474-479.
- Page, R.E. and Fondrk, M.K., 1995. The effects of colony-level selection on the social organization of honey bee (*Apis mellifera* L.) colonies: colony-level components of pollen hoarding. *Behavioral Ecology and Sociobiology* 36: 135-144.
- Palma, M.S. and Brochetto-Braga, M., 1993. Biochemical variability between venoms from different honey-bee (*Apis mellifera*) races. *Comparative Biochemistry and Physiology Part C: Pharmacology, Toxicology and Endocrinology* 106: 423-427.
- Parajulee, M.N., Defoliart, G.R. and Hogg, D.B., 1993. Model for use in mass-production of *Acheta domesticus* (Orthoptera: Gryllidae) as food. *Journal of Economic Entomology* 86: 1424-1428.
- Park, S., Choi, H., Choi, J.-Y. and Jeong, G., 2017. Population structure of the exotic black soldier fly, *Hermetia illucens* (Diptera: Stratiomyidae) in Korea. *Korean Journal of Environment and Ecology* 31: 520-528. <https://doi.org/10.13047/kjee.2017.31.6.520>
- Park, S.I., Kim, J.W. and Yoe, S.M., 2015. Purification and characterization of a novel antibacterial peptide from black soldier fly (*Hermetia illucens*) larvae. *Developmental and Comparative Immunology* 52: 98-106. <https://doi.org/10.1016/j.dci.2015.04.018>
- Pashley, D.P., 1988. Current status of fall armyworm host strains. *Florida Entomologist* 71: 227-234.
- Perez-Sato, J.A., Chaline, N., Martin, S.J., Hughes, W.O. and Ratnieks, F.L., 2009. Multi-level selection for hygienic behaviour in honeybees. *Heredity* 102: 609-615. <https://doi.org/10.1038/hdy.2009.20>
- Petitpierre, E., Gatewood, J. and Schmid, C., 1988. Satellite DNA from the beetle *Tenebrio molitor*. *Experientia* 44: 498-499.
- Pianka, E.R., 1970. On R- and K-selection. *American Naturalist* 104: 592-597.
- Poveda, J., Jiménez-Gómez, A., Saati-Santamaría, Z., Usategui-Martín, R., Rivas, R. and García-Fraile, P., 2019. Mealworm frass as a potential biofertilizer and abiotic stress tolerance-inductor in plants. *Applied Soil Ecology* 142: 110-122.
- Prabhakar, S., Chen, M.S., Elpidina, E., Vinokurov, K., Smith, C., Marshall, J. and Oppert, B., 2007. Sequence analysis and molecular characterization of larval midgut cDNA transcripts encoding peptidases from the yellow mealworm, *Tenebrio molitor* L. *Insect Molecular Biology* 16: 455-468.
- Pradeep, A.R., Chatterjee, S.N. and Nair, C.V., 2005. Genetic differentiation induced by selection in an inbred population of the silkworm *Bombyx mori*, revealed by RAPD and ISSR marker systems. *Journal of Applied Genetics* 46: 291.
- Przemieniecki, S.W., Kosewska, A., Ciesielski, S. and Kosewska, O., 2020. Changes in the gut microbiome and enzymatic profile of *Tenebrio molitor* larvae biodegrading cellulose, polyethylene and polystyrene waste. *Environmental Pollution* 256: 113265. <https://doi.org/10.1016/j.envpol.2019.113265>
- Quezada-Euán, J.J.G., Echazarreta, C.M. and Paxton, R.J., 1996. The distribution and range expansion of Africanized honey bees (*Apis mellifera*) in the state of Yucatan, Mexico. *Journal of Apicultural Research* 35: 85-95. <https://doi.org/10.1080/00218839.1996.11100917>
- Rahmathulla, V.K., 2012. Management of climatic factors for successful silkworm (*Bombyx mori* L.) crop and higher silk production: a review. *Psyche: A Journal of Entomology* 2012: Article ID 121234. <https://doi.org/10.1155/2012/121234>

- Ran, F.A., Hsu, P.D., Wright, J., Agarwala, V., Scott, D.A. and Zhang, F., 2013. Genome engineering using the CRISPR-Cas9 system. *Nature Protocols* 8: 2281-2308. <https://doi.org/10.1038/nprot.2013.143>
- Rehman, K.u., Rehman, A., Cai, M., Zheng, L., Xiao, X., Somroo, A.A., Wang, H., Li, W., Yu, Z. and Zhang, J., 2017. Conversion of mixtures of dairy manure and soybean curd residue by black soldier fly larvae (*Hermetia illucens* L.). *Journal of Cleaner Production* 154: 366-373. <https://doi.org/10.1016/j.jclepro.2017.04.019>
- Rhode, C., Badenhorst, R., Hull, K.L., Greenwood, M.P., Bester-van der Merwe, A.E., Andere, A.A., Picard, C.J. and Richards, C., 2020. Genetic and phenotypic consequences of early domestication in black soldier flies (*Hermetia illucens*). *Animal Genetics* 51: 752-762. <https://doi.org/10.1111/age.12961>
- Ribeiro, N., Abelho, M. and Costa, R., 2018. A review of the scientific literature for optimal conditions for mass rearing *Tenebrio molitor* (Coleoptera: Tenebrionidae). *Journal of Entomological Science* 53: 434-454.
- Rimoldi, S., Gini, E., Iannini, F., Gasco, L. and Terova, G., 2019. The effects of dietary insect meal from *Hermetia illucens* prepupae on autochthonous gut microbiota of rainbow trout (*Oncorhynchus mykiss*). *Animals* 9(4): 143. <https://doi.org/10.3390/ani9040143>
- Ross-Ibarra, J., Morrell, P.L. and Gaut, B.S., 2007. Plant domestication, a unique opportunity to identify the genetic basis of adaptation. *Proceedings of the National Academy of Sciences* 104 Suppl 1: 8641-8648. <https://doi.org/10.1073/pnas.0700643104>
- Ruiz, X. and Almanza, M., 2018. Implications of genetic diversity in the improvement of silkworm *Bombyx mori* L. *Chilean journal of agricultural research* 78: 569-579. <https://doi.org/10.4067/s0718-58392018000400569>
- Russo, J., Brehelin, M. and Carton, Y., 2001. Haemocyte changes in resistant and susceptible strains of *D. melanogaster* caused by virulent and avirulent strains of the parasitic wasp *Leptopilina boulardi*. *Journal of Insect Physiology* 47: 167-172.
- Ryder, J. and Siva-Jothy, M., 2001. Quantitative genetics of immune function and body size in the house cricket, *Acheta domesticus*. *Journal of Evolutionary Biology* 14: 646-653.
- Schiavone, A., Cullere, M., De Marco, M., Meneguz, M., Biasato, I., Bergagna, S., Dezzutto, D., Gai, F., Dabbou, S., Gasco, L. and Dalle Zotte, A., 2017. Partial or total replacement of soybean oil by black soldier fly larvae (*Hermetia illucens* L.) fat in broiler diets: effect on growth performances, feed-choice, blood traits, carcass characteristics and meat quality. *Italian Journal of Animal Science* 16: 93-100. <https://doi.org/10.1080/1828051x.2016.1249968>
- Schwenke, R.A., Lazzaro, B.P. and Wolfner, M.F., 2016. Reproduction-immunity trade-offs in insects. *Annual Review of Entomology* 61: 239-256. <https://doi.org/10.1146/annurev-ento-010715-023924>
- Scott Schneider, S., DeGrandi-Hoffman, G. and Smith, D.R., 2004. The African honey bee: factors contributing to a successful biological invasion. *Annual Review of Entomology* 49: 351-376. <https://doi.org/10.1146/annurev.ento.49.061802.123359>
- Seeley, T.D. and Tarpay, D.R., 2007. Queen promiscuity lowers disease within honeybee colonies. *Proceedings of the Royal Society B: Biological Sciences* 274: 67-72.
- Seong, K.M., Mittapalli, O., Clark, J.M. and Pittendrigh, B.R., 2019. A review of DDT resistance as it pertains to the 91-C and 91-R strains in *Drosophila melanogaster*. *Pesticide Biochemistry and Physiology* 161: 86-94. <https://doi.org/10.1016/j.pestbp.2019.06.003>
- Sevala, V., Sevala, V. and Loughton, B., 1993. Insulin-like molecules in the beetle *Tenebrio molitor*. *Cell and tissue research* 273: 71-77.
- Shekar, K.C. and Basavaraja, H., 2008. Changes in qualitative and quantitative characters in bivoltine silkworm breeds of *Bombyx mori* L. under different selection methods. *Indian Journal of Sericulture* 47: 175-182.
- Sheppard, C., 1983. House fly and lesser fly control utilizing the black soldier fly in manure management systems for caged laying hens. *Environmental entomology* 12: 1439-1442.
- Sheppard, D.C., Newton, G.L., Thompson, S.A. and Savage, S., 1994. A value added manure management system using the black soldier fly. *Bioresource technology* 50: 275-279.
- Sheppard, D.C., Tomberlin, J.K., Joyce, J.A., Kiser, B.C. and Sumner, S.M., 2002. Rearing methods for the black soldier fly (Diptera: Stratiomyidae). *Journal of Medical Entomology* 39: 695-698.
- Sheppard, W.S. and Meixner, M.D., 2003. *Apis mellifera pomonella*, a new honey bee subspecies from Central Asia. *Apidologie* 34: 367-375. <https://doi.org/10.1051/apido:2003037>
- Simmonds, F., 1947. Improvement of the sex-ratio of a parasite by selection. *The Canadian Entomologist* 79: 41-44.
- Singh, T., Bhat, M.M. and Khan, M.A., 2011. Critical analysis of correlation and heritability phenomenon in the silkworm, *Bombyx mori*; (Lepidoptera: Bombycidae). *Advances in Bioscience and Biotechnology* 02: 347-353. <https://doi.org/10.4236/abb.2011.25051>
- Smith, J.M. and Haigh, J., 1974. The hitch-hiking effect of a favourable gene. *Genetics Research* 23: 23-35.
- Solignac, M., Vautrin, D., Loiseau, A., Mougel, F., Baudry, E., Estoup, A., Garnery, L., Haberl, M. and Cornuet, J.-M., 2003. Five hundred and fifty microsatellite markers for the study of the honeybee (*Apis mellifera* L.) genome. *Molecular Ecology Notes* 3: 307-311. <https://doi.org/10.1046/j.1471-8286.2003.00436.x>
- Sorati, M., Newman, M. and Hoffman, A.A., 1996. Inbreeding and incompatibility in *Trichogramma nr. brassicae*: evidence and implications for quality control. *Entomologia experimentalis et applicata* 78: 283-290.
- Sørensen, J.G., Addison, M.F. and Terblanche, J.S., 2012. Mass-rearing of insects for pest management: challenges, synergies and advances from evolutionary physiology. *Crop Protection* 38: 87-94.
- Southwick, E.E. and Southwick Jr, L., 1992. Estimating the economic value of honey bees (Hymenoptera: Apidae) as agricultural pollinators in the United States. *Journal of economic entomology* 85: 621-633.
- Spötter, A., Gupta, P., Mayer, M., Reinsch, N. and Bienefeld, K., 2016. Genome-wide association study of a *Varroa*-specific defense behavior in honeybees (*Apis mellifera*). *Journal of Heredity* 107: 220-227.
- Srikanth, K., Park, J.E., Lim, D., Cha, J., Cho, S.R., Cho, I.C. and Park, W., 2020. A comparison between hi-C and 10X genomics linked read sequencing for whole genome phasing in Hanwoo cattle. *Genes* 11: 332. <https://doi.org/10.3390/genes11030332>

- Srivastava, S., Srikanth, K., Won, S., Son, J.H., Park, J.E., Park, W., Chai, H.H. and Lim, D., 2020. Haplotype-based genome-wide association study and identification of candidate genes associated with carcass traits in Hanwoo cattle. *Genes* 11: 551. <https://doi.org/10.3390/genes11050551>
- Stahls, G., Meier, R., Sandrock, C., Hauser, M., Sasic Zoric, L., Laiho, E., Aracil, A., Doderovic, J., Badenhorst, R., Unadirekku, P., Mohd Adom, N.A.B., Wein, L., Richards, C., Tomberlin, J.K., Rojo, S., Veselic, S. and Parviainen, T., 2020. The puzzling mitochondrial phylogeography of the black soldier fly (*Hermetia illucens*), the commercially most important insect protein species. *BMC Evolutionary Biology* 20: 60. <https://doi.org/10.1186/s12862-020-01627-2>
- Stearns, S.C., 2000. Life history evolution: successes, limitations, and prospects. *Naturwissenschaften* 87: 476-486. <https://doi.org/10.1007/s001140050763>
- Sun, D., Guo, Z., Liu, Y. and Zhang, Y., 2017. Progress and prospects of CRISPR/Cas systems in insects and other arthropods. *Frontiers in physiology* 8: 608.
- Tabashnik, B.E., Van Rensburg, J. and Carrière, Y., 2009. Field-evolved insect resistance to *Bt* crops: definition, theory, and data. *Journal of economic entomology* 102: 2011-2025.
- Tanaka, Y., 1953. Genetics of the silkworm, *Bombyx mori*. *Advances in Genetics* 5: 239-317. [https://doi.org/10.1016/S0065-2660\(08\)60409-5](https://doi.org/10.1016/S0065-2660(08)60409-5)
- Tennis, P., 1985. Long-term divergence in body size produced by food size in laboratory populations of *Acheta domesticus* (Orthoptera: Gryllidae). *Canadian Journal of Zoology* 63: 1395-1401.
- The Bovine Genome Sequencing and Analysis Consortium, Elsik, C.G., Tellam, R.L., Worley, K.C., Gibbs, R.A., Muzny, D.M., Weinstock, G.M., Adelson, D.L., Eichler, E.E., Elnitski, L., Guigo, R., Hamernik, D.L., Kappes, S.M., Lewin, H.A., Lynn, D.J., Nicholas, F.W., Raymond, A., Rijkens, M., Skow, L.C., Zdobnov, E.M., Schook, L., Womack, J., Alioto, T., Antonarakis, S.E., Astashyn, A., Chapple, C.E., Chen, H.C., Chrast, J., Camara, F., Ermolaeva, O., Henrichsen, C.N., Hlavina, W., Kapustin, Y., Kiryutin, B., Kitts, P., Kokocinski, F., Landrum, M., Maglott, D., Pruitt, K., Sapojnikov, V., Searle, S.M., Solovyev, V., Souvorov, A., Ucla, C., Wyss, C., Anzola, J.M., Gerlach, D., Elhaik, E., Graur, D., Reese, J.T., Edgar, R.C., McEwan, J.C., Payne, G.M., Raison, J.M., Junier, T., Kriventseva, E.V., Eyas, E., Plass, M., Donthu, R., Larkin, D.M., Reecy, J., Yang, M.Q., Chen, L., Cheng, Z., Chitko-McKown, C.G., Liu, G.E., Matukumalli, L.K., Song, J., Zhu, B., Bradley, D.G., Brinkman, F.S., Lau, L.P., Whiteside, M.D., Walker, A., Wheeler, T.T., Casey, T., German, J.B., Lemay, D.G., Maqbool, N.J., Molenaar, A.J., Seo, S., Stothard, P., Baldwin, C.L., Baxter, R., Brinkmeyer-Langford, C.L., Brown, W.C., Childers, C.P., Connelley, T., Ellis, S.A., Fritz, K., Glass, E.J., Herzig, C.T., Iivanainen, A., Lahmers, K.K., Bennett, A.K., Dickens, C.M., Gilbert, J.G., Hagen, D.E., Salih, H., Aerts, J., Caetano, A.R., Dalrymple, B., Garcia, J.F., Gill, C.A., Hiendler, S.G., Memili, E., Spurlock, D., Williams, J.L., Alexander, L., Brownstein, M.J., Guan, L., Holt, R.A., Jones, S.J., Marra, M.A., Moore, R., Moore, S.S., Roberts, A., Taniguchi, M., Waterman, R.C., Chacko, J., Chandrabose, M.M., Cree, A., Dao, M.D., Dinh, H.H., Gabisi, R.A., Hines, S., Hume, J., Jhangiani, S.N., Joshi, V., Kovar, C.L., Lewis, L.R., Liu, Y.S., Lopez, J., Morgan, M.B., Nguyen, N.B., Okwuonu, G.O., Ruiz, S.J., Santibanez, J., Wright, R.A., Buhay, C., Ding, Y., Dugan-Rocha, S., Herdandez, J., Holder, M., Sabo, A., Egan, A., Goodell, J., Wilczek-Boney, K., Fowler, G.R., Hitchens, M.E., Lozado, R.J., Moen, C., Steffen, D., Warren, J.T., Zhang, J., Chiu, R., Schein, J.E., Durbin, K.J., Havlak, P., Jiang, H., Liu, Y., Qin, X., Ren, Y., Shen, Y., Song, H., Bell, S.N., Davis, C., Johnson, A.J., Lee, S., Nazareth, L.V., Patel, B.M., Pu, L.L., Vattathil, S., Williams, R.L., Jr, Curry, S., Hamilton, C., Sodergren, E., Wheeler, D.A., Barris, W., Bennett, G.L., Eggen, A., Green, R.D., Harhay, G.P., Hobbs, M., Jann, O., Keele, J.W., Kent, M.P., Lien, S., McKay, S.D., McWilliam, S., Ratnakumar, A., Schnabel, R.D., Smith, T., Snelling, W.M., Sonstegard, T.S., Stone, R.T., Sugimoto, Y., Takasuga, A., Taylor, J.F., Van Tassell, C.P., Macneil, M.D., Abatepaulo, A.R., Abbey, C.A., Ahola, V., Almeida, I.G., Amadio, A.F., Anatriello, E., Bahadue, S.M., Biase, F.H., Boldt, C.R., Carroll, J.A., Carvalho, W.A., Cervelatti, E.P., Chacko, E., Chapin, J.E., Cheng, Y., Choi, J., Colley, A.J., de Campos, T.A., De Donato, M., Santos, I.K., de Oliveira, C.J., Deobald, H., Devinoy, E., Donohue, K.E., Dovc, P., Eberlein, A., Fitzsimmons, C.J., Franzin, A.M., Garcia, G.R., Genini, S., Gladney, C.J., Grant, J.R., Greaser, M.L., Green, J.A., Hadsell, D.L., Hakimov, H.A., Halgren, R., Harrow, J.L., Hart, E.A., Hastings, N., Hernandez, M., Hu, Z.L., Ingham, A., Iso-Touru, T., Jamis, C., Jensen, K., Kapetis, D., Kerr, T., Khalil, S.S., Khatib, H., Kolbehdari, D., Kumar, C.G., Kumar, D., Leach, R., Lee, J.C., Li, C., Logan, K.M., Malinverni, R., Marques, E., Martin, W.F., Martins, N.F., Maruyama, S.R., Mazza, R., McLean, K.L., Medrano, J.F., Moreno, B.T., More, D.D., Muntean, C.T., Nandakumar, H.P., Nogueira, M.F., Olsaker, I., Pant, S.D., Panzitta, F., Pastor, R.C., Poli, M.A., Poslusny, N., Rachagani, S., Ranganathan, S., Razpet, A., Riggs, P.K., Rincon, G., Rodriguez-Osorio, N., Rodriguez-Zas, S.L., Romero, N.E., Rosenwald, A., Sando, L., Schmutz, S.M., Shen, L., Sherman, L., Southey, B.R., Lutzow, Y.S., Sweedler, J.V., Tammen, I., Telugu, B.P., Urbanski, J.M., Utsunomiya, Y.T., Verschoor, C.P., Waardenberg, A.J., Wang, Z., Ward, R., Weikard, R., Welsh, T.H., Jr, White, S.N., Wilming, L.G., Wunderlich, K.R., Yang, J. and Zhao, F.Q., 2009. The genome sequence of taurine cattle: a window to ruminant biology and evolution. *Science* 324: 522-528. <https://doi.org/10.1126/science.1169588>
- The Honeybee Genome Sequencing Consortium, 2006. Insights into social insects from the genome of the honeybee *Apis mellifera*. *Nature* 443: 931.
- The International Silkworm Genome Consortium, 2008. The genome of a lepidopteran model insect, the silkworm *Bombyx mori*. *Insect biochemistry and molecular biology* 38: 1036-1045.
- Tribolium* Genome Sequencing Consortium, Richards, S., Gibbs, R.A., Weinstock, G.M., Brown, S.J., Denell, R., Beeman, R.W., Gibbs, R., Beeman, R.W., Brown, S.J., Bucher, G., Friedrich, M., Grimmekhuijzen, C.J., Klingler, M., Lorenzen, M., Richards, S., Roth, S., Schroder, R., Tautz, D., Zdobnov, E.M., Muzny, D., Gibbs, R.A., Weinstock, G.M., Attaway, T., Bell, S., Buhay, C.J., Chandrabose, M.N., Chavez, D., Clerk-Blankenburg, K.P., Cree, A., Dao, M., Davis, C., Chacko, J., Dinh, H., Dugan-Rocha, S., Fowler, G., Garner, T.T., Garnes, J., Gnirke, A., Hawes, A., Hernandez, J., Hines, S., Holder, M., Hume, J., Jhangiani, S.N., Joshi, V., Khan, Z.M., Jackson, L., Kovar, C., Kowis, A., Lee, S., Lewis, L.R., Margolis, J., Morgan, M., Nazareth, L.V., Nguyen, N., Okwuonu, G., Parker, D., Richards, S., Ruiz, S.J., Santibanez, J., Savard, J., Scherer, S.E.,

- Schneider, B., Sodergren, E., Tautz, D., Vattahil, S., Villasana, D., White, C.S., Wright, R., Park, Y., Beeman, R.W., Lord, J., Oppert, B., Lorenzen, M., Brown, S., Wang, L., Savard, J., Tautz, D., Richards, S., Weinstock, G., Gibbs, R.A., Liu, Y., Worley, K., Weinstock, G., Elsik, C.G., Reese, J.T., Elhaik, E., Landan, G., Graur, D., Arensburger, P., Atkinson, P., Beeman, R.W., Beidler, J., Brown, S.J., Demuth, J.P., Drury, D.W., Du, Y.Z., Fujiwara, H., Lorenzen, M., Maselli, V., Osanai, M., Park, Y., Robertson, H.M., Tu, Z., Wang, J.J., Wang, S., Richards, S., Song, H., Zhang, L., Sodergren, E., Werner, D., Stanke, M., Morgenstern, B., Solovoyev, V., Kosarev, P., Brown, G., Chen, H.C., Ermolaeva, O., Hlavina, W., Kapustin, Y., Kiryutin, B., Kitts, P., Maglott, D., Pruitt, K., Sapojnikov, V., Souvorov, A., Mackey, A.J., Waterhouse, R.M., Wyder, S., Zdobnov, E.M., Zdobnov, E.M., Wyder, S., Kriventseva, E.V., Kadowaki, T., Bork, P., Aranda, M., Bao, R., Beerhmann, A., Berns, N., Bolognesi, R., Bonneton, F., Bopp, D., Brown, S.J., Bucher, G., Butts, T., Chaumot, A., Denell, R.E., Ferrier, D.E., Friedrich, M., Gordon, C.M., Jindra, M., Klingler, M., Lan, Q., Lattorff, H.M., Laudet, V., von Levetzow, C., Liu, Z., Lutz, R., Lynch, J.A., da Fonseca, R.N., Posnien, N., Reuter, R., Roth, S., Savard, J., Schinko, J.B., Schmitt, C., Schoppmeier, M., Schroder, R., Shippy, T.D., Simonnet, F., Marques-Souza, H., Tautz, D., Tomoyasu, Y., Trauner, J., Van der Zee, M., Vervoort, M., Wittkopp, N., Wimmer, E.A., Yang, X., Jones, A.K., Sattelle, D.B., Ebert, P.R., Nelson, D., Scott, J.G., Beeman, R.W., Muthukrishnan, S., Kramer, K.J., Arakane, Y., Beeman, R.W., Zhu, Q., Hogenkamp, D., Dixit, R., Oppert, B., Jiang, H., Zou, Z., Marshall, J., Elpidina, E., Vinokurov, K., Oppert, C., Zou, Z., Evans, J., Lu, Z., Zhao, P., Sumathipala, N., Altincicek, B., Vilcinskis, A., Williams, M., Hultmark, D., Hetru, C., Jiang, H., Grimmelikhuijzen, C.J., Hauser, F., Cazzamali, G., Williamson, M., Park, Y., Li, B., Tanaka, Y., Predel, R., Neupert, S., Schachtner, J., Verleyen, P., Raible, F., Bork, P., Friedrich, M., Walden, K.K., Robertson, H.M., Angeli, S., Foret, S., Bucher, G., Schuetz, S., Maleszka, R., Wimmer, E.A., Beeman, R.W., Lorenzen, M., Tomoyasu, Y., Miller, S.C., Grossmann, D. and Bucher, G., 2008. The genome of the model beetle and pest *Tribolium castaneum*. *Nature* 452: 949-955. <https://doi.org/10.1038/nature06784>
- Tschirner, M. and Simon, A., 2015. Influence of different growing substrates and processing on the nutrient composition of black soldier fly larvae destined for animal feed. *Journal of Insects as Food and Feed* 1: 249-259. <https://doi.org/10.3920/jiff2014.0008>
- Turnbull, A.L. and Chant, D.A., 1961. The practice and theory of biological control of insects in Canada. *Canadian Journal of Zoology* 39: 697-753.
- Urs, K. and Hopkins, T., 1973. Effect of moisture on growth rate and development of two strains of *Tenebrio molitor* L. (Coleoptera, Tenebrionidae). *Journal of Stored Products Research* 8: 291-297.
- Uzunov, A., Brascamp, E.W. and Büchler, R., 2017. The basic concept of honey bee breeding programs. *Bee World* 94: 84-87. <https://doi.org/10.1080/0005772x.2017.1345427>
- Van Bergeijk, K., Bigler, F., Kaashoek, N. and Pak, G., 1989. Changes in host acceptance and host suitability as an effect of rearing *Trichogramma maidis* on a factitious host. *Entomologia Experimentalis et Applicata* 52: 229-238.
- Van Broekhoven, S., Gutierrez, J.M., De Rijk, T., De Nijs, W. and Van Loon, J.J.A., 2017. Degradation and excretion of the *Fusarium* toxin deoxynivalenol by an edible insect, the yellow mealworm (*Tenebrio molitor* L.). *World Mycotoxin Journal* 10: 163-169. <https://doi.org/10.3920/WMJ2016.2102>
- Van Den Bosch, R. and Messenger, P., 1973. Entomophagous insects. Biological control. Intext Press, Inc., New York, NY, USA, pp. 35-47.
- Van Huis, A., 2013. Potential of insects as food and feed in assuring food security. *Annual Review of Entomology* 58: 563-583. <https://doi.org/10.1146/annurev-ento-120811-153704>
- Van Huis, A., Dicke, M. and Van Loon, J.J.A., 2015. Insects to feed the world. *Journal of Insects as Food and Feed* 1: 3-5. <https://doi.org/10.3920/JIFF2015.x002>
- Van Lenteren, J.C. and Nicoli, G., 2004. Quality control of mass produced beneficial insects. In: Heinz, R., Van Driesche, R. and Parrella, M.P. (eds) Biological control of arthropod pests in protected cultures. Ball Publishing, Batavia, IL, USA, pp 503-526.
- Varotto Boccazzi, I., Ottoboni, M., Martin, E., Comandatore, F., Vallone, L., Spranghers, T., Eeckhout, M., Mereghetti, V., Pinotti, L. and Epis, S., 2017. A survey of the mycobiota associated with larvae of the black soldier fly (*Hermetia illucens*) reared for feed production. *PLoS ONE* 12: e0182533. <https://doi.org/10.1371/journal.pone.0182533>
- Veldkamp, T. and Bosch, G., 2015. Insects: a protein-rich feed ingredient in pig and poultry diets. *Animal Frontiers* 5: 45-50.
- Venter, J.C., Adams, M.D., Myers, E.W., Li, P.W., Mural, R.J., Sutton, G.G., Smith, H.O., Yandell, M., Evans, C.A., Holt, R.A., Gocayne, J.D., Amanatides, P., Ballew, R.M., Huson, D.H., Wortman, J.R., Zhang, Q., Kodira, C.D., Zheng, X.H., Chen, L., Skupski, M., Subramanian, G., Thomas, P.D., Zhang, J., Gabor Miklos, G.L., Nelson, C., Broder, S., Clark, A.G., Nadeau, J., McKusick, V.A., Zinder, N., Levine, A.J., Roberts, R.J., Simon, M., Slayman, C., Hunkapiller, M., Bolanos, R., Delcher, A., Dew, I., Fasulo, D., Flanigan, M., Florea, L., Halpern, A., Hannenhalli, S., Kravitz, S., Levy, S., Mobarry, C., Reinert, K., Remington, K., Abu-Threideh, J., Beasley, E., Biddick, K., Bonazzi, V., Brandon, R., Cargill, M., Chandramouliswaran, I., Charlab, R., Chaturvedi, K., Deng, Z., Di Francesco, V., Dunn, P., Eilbeck, K., Evangelista, C., Gabrielian, A.E., Gan, W., Ge, W., Gong, F., Gu, Z., Guan, P., Heiman, T.J., Higgins, M.E., Ji, R.R., Ke, Z., Ketchum, K.A., Lai, Z., Lei, Y., Li, Z., Li, J., Liang, Y., Lin, X., Lu, F., Merkulov, G.V., Milshina, N., Moore, H.M., Naik, A.K., Narayan, V.A., Neelam, B., Nusskern, D., Rusch, D.B., Salzberg, S., Shao, W., Shue, B., Sun, J., Wang, Z., Wang, A., Wang, X., Wang, J., Wei, M., Wides, R., Xiao, C., Yan, C., Yao, A., Ye, J., Zhan, M., Zhang, W., Zhang, H., Zhao, Q., Zheng, L., Zhong, F., Zhong, W., Zhu, S., Zhao, S., Gilbert, D., Baumhueter, S., Spier, G., Carter, C., Cravchik, A., Woodage, T., Ali, F., An, H., Awe, A., Baldwin, D., Baden, H., Barnstead, M., Barrow, I., Beeson, K., Busam, D., Carver, A., Center, A., Cheng, M.L., Curry, L., Danaher, S., Davenport, L., Desilets, R., Dietz, S., Dodson, K., Doup, L., Ferriera, S., Garg, N., Gluecksmann, A., Hart, B., Haynes, J., Haynes, C., Heiner, C., Hladun, S., Hostin, D., Houck, J., Howland, T., Ibegwam, C., Johnson, J., Kalush, F., Kline, L., Koduru, S., Love, A., Mann, F., May, D., McCawley, S., McIntosh, T., McMullen, L., Moy, M., Moy, L., Murphy, B., Nelson, K., Pfannkoch, C., Pratts, E., Puri, V., Qureshi, H., Reardon, M., Rodriguez, R., Rogers, Y.H., Romblad, D., Ruhfel, B., Scott, R., Sitter, C., Smallwood, M., Stewart,

- E., Strong, R., Suh, E., Thomas, R., Tint, N.N., Tse, S., Vech, C., Wang, G., Wetter, J., Williams, S., Williams, M., Windsor, S., Winn-Deen, E., Wolfe, K., Zaveri, J., Zaveri, K., Abril, J.F., Guigo, R., Campbell, M.J., Sjolander, K.V., Karlak, B., Kejariwal, A., Mi, H., Lazareva, B., Hatton, T., Narechania, A., Diemer, K., Muruganujan, A., Guo, N., Sato, S., Bafna, V., Istrail, S., Lippert, R., Schwartz, R., Walenz, B., Yooseph, S., Allen, D., Basu, A., Baxendale, J., Blick, L., Caminha, M., Carnes-Stine, J., Caulk, P., Chiang, Y.H., Coyne, M., Dahlke, C., Mays, A., Dombroski, M., Donnelly, M., Ely, D., Esparham, S., Fosler, C., Gire, H., Glanowski, S., Glasser, K., Glodek, A., Gorokhov, M., Graham, K., Gropman, B., Harris, M., Heil, J., Henderson, S., Hoover, J., Jennings, D., Jordan, C., Jordan, J., Kasha, J., Kagan, L., Kraft, C., Levitsky, A., Lewis, M., Liu, X., Lopez, J., Ma, D., Majoros, W., McDaniel, J., Murphy, S., Newman, M., Nguyen, T., Nguyen, N., Nodell, M., Pan, S., Peck, J., Peterson, M., Rowe, W., Sanders, R., Scott, J., Simpson, M., Smith, T., Sprague, A., Stockwell, T., Turner, R., Venter, E., Wang, M., Wen, M., Wu, D., Wu, M., Xia, A., Zandieh, A. and Zhu, X., 2001. The sequence of the human genome. *Science* 291: 1304-1351. <https://doi.org/10.1126/science.1058040>
- Vigneron, A., Jehan, C., Rigaud, T. and Moret, Y., 2019. Immune defenses of a beneficial pest: the mealworm beetle, *Tenebrio molitor*. *Frontiers in Physiology* 10: 138. <https://doi.org/10.3389/fphys.2019.00138>
- Wallberg, A., Glemin, S. and Webster, M.T., 2015. Extreme recombination frequencies shape genome variation and evolution in the honeybee, *Apis mellifera*. *PLoS Genetics* 11: e1005189. <https://doi.org/10.1371/journal.pgen.1005189>
- Wang, Y.S. and Shelomi, M., 2017. Review of black soldier fly (*Hermetia illucens*) as animal feed and human food. *Foods* 6(10): 91. <https://doi.org/10.3390/foods6100091>
- Wei, W., Xin, H., Roy, B., Dai, J., Miao, Y. and Gao, G., 2014. Heritable genome editing with CRISPR/Cas9 in the silkworm, *Bombyx mori*. *PLoS ONE* 9: e101210. <https://doi.org/10.1371/journal.pone.0101210>
- Wen, H., Lan, X., Zhang, Y., Zhao, T., Wang, Y., Kajiura, Z. and Nakagaki, M., 2010. Transgenic silkworms (*Bombyx mori*) produce recombinant spider dragline silk in cocoons. *Molecular biology reports* 37: 1815-1821.
- Werren, J.H., Baldo, L. and Clark, M.E., 2008. *Wolbachia*: master manipulators of invertebrate biology. *Nature Reviews Microbiology* 6: 741-751. <https://doi.org/10.1038/nrmicro1969>
- Werren, J.H. and Windsor, D.M., 2000. *Wolbachia* infection frequencies in insects: evidence of a global equilibrium? *Proceedings of the Royal Society B: Biological Sciences* 267: 1277-1285. <https://doi.org/10.1098/rspb.2000.1139>
- White, E.B., Debach, P. and Garber, M.J., 1970. Artificial selection for genetic adaptation to temperature extremes in *Aphytis lingnanensis* Compere (Hymenoptera: Aphelinidae). *Hilgardia* 40: 161-192.
- Wilkes, A., 1942. The influence of selection on the preferendum of a chalcid (*Microplectron fuscipennis* Zett.) and its significance in the biological control of an insect pest. *Proceedings of the Royal Society of London. Series B-Biological Sciences* 130: 400-415.
- Wilkes, A., 1947. The effects of selective breeding on the laboratory propagation of insect parasites. *Proceedings of the Royal Society of London. Series B-Biological Sciences* 134: 227-245.
- Wilkes, A., Pielou, D. and Glasser, R., 1952. Selection for DDT tolerance in a beneficial insect. In: *Conference on Insecticide Resistance and Insect Physiology*, December 8-9, 1951, University of Cincinnati. National Academy of Sciences, National Research Council, Vol. 219, pp. 78-81.
- Wilkie, R.M., 2018. 'Minilivestock' farming: who is farming edible insects in Europe and North America? *Journal of Sociology* 54: 520-537.
- Wilson, A.D.M., Whattam, E.M., Bennett, R., Visanuvimol, L., Lauzon, C. and Bertram, S.M., 2010. Behavioral correlations across activity, mating, exploration, aggression, and antipredator contexts in the European house cricket, *Acheta domesticus*. *Behavioral Ecology and Sociobiology* 64: 703-715. <https://doi.org/10.1007/s00265-009-0888-1>
- Winston, M.L. and Katz, S.J., 1982. Foraging differences between cross-fostered honeybee workers (*Apis mellifera*) of European and Africanized races. *Behavioral Ecology and Sociobiology* 10: 125-129.
- Worden, B.D. and Parker, P.G., 2001. Polyandry in grain beetles, *Tenebrio molitor*, leads to greater reproductive success: material or genetic benefits? *Behavioral Ecology* 12: 761-767.
- Xia, Q., Guo, Y., Zhang, Z., Li, D., Xuan, Z., Li, Z., Dai, F., Li, Y., Cheng, D. and Li, R., 2009. Complete resequencing of 40 genomes reveals domestication events and genes in silkworm (*Bombyx*). *Science* 326: 433-436.
- Xu, J., Chen, R.M., Chen, S.Q., Chen, K., Tang, L.M., Yang, D.H., Yang, X., Zhang, Y., Song, H.S. and Huang, Y.P., 2019. Identification of a germline-expression promoter for genome editing in *Bombyx mori*. *Insect Science* 26: 991-999. <https://doi.org/10.1111/1744-7917.12657>
- Xu, J., Dong, Q., Yu, Y., Niu, B., Ji, D., Li, M., Huang, Y., Chen, X. and Tan, A., 2018. Mass spider silk production through targeted gene replacement in *Bombyx mori*. *Proceedings of the National Academy of Sciences* 115: 8757-8762. <https://doi.org/10.1073/pnas.1806805115>
- Yang, S.S., Brandon, A.M., Andrew Flanagan, J.C., Yang, J., Ning, D., Cai, S.Y., Fan, H.Q., Wang, Z.Y., Ren, J., Benbow, E., Ren, N.Q., Waymouth, R.M., Zhou, J., Criddle, C.S. and Wu, W.M., 2018a. Biodegradation of polystyrene wastes in yellow mealworms (larvae of *Tenebrio molitor* Linnaeus): factors affecting biodegradation rates and the ability of polystyrene-fed larvae to complete their life cycle. *Chemosphere* 191: 979-989. <https://doi.org/10.1016/j.chemosphere.2017.10.117>
- Yang, S.S., Wu, W.M., Brandon, A.M., Fan, H.Q., Receveur, J.P., Li, Y., Wang, Z.Y., Fan, R., McClellan, R.L., Gao, S.H., Ning, D., Phillips, D.H., Peng, B.Y., Wang, H., Cai, S.Y., Li, P., Cai, W.W., Ding, L.Y., Yang, J., Zheng, M., Ren, J., Zhang, Y.L., Gao, J., Xing, D., Ren, N.Q., Waymouth, R.M., Zhou, J., Tao, H.C., Picard, C.J., Benbow, M.E. and Criddle, C.S., 2018b. Ubiquity of polystyrene digestion and biodegradation within yellow mealworms, larvae of *Tenebrio molitor* Linnaeus (Coleoptera: Tenebrionidae). *Chemosphere* 212: 262-271. <https://doi.org/10.1016/j.chemosphere.2018.08.078>
- Zatsepina, O.G., Velikodvorskaia, V.V., Molodtsov, V.B., Garbuz, D., Lerman, D.N., Bettencourt, B.R., Feder, M.E. and Evgenev, M.B., 2001. A *Drosophila melanogaster* strain from sub-equatorial Africa has exceptional thermotolerance but decreased Hsp70 expression. *Journal of Experimental Biology* 204: 1869-1881.

- Zhan, S., Fang, G., Cai, M., Kou, Z., Xu, J., Cao, Y., Bai, L., Zhang, Y., Jiang, Y., Luo, X., Xu, J., Xu, X., Zheng, L., Yu, Z., Yang, H., Zhang, Z., Wang, S., Tomberlin, J.K., Zhang, J. and Huang, Y., 2020. Genomic landscape and genetic manipulation of the black soldier fly *Hermetia illucens*, a natural waste recycler. *Cell Research* 30: 50-60. <https://doi.org/10.1038/s41422-019-0252-6>
- Zhou, F., Tomberlin, J.K., Zheng, L., Yu, Z. and Zhang, J., 2013. Developmental and waste reduction plasticity of three black soldier fly strains (Diptera: Stratiomyidae) raised on different livestock manures. *Journal of Medical Entomology* 50: 1224-1230. <https://doi.org/10.1603/me13021>
- Zhou, Z., Yang, H. and Zhong, B., 2008. From genome to proteome: great progress in the domesticated silkworm (*Bombyx mori* L.). *Acta Biochimica et Biophysica Sinica* 40: 601-611. <https://doi.org/10.1111/j.1745-7270.2008.00432.x>
- Zhu, Z., Rehman, K.U., Yu, Y., Liu, X., Wang, H., Tomberlin, J.K., Sze, S.H., Cai, M., Zhang, J., Yu, Z., Zheng, J. and Zheng, L., 2019. De novo transcriptome sequencing and analysis revealed the molecular basis of rapid fat accumulation by black soldier fly (*Hermetia illucens*, L.) for development of insectival biodiesel. *Biotechnology for Biofuels* 12: 194. <https://doi.org/10.1186/s13068-019-1531-7>