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SPECIAL ISSUE: INSECTS IN PRODUCTION

Insects in production – an introduction

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Abstract

Insects have been on the menu of humans for centuries, but only recently we have begun to mass produce them for human food and animal feed. This introduction first paints a synopsis of mass cultured insects and their application. The new insect production industry raises many interesting fundamental and applied questions about insect biology and fitness. The second part of the introduction to this special issue addresses the 13 articles dealing with the improvement of mass-rearing efforts for a range of insects. The various studies focus on the effects of diet and microorganisms on relevant life-history traits and economic value of the insects. They reflect the current rapid developments in the insect production industry.

Introduction

Insects have been on the menu for centuries, but only recently their mass production for human food and animal feed has started to take off. Both fundamental and applied research is of importance for mass production of insects. More general knowledge about insect biology is needed as basis for insect rearing. In addition, various applied aspects make research on production insects of particular interest. For instance, as production insects are typically bred in large numbers and under artificial conditions, much applied research focuses on traits related to their breeding efficacy and economic value. An important aim is how the culturing conditions can be optimized to gain maximum yield and quality of the insect products. For example, the effect of diet on the growth and health of the insect is receiving a lot of attention. Another research topic is the role of microorganisms, not just in terms of risk of infection and diseases, but also their potential benefit in the production process. The articles in this special journal issue address these and other topics in a variety of insect species that are in different phases of commercialization. Before considering these studies in more detail, we briefly inventory the most important commercial insect species and indicate for what purpose they are bred.

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Insects in production: an overview

Although contemporary agriculture is undergoing rapid technological development, worldwide insect farming is still largely manual and run by smallholder farmers (Kenis et al., 2018). Besides rearing for human consumption and for the animal food market, small-scale businesses involve production of fish baits, prey for insectivorous pets, medical applications, and culturing insects by hobbyists and for educational purposes. These operations require manual labour and contribute to local economies. In order to address scientific need, production of standardized insect models has been established in stock centres. For example, a broad range of wild-type and mutant strains of *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) can be purchased for research purposes, and more than 1 000 strains of silkworms are maintained at stock centres in silk-producing countries (Goldsmith et al., 2005). The increasing demand for large numbers of specimens led to up-scaling of insect breeding facilities and developing more efficient and economical production methods. One successful example are the 20 000 cricket farms in Thailand that increased their production capacities to medium and large scale (Hanboonsong et al., 2013). We currently witness an exponential growth in companies that establish standardized pipelines to mass produce insects for commercial use (Fanson et al., 2014; Orzoco-Dávila et al., 2017). Insect-based food and feed industry already produces tons of insects daily (van Huis, 2016), but the variety of insect species and their production amounts are expected to increase rapidly. These industrial-scale facilities present a constant and reliable source of insects.

Nutritional and other health benefits of edible insects have been documented by many authors (e.g., Di Mattia et al., 2019). As global interest in entomophagy is rising, the availability of products generated from the harvested insects is increasing as well. Crickets and mealworms are among the most commonly consumed taxa (Table 1), and their production operations range from small-scale 'subsistence' to large industrial factories (Oonincx & de Boer, 2012; Hanboonsong et al., 2013). Moreover, insects are increasingly considered as suitable protein source for incorporation into animal feed. Within the insect-as-feed sector, research and innovation efforts are mostly concentrated on the production of the black soldier fly (BSF), *Hermetia illucens* L. (Diptera: Stratiomyidae), at an industrial scale (Gobbi et al., 2013; Chia et al., 2018). In addition, technological and ecological aspects of waste processing by fly larvae and their commercial potential are receiving renewed interest (Barnard et al., 1998; Zhang et al., 2012; Wang et al., 2013). Use of larvae of BSF and the common housefly, *Musca domestica* L. (Diptera: Muscidae), to treat organic wastes or livestock manure is proposed as a promising and effective technology (Sheppard et al., 1994; Wang et al., 2013). As such, various approaches and rearing systems are being developed worldwide, ranging from small-scale rearing operations on locally available substrates (Koné et al., 2017; Mafwila et al., 2019), to large-scale composting systems with capacity of processing 35 tons of raw swine manure per day (Zhang et al., 2012).

Insects are not just bred for food and feed. Mass-rearing programmes have also been developed for sustainable pest management and release technologies. Both, government-owned production units and multinational agro-chemical companies are involved in the mass-rearing of biological control agents (van Lenteren et al., 2018). The history of commercial mass production of biocontrol agents spans a period of over 100 years (van Lenteren et al., 2018). A lot of research has been conducted and progress has been made on reducing the economic, health, and environmental risks while maximizing pest control. Over 6 000 introductions of more than 2 000 insect biological control agents have been carried out worldwide to control insect pests (Cock et al., 2016). Among them, Hymenoptera, Acari, and Coleoptera are the taxa most commonly produced and sold commercially (van Lenteren, 2012). Being predators of key pests in diverse crop systems, parasitoid wasps (Hymenoptera) in the families Aphelinidae, Trichogrammatidae, and Braconidae are mass reared globally (Wang et al., 2019). Flower bugs (Hemiptera: Anthocoridae) of the genera *Orius* and *Anthocoris* are mass produced as polyphagous predators that feed on a wide array of arthropod prey. The predatory mite species *Amblyseius swirskii* Athias-Henriot and *Neoseiulus cucumeris* (Oudemans) (both Acari: Phytoseiidae) are among the economically most important control agents (van Lenteren, 2012).

The sterile insect technique (SIT), which is based on mass release of factory-bred specimens, has proven successful for irradiating a range of insect pests. One of the best examples is the screwworm *Cochliomyia hominivorax* (Coquerel) (Diptera: Calliphoridae) that has been reared on a massive scale in Mexico since 1976. Additional examples of SIT success include the area-wide release of sterile fruit flies (Tephritidae), such as the Mexican fruit fly, *Anastrepha ludens* (Loew) (Rull et al., 2005) and the Mediterranean fruit fly, *Ceritatis capitata* (Wiedemann) (Robinson, 2002), mosquitoes, such as *Aedes aegypti* (L.) (Diptera: Culicidae) (Puggioli et al., 2013; Zheng et al., 2015), and tsetse flies (*Glossina* spp.) (Vreysen et al., 2000).

There are additional purposes for breeding insects, such as medical applications and other human benefits (Table 1). Although the European honey bee, *Apis mellifera* L. (Hymenoptera: Apidae), plays an important role in the food industry with the annual production of around 1.2 million tons of commercial honey (FAO, 2009), it is also managed for pollination service (Brittain et al., 2013). In addition, together with the common green bottle fly, *Lucilia sericata* (Meigen) (Diptera: Calliphoridae), and the American cockroach, *Periplaneta americana* (L.) (Blattodea: Blattidae), honey bees are examples of insects used in human therapy and cosmetics (Table 1). The domestic silk moth, *Bombyx mori* L. (Lepidoptera: Bombicidae), is one of the best known insects in production (van Huis, 2016). By controlled breeding and selection for beneficial production traits, production strains of *B. mori* became domesticated and entirely depended on humans for their survival and reproduction (International Silkworm Genome Consortium, 2008). Besides textile, silk moths provide humans with a variety of other valuable products such as paint, pharmaceuticals, soap, and bio-fuel (Trivedy et al., 2008).

Insects in production: this special issue

The articles presented in this special journal issue provide a snapshot of current research in commercial insect production. There are two main focuses: the role of abiotic factors, such as diet and temperature, and the role of the microbiome in raising various insect species.

Abiotic factors: diet and temperature

Insects have traditionally been part of human food and still make up a sizable component of the diet in some parts of

Table 1 Overview of insects in production

Purpose	Common name	Scientific name	Specifics	References
Food	European honey bee	*Apis mellifera* L.	Bee products such as honey, propolis, and pollen	Rinderer et al. (1985)
	Domestic house cricket Jamaican field cricket Two-spotted cricket Cambodian field cricket	*Acheta domesticus* (L.) *Gryllus assimilis* Fabricius *Gryllus bimaculatus* De Geer *Teleogryllus testaceus* (Walker)	Farmed on several continents for human consumption and as pet food	Finke (2002); Weissman et al. (2012); Hanboonsong et al. (2013); Caparros Megido et al. (2016)
	Palm weevil	*Rhynchophorus ferrugineus* (Olivier)	Reared mostly in regions where food sources (i.e., sago palm trees or lan phru trees) are available	Kaakeh et al. (2001); Hanboonsong et al. (2013)
	Yellow mealworm	*Tenebrio molitor* L.	Easy rearing requirements and high capacity in industrial-scale production	Ghaly & Alkoaik (2009); Oonincx & de Boer (2012)
Feed	Black soldier fly Common housefly Yellow mealworm Giant/ super mealworm	*Hermetia illucens* (L.) *Musca domestica* L. *T. molitor* *Zophobas morio* Fabricius	Larvae and pupae are a significant source of protein for livestock and pet feed	Finke (2002); van Huis (2016)
	Madagascar hissing cockroach	*Gromphadorhina portentosa* (Schaum)	Common feed for insectivorous pets	Oonincx & Dierenfeld (2012)
Industrial products	Domestic silk moth	*Bombyx mori* L.	The caterpillar is used in sericulture, larvae and pupae are used for industrial production of recombinant eukaryotic proteins and baculoviruses	Tomita et al. (2003); Motohashi et al. (2005)
	New World cochineal	*Dactylopius coccus* Costa	Production of carminic acid - colorant used in cosmetics, food, textile, and pharmaceuticals	Borges et al. (2012)
	Common Indian lac insect	*Kerria lacca* (Kerr)	Widely exploited for lac cultivation, used in production of wood polishes and finishes	Sharma et al. (2006)
Biological control – Augmentative approach	Greater wax moth	*Galleria mellonella* L.	Hosts or prey for mass-rearing parasitic and predaceous insects and entomopathogenic nematodes	Metwally et al. (2012)
	Fam. Aphelinidae Fam. Braconiadae	*Aphelinus abdominalis* (Dalman) *Eretmocerus eremicus* Rose & Zolnerowich *Encarsia formosa* Gahan *Aphidius colemani* Viereck *Dacnusa sibirica* Telenga	A selection of some of the most important parasitioid wasps - biocontrol agents of various species of aphids, mealybugs,	van Lenteren (2012); Wang et al. (2019)

Table 1 Continued

Purpose	Common name	Scientific name	Specifics	References
	Fam. Eulophidea	*Diglyphus isaea* (Walker)	whiteflies, leaf miners, moths, etc.	
	Fam. Trichogrammatidae	*Trichogramma evanescens* Westwood		
	Fam. Encyrtidae	*Anagyrus pseudococci* (Girault)		
	Fam. Pteromalidae	*Muscidifurax raptorellus* Kogan & Legner		
		Spalangia spp.		
	Two-spot ladybird	*Adalia bipunctata* (L.)	Some of the most common predators – biocontrol agents of agricultural insect pests and in livestock hygiene management, used against various species/life stages of aphids, thrips, leaf miners, mites, whiteflies, filth flies, lesser flies, etc.	Cock et al. (2016); Kenis et al. (2017); Cock (2019)
	Common flower bug	*Anthocoris nemoralis* (Fabricius)		
	Swirski mite	*Amblyseius swirskii* Athias-Henriot		
	Aphid midge	*Aphidoletes aphidimyza* (Rondani)		
	Common green lacewing	*Chrysoperla* carnea (Stephens)		
	Mealybug	*Cryptolaemus montrouzieri* Mulsant		
	Asian ladybeetle	*Harmonia axyridis* (Pallas)		
	Whitefly predatory ladybeetle	*Delphastus catalinae* (Horn)		
	–	*Macrolophus pygmaeus* (Rambur)		
	Pirate bug	*Orius laevigatus* (Fieber)		
	Soil-dwelling mite	*Stratiolaelaps scimitus* (Womersley)		
	Cucumeris mite	*Neoseiulus cucumeris* (Oudemans)		
Biological control - Sterile insect technique	New World screwworm	*Cochliomyia hominivorax* (Coquerel)	Larvae eat the living tissue of warm-blooded animals	Richardson et al. (1982); Vargas-Terán et al. (2005)
	Mediterranean fruit fly	*Ceratitis capitata* (Wiedemann)	One of the most destructive fruit pests	Robinson (2002)
	Melon fly	*Bactrocera cucurbitae* (Coquillett)	Major pest of cucurbitaceous vegetables	Koyama et al. (2004)
	Mexican fruit fly	*Anastrepha ludens* (Loew)	Major pest in citrus-producing areas	Rull et al. (2005)
	Codling moth	*Cydia pomonella* (L.)	Major pest of apples and pears	Hansen & Anderson (2006)
	Pink bollworm	*Pectinophora gossypiella* (Saunders)	Major pest in cotton-growing areas	Henneberry (2007)
	Tsetse flies	*Glossina* spp.	Vectors of human and animal trypanosomiasis throughout sub-Saharan Africa	Vreysen et al. (2000)
	Yellow fever mosquito	*Aedes aegypti* (L.)	Vectors of several arboviruses including dengue and chikungunya	Puggioli et al. (2013); Zheng et al. (2015)
	Tiger mosquito	*Aedes albopictus* (Skuse)		

Table 1 Continued

Purpose	Common name	Scientific name	Specifics	References
Waste management	Common housefly Black soldier fly	*M. domestica* *H. illucens*	Sustainable management of a wide range of organic wastes	Diener et al. (2009); Wang et al. (2013); Nyakeri et al. (2019)
Medicine and cosmetics	European honey bee	*A. mellifera*	Production of royal jelly, beewax, bee venom	Rinderer et al. (1985)
	American cockroach	*Periplaneta americana* (L.)	Product called 'potion of recovery' used in immunotherapy, respiratory, gastric, and other diseases	Mao et al. (2003); Srivastava et al. (2011); Ting Shun et al. (2012)
	Common green bottle fly	*Lucilia sericata* (Meigen)	Maggot therapy – larvae used for cleaning the necrotic tissue within a wound	Sherman (2009); Gasz & Harvey (2017); Yan et al. (2018)
Pollination	European honey bee	*A. mellifera*	Dominant role in managed pollination service	Brittain et al. (2013)
	Bumble bee	*Bombus terrestris* (L.)	For pollination of more than 100 crops	Goulson (2013)
	Alfalfa leafcutting bee	*Megachile rotundata* (Fabricius)	Alfalfa and canola pollination	Pitts-Singer & Cane (2011)
	Common green bottle fly	*L. sericata*	Pollination of crops from Cruciferae, Umbeliferae, and Amaryllidaceae families	Herrmann et al. (2019)
Research	Common fruit fly	*Drosophila melanogaster* Meigen	Model organisms produced in stock centres for scientific purposes	https://bdsc.indiana.edu
	Domestic silk moth	*B. mori*		International Silkworm Genome Consortium (2008)
	Greater wax moth	*Galleria mellonella* L.	Model organism for study of host-pathogen interactions	Fuchs et al. (2010)
	Red flour beetle	*Tribolium castaneum* (Herbst)	A pest of stored products but also a model for study of developmental biology	Tribolium Genome Sequencing Consortium; https://www.nature.com/articles/nature06784
	Hide beetle	*Dermestes maculatus* De Geer	Skeletal cleaning in museums	Pahl (2020)

the world. The edible bush-cricket, *Ruspolia differens* (Serville) (Orthoptera: Tettigoniidae), is an important food source in Africa and has been bred commercially for a long time, albeit not yet on a mass-rearing scale (Agea et al., 2008). In nature, this grasshopper feeds on a wide variety of grasses and sedges, suggesting that it is a generalist feeder that can be reared on many substrates. To gain insight into nutrient requirements of *R. differens*, Malinga et al. (2020) test a range of plant species for their suitability as host. Developmental time, survival, and adult weight varied considerably between host plants and the highest performance was obtained on a diverse mixture of inflorescenses. The strongest diet effects are observed on the mono-saturated fraction of fatty acids. Sorjonen et al. (2020) take this work further by investigating the potential of various by-products from the food industry added to the diet. They find that increased protein levels in by-products containing barley and potato enhanced growth, development time, and survival of the grasshoppers. These findings are important to further improve large-scale rearing programmes for *R. differens*.

The BSF (*H. illucens*) is one of the insect species for which mass-rearing facilities are being developed at large scale. It can be bred on a range of substrates and serves as an alternative protein source for feed and food. Chia et al. (2020) investigate the nutritional composition of BSF larvae on various side-streams from the agro-industry, in particular from breweries. They find significant effects of diet on protein and fat content, as well as on mineral levels of larvae. These results are important for further developing this fly as an alternative feed source for livestock, such as fish and poultry, in a circular economy.

Although *D. melanogaster* is not mass produced for food and feed, it can serve as guide species for many other production insects. It is reared at many research laboratories in the world and at small scale as food for pets, such as reptiles and amphibians. Kim et al. (2020) investigate how life-history traits are affected in various strains by the balance between proteins (P) and carbohydrates (C) in the diet. In general, adult lifespan decreased whereas egg production increased at higher P:C ratio. Effects on larvae are different, with the lowest P:C ratio causing high mortality, longer developmental time, and lower body mass. Although these effects were qualitatively similar between strains, the authors also find significant strain*diet interactions on the magnitude of effects. Consistent with many previous studies, these results confirm that diet can have an important effect on insect life-history traits. They also highlight the importance of variation between strains in response to culturing conditions, which may be exploited in insect mass-rearing programmes.

Effects of diet on insect performance are also important in the pest control industry, such as in the production of biological control agents and the production of insects for release in SIT programmes. To reduce rearing costs, Montoro et al. (2020) test effects of artificial diets with different macronutrient composition on the fitness of the predatory bug *Orius majusculus* (Reuter) (Hemiptera: Anthocoridae). This bug is an important biocontrol agent and normally reared on eggs of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae). Female size and fecundity are significantly reduced on the artificial diets indicating that some crucial components were still missing from the formulations. In another study, Aceituno-Medina et al. (2020) measured the fitness of fruit flies *A. ludens* and *Anastrepha obliqua* (Macquart) (Diptera: Tephritidae) on two artificial diets. These flies are important pests in the fruit industry and mass reared for SIT application. To prevent laborious mixing of ingredients the authors developed two pelleted rearing substrates. Pelletizing of the diet yielded heavier larvae and pupae but did not affect any other life-history traits. Thus, pelleted diets can improve the efficiency of mass-rearing programmes by reducing labour without affecting the efficacy of the insects in SIT programmes. van Emden & Wild (2020) complete this section on the role of diet on artificial rearing of the aphid *Myzus persicae* (Sulzer) (Hemiptera: Aphididae). Aphids are sap-sucking insects that can cause large damage to cultivated plants (Blackman & Eastop, 2000). The authors describe a method by which they have maintained a *M. persicae* culture in the laboratory for over 30 years. As some aphid species are used as hosts for rearing parasitoid wasps in biological control programmes, sharing knowledge about artificial rearing methods of them is relevant.

Besides diet, abiotic factors such as temperature may significantly affect the success and sustainability of mass-rearing programmes. Francuski et al. (2020) measured fecundity at two temperatures in a Spanish and a Dutch strain of the common housefly, *M. domestica*. Consistent with the theory of life-history trade-offs, increasing temperature from 25 to 32 °C shortened the sexual maturation time and increased daily egg production, but reduced adult longevity and lifetime egg production. The results are relevant for choosing the optimal temperature in mass-rearing programmes of houseflies. Maximization of the production process may be attained at a particular balance between birth rate (i.e., the rate at which new individuals are added to the population) and adult survival.

Microbiome

The microbiome is an integral part of insect life. It encompasses bacteria, archaea, fungi, viruses, and protozoa that as a community might play influential roles in the life history of the insect (Gurung et al., 2019). Examples include provisioning of essential nutrients (Gonella et al., 2019), aiding pheromone communication (Engl & Kaltenpoth, 2018), and conferring parasitoid resistance (Vorburger, 2017). Next to beneficial effects, microorganisms can be neutral or detrimental to insect fitness and health. As such, they may be exploited for improving insect rearing, but also form a threat for infections and diseases in insect monocultures (e.g., Nair et al., 2019). In particular, large monocultures increase the risk of pathogenic infections and some devastating outbreaks of diseases in insect mass cultures have been reported (reviewed by Eilenberg et al., 2015).

Joosten et al. (2020) provide a comprehensive review of the pathogens and diseases of BSF and compare their literature data to immunological and disease information of other dipterans. The most important threats to insect cultures are entomopathogenic fungi, viruses, protozoa, and bacteria. In contrast to other production insects, BSF appears to be particularly devoid of pathogen infections and no disease outbreaks have yet been reported from mass rearings. The reasons for this remain unclear, but it may have to do with the septic environment in which the larvae develop. The information presented in this review provides basic knowledge to inform guidelines for the sustainable production of BSF and other production insects.

Microorganisms are receiving increasing appreciation as a way to improve pest control strategies (Trienens & Beukeboom, 2019). This issue contains two contributions from Koskinioti et al. (2020a, 2020b) on the role of microbiota, added as probiotics to the diet, in the rearing of the olive fly, *Bactrocera oleae* (Rossi) (Diptera: Tephritidae), and its parasitoid *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae). The olive fly is a specialist feeder on olives and causes severe economic harm to the olive industry. SIT applications for this species have been hampered by problems of rearing the flies in large numbers on artificial diet. A major reason appears to be the reliance of *B. oleae* on specific microbes for digesting the olive's secondary compounds. The authors test the effect of adding various gut bacteria, including *Bacillus*, *Serratia*, *Providencia*, and *Enterobacter* spp., to artificial larval diets. They observe both harmful and beneficial effects depending on bacterial species and conclude that *Enterobacter* sp. AA26 is most promising for improving SIT application. In an accompanying study, the authors investigate the extent to which probiotic improvement of *B. oleae* rearing benefits the development of its parasitoid that is being reared on *B. oleae*. They observe various positive and negative effects on parasitoid fitness depending on bacterial species in the host's diet. Specific isolates of *Providencia*, *Bacillus*, and *Serratia* resulted in faster emergence, increased fecundity, improved parasitism rate, and more female-biased progeny sex ratios, whereas *Klebsiella* and *Enterobacter* spp. negatively affected these fitness parameters. These studies are instrumental for improving olive fly control programmes, both in terms of releasing sterile males as part of SIT and of rearing parasitoids for integrated pest management programmes.

Wolbachia is a widespread symbiont of insects and can manipulate host reproduction in several ways (Werren et al., 2008). Some of these effects may be exploited for insect pest control. One form of host reproduction manipulation is cytoplasmic incompatibility, the sterilization of females following mating with infected males due to sperm chromosome modification by *Wolbachia* (Vreysen et al., 2007). Carvalho et al. (2020) investigate the potential of the incompatible insect technique (IIT) for the control of the mosquito *A. aegypti*. They introgressed the *Wolbachia* WB2 strain into a Brazilian and Mexican *A. aegypti* strain that were free of the bacterium. They observed no effect on the Brazilian strain, but several fitness components were negatively affected in the Mexican strain. These results indicate that variation in host genomic background needs to be taken into account upon choosing the strain for mass rearing in SIT programmes.

This special issue is completed by a study of Ulanova et al. (2020) on the microbiome composition of the green blowfly (*L. sericata*) raised on fish wastes. This cosmopolitan fly is of great economic and medical importance, as it can cause severe disease in cattle and sheep, but its larvae are also used for wound healing in human patients. The microbiome consists predominantly of *Xanthomonadaceae*, *Enterobacteriaceae*, and *Lactobacillaceae*, and to a lesser extent *Clostridium*, *Erypelothrix*, and *Oceanispherum* bacterial species. This knowledge is useful for evaluating the potential of this fly as a disease vector in the livestock industry as well as for its safety in human medical applications.

The studies comprising this special issue contribute to the basic knowledge of the biology of insects in production. They also provide important information about improvement of conditions for commercial and safe rearing of the insects. It is clear that for most species considered much more research is needed to fully exploit their potential as feed and food producers, and to further improve their rearing conditions as part of pest control programmes. Although diet and temperature are proven abiotic factors that can be varied to optimize life-history traits and increase yield, there are additional environmental variables that are not covered in this issue and need to be considered in the near future, such as light periodicity and wavelengths. An undervalued field in commercial insect research is genetics – for example, how can artificial selection be exploited to improve traits of commercial interest (e.g., Lirakis & Magalhães, 2019). Another promising future field of research is 'high density entomology' – in successful mass-rearing programmes insect density is, by default, unnaturally high but to what extent do these high densities affect the behaviour, performance, and well-being of the insects?

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