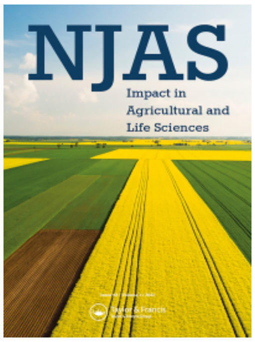

NJAS: Impact in Agricultural and Life Sciences

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/tjls21

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To cite this article: Anna Voulgari-Kokota, Martijn S. van Loon & Bernice Bovenkerk (2023) Insects as mini-livestock: Considering insect welfare in feed production, NJAS: Impact in Agricultural and Life Sciences, 95:1, 2191797, DOI: 10.1080/27685241.2023.2191797

To link to this article: https://doi.org/10.1080/27685241.2023.2191797

Published online: 22 Mar 2023.

NJAS: IMPACT IN AGRICULTURAL AND LIFE SCIENCES
2023, VOL. 95, NO. 1, 2191797
https://doi.org/10.1080/27685241.2023.2191797

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Insects as mini-livestock: Considering insect welfare in feed production

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ABSTRACT
Insect farming for animal feed production is considered a promising alternative to the traditional feed manufacturing sector, because of its low ecological footprint and circular use of required resources. However, treating insects as mini-livestock is accompanied by various questions on the suitable rearing conditions needed to achieve high-quality products, while considering insect welfare. Although there are concepts which have long served as a compass for animal welfare regulations, these have been under increasing criticism. Also, they have been drawn up for vertebrate animals and are, therefore, not entirely applicable to insects. We hold that the development of commonly accepted methods for keeping insects as mini-livestock demands deep knowledge on insect biology and a dynamic discussion on insect welfare. We plead for an evaluation of the relevant ethical and empirical aspects of insect rearing conditions and for establishing welfare criteria based on these evaluations. By addressing several questions and uncertainties from an interdisciplinary perspective of entomology, animal ethics and philosophy of mind, we argue that taking into account current knowledge on insect biology could aid in the emergence of a novel, well-informed and integrated perspective on insect welfare. Ultimately, our goal is to trace the necessary biological factors for designing implementable and appropriate insect rearing conditions, in order to avoid ethical mistakes that have historically been made in animal production systems.

ARTICLE HISTORY Received 15 November 2022; Accepted 10 March 2023; Publish online 18 March 2023

KEYWORD Animal welfare; insects; Musca domestica; Hermetia illucens; insect feed; mini-livestock

1. Introduction

Livestock production demands 33% of the world's agricultural land for feed production (Gerber et al., 2013). Insect feed, which was recently licenced for use in poultry and pig feed in the EU 2021, has significantly less requirements and could aid in the reduction of greenhouse gas emissions (van Huis &

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Gasco, 2023). At the same time, certain insects could be reared on organic leftover streams of the agricultural sector to achieve circular use of resources (van Huis et al., 2013). Therefore, the use of insects for feed is often considered a good and sustainable alternative to traditional feed production (Dicke, 2018). While large-scale insect production is growing rapidly in response to this promising innovation, the use of insects as production animals raises ethical considerations on the environmental impact, the product quality and the respect for animal welfare in such enterprises (Gjerris et al., 2016). In this paper, we address the latter, and discuss the ethical and empirical aspects of suitable production conditions.

Unlike other animals used in economic enterprises, insect species too often escape ethical reflection. Loo and Sellbach (2013) refer to the insects as "leftovers of agricultural production" and consequently as "the leftovers of animal ethics". To avoid ethical mistakes which have been done in the past with the exploitation of vertebrate animals, we call for a joint effort combining biology and ethics to propose an interdisciplinary research scheme (Webster, 1998) as necessary for the emergence of a novel, well-informed and integrated perspective on insect welfare, independent of economic considerations and entrepreneurism, which should accompany the growing insect feed sector.

Among the insect species that could potentially be reared as animal feed, the black soldier fly (*Hermetia illucens*), the common house fly (*Musca domestica*) and mealworms, such as the yellow mealworm (*Tenebrio molitor*), are currently mainly used (van Huis & Gasco, 2023). Academic interest has risen considerably during the last years, considering that 80–90% of all publications dealing with this subject have been published during the last six years, with the black soldier fly being the leader in literature for edible insects and insects for feed (Van Huis, 2023). Given the enormous diversity within Insecta, we support that insect welfare should be examined with respect to the characteristics of each species. For that, we will focus on the black soldier fly (*Hermetia illucens*) and the housefly (*Musca domestica*). We will examine these two species together, because they are characterised by similar life cycles in terms of duration and developmental stages and due to their relative phylogenetic proximity (Order: Diptera) (Kortsmit et al., 2022). Also, these two species are rapidly developing as mini-livestock, due to their capacity to convert organic left-over streams from agriculture into animal protein with high nutritive value (Barragan-Fonseca et al., 2017), resulting in a circular use of resources (van Zanten et al., 2015). We will also rely to a certain extent on literature about other insect species that have been more extensively studied, mainly other flies like *Drosophila* and bee species which have been examined for the capacity to feel, to borrow research questions and hypotheses which need to be tested in order to draw correct welfare regulations.

Insect production is not a new idea. Insects for human, livestock and pet food have been produced in many facilities, both large and small, for many years throughout the world. In general, people have long recognised the high potential of services and products provided by insects. Boppré and Vane-Wright (2019) provide an extensive overview of such historic and contemporary examples, including honey and silk, but also the fertilisation of crops and cleaning up of waste, illustrating the great instrumental and economic value of insects. With respect to our morals, however, it is not clear how insects should be valued. Traditionally, invertebrates, including insects, have often been subject to the belief that they do not meet the appropriate criteria to be morally considerable. The reason for this relates to the lack of consensus on whether insects are "sentient creatures" and to their (supposed) inability to experience emotions (Allen-Hermanson, 2008). What is more, there are cases where discussion about insect farming is accompanied by avoidance to refer to insects as animals and rather referring to them as products (Santaoja & Niva, 2019). However, van Huis mentions in his 2019 editorial on the welfare of farmed insects that even though nobody used to ask about insect welfare before the emergence of the industry which uses insects as food and feed, the situation has started to change. He mentions that this is due to the connection people make, associating insects with what they perceive as "conventional" livestock (van Huis, 2019). Consequently, we believe that maintaining insects as production animals should raise similar questions to the ones that have previously been raised about conventional livestock.

Historically, changes in the perception towards the ethical treatment of animals led to the emergence of animal welfare standards in the 1960s, with respect to vertebrates kept under intensive industrial conditions (Brambell, 1965). Moral considerations with respect to the welfare and well-being of animals, however, have relatively recently been extended to fish (Bovenkerk & Meijboom, 2013), as well as to certain groups of invertebrates (e.g. Cephalopod, Decaphods), thus including insects into our scope of moral concerns (Barrett et al., 2022; Boppré & Vane-Wright, 2019; Drinkwater et al., 2019; Mather, 2001; Singer, 2016). Nevertheless, these concerns are not translated into legislation with the exception of a few national regulations (see Lotta, 2019). In the absence of official regulations for insects, insect producers have individually developed production practices (Barrett et al., 2022; De Goede et al., 2013; Erens et al., 2012). Insect producers not only have to figure out how to care for their mini-livestock but also whether it makes sense to care at all (Bear, 2021).

Furthermore, the existing framework for protecting insect welfare in most cases is the concept of Brambell's Five Freedoms (De Goede et al., 2013; Erens et al., 2012; The Dutch Council of Animal Affairs, 2018; van Huis et al., 2013), which brings a number of important limitations (see Box). Firstly, applying animal welfare concepts originally designed for conventional livestock

Table 1. Animal welfare requirements: a brief summary.

The Brambell Commission was set up by the British government, in response to public concerns after the publication of Ruth Harrison's book *Animal Machines*, which described the conditions of animals living in modern production systems. Findings in the Brambell Report were developed into the so-called Five Freedoms by the Farm Animal Welfare Council (FAWC). These freedoms should safeguard the animals against: (1) thirst, hunger and malnutrition; (2) physical and physiological discomfort; (3) pain, injury and disease; (4) fear, distress and chronic stress; (5) limitation of natural behaviour. These freedoms influenced European animal welfare regulations, as this concept has served as a baseline for regulatory decisions (Simonin & Gavinelli, 2019). The Dutch Council of Animal Affairs (2018) maintain that welfare requirements for insects should follow the so-called *Five Freedoms* concept.
However, this concept has faced criticism for its limitations, related to normative assumptions underlying the (supposed) objective measurements of animal welfare. Specifically, welfare is construed negatively, limited to the absence of negative states (Korte et al., 2007; Mellor, 2016a, 2016b; Mellor & Beausoleil, 2015; Yeates & Main, 2008). Such welfarism has been criticised for accepting most uses of animals, as long as it minimizes pain and suffering (Haynes, 2011). Moreover, it excludes definitions of welfare that focus on the whole course of an animal's life and a wide spectrum of natural behaviours (Fraser et al., 1997). The so-called "allostasis model", for example, illustrates that the capacity to adapt and change are important determinants of welfare and therefore, the Five Freedoms concept is too static (Korte et al., 2007; McEwen & Wingfield, 2003). Short-term stressors are not necessarily problematic, as long as the animal reaches a base level of welfare rapidly after the perturbation; challenging animals by exposing them to diverse environments is likely to contribute to positive welfare (Mellor & Beausoleil, 2015, p. 245; Spinka & Wemesfelder, 2011, p. 27). Being able to exercise one's agency (Wemelsfelder, 1997) results in the positive experience of being in control (Mellor & Beausoleil, 2015, p. 247).
Mellor and Beausoleil (2015) propose an alternative to the Five Freedoms – an "extended Five Domains model" - which is more fine-grained, takes into account positive welfare, considers both welfare experienced at a particular point in time as well as over a longer period, and distinguishes between different animal species, lifecycle stages and keeping contexts (e.g. farming, zoos, companion). Another initiative to include a wider range of criteria, in particular positive welfare as well as contextual parameters (Blokhuis et al., 2010) is offered by the Welfare Quality Network (Blokhuis et al., 2013). For example, when considering the welfare of fly larvae, it may be beneficial to prioritize factors such as substrate preference, or abiotic conditions that mimic natural day and night cycles (fluctuating temperatures and varying light exposure). Such an approach is likely to differ from one focused solely on maximizing growth, which may not align with the animals' natural environment, behaviour and needs.
The inclusion of a wider range of both negative and positive effects shifts the focus from providing minimum conditions to environmental enrichment. For example, Mallory et al. (2016) have shown that environmental enrichment affects the memory of adult house crickets (*Acheta domesticus*), and Julita et al. (2020) demonstrated that, under direct and full sunlight in tropical environments, the black soldier fly exhibits optimal mating and reproductive behaviour, that is, when kept in semi-outdoor conditions. Note, however, that semi-outdoor conditions in regions with temperate climates are unlikely to provide an enriching environment due to the lower temperatures and relatively low lengths of light periods. Finally, a focus on positive welfare could impact the environmental benefits, economic feasibility, and final eco-efficiency of the entire system (Spykman et al., 2021).

ignores that many insect species may need radically different living conditions from the animals for which this framework was drawn. The freedom "to stand up; lie down; turn around; groom themselves; and stretch their limbs", for example, could not apply to the larvae of our target insect species. "Ready access to clean food and water", is also not a prerequisite to many insect species which naturally reside in septic environments. For other freedoms, such as the "avoidance of chronic suffering" or "boredom", little research has been done to prove the capacity of insects to be in such states. Therefore, the Dutch Council of Animal Affairs has called for an investigation to determine which would be the "optimum housing and growing conditions, such as climate, light, substrate, and population densities" (The Dutch Council of Animal Affairs, 2018, p. 30) for insect production. That issue is of great importance, particularly if one considers the need to specialise welfare regulations even within vertebrates (Bracke, 2006). Secondly, the concept has received increased criticism, mainly because it excludes states of positive welfare (Mellor, 2016a) and it ignores animal agency (Spinka & Wemesfelder, 2011) (see Box).

Our approach intends to work on two fronts. First, we will discuss to what extent moral concerns about the welfare and well-being of conventional livestock extend to insects. In general, insects have been often excluded from ethical deliberations. Here, we want to briefly discuss the reasons for that and evaluate their validity. Secondly, we will identify welfare requirements currently used to evaluate animal welfare and discuss relevant research done to insects. We will include requirements which are either part of or derive from traditional welfare concepts, but also requirements of positive welfare (Mellor, 2016a, 2016b), which are often ignored. These requirements will be grouped in more general categories, as previously done (Appleby et al., 2018; Mellor & Beausoleil, 2015) and adapted in line with current knowledge on insect biology. We aim at including all relevant aspects of biological research, including studies on insect behaviour, immunity, microbiome, and population dynamics, combined with insights from animal ethics and philosophy of mind, to explore how to understand the ethical treatment of insects and insect welfare. Ultimately, our goal is rather pragmatic, and we primarily aim at tracing the necessary biological factors for designing implementable and appropriate insect rearing conditions.

2. Insect sentience, moral standing & welfare considerations

As stated in the introduction, we will argue that maintaining insects as mini-livestock should raise similar questions that have previously been asked about conventional livestock, in order to prevent moral missteps done in animal husbandry systems. This point of departure, however, is not commonplace: many invertebrates, including insects, are often excluded from ethical deliberations and largely exempt in welfare legislation. In the European Union, for example, the Council Directive concerning the protection of animals kept for farming purposes (98/58/EC) explicitly states that it does not apply to "any invertebrate animal" (article 1, paragraph d). This means that, while large-scale insect rearing companies are already in production, insect producers in the European Union are currently excluded from any legal obligations with regard to animal welfare. Invertebrate welfare has, therefore, been rightly called an overlooked issue (Horvath et al., 2013).

The reason for this exclusion relates to uncertainty about whether insects (and other invertebrates) are "sentient creatures": given their relatively simple nervous system (compared to vertebrates), an implicit assumption that these animals cannot be sentient appears. This assumption undermines the moral significance of insects, at least according to utilitarian – and welfarist – branches of ethics, as they rely upon the capacity for sentience to determine whether an animal deserves moral status. This position echoes the claim of classic utilitarian Jeremy Bentham (1748–1832) that the capacity to experience pain and suffering should be the starting point for our ethical deliberations. Sentience is, along these lines, often defined as the capacity of pain and suffering, and, historically, there have been doubts about whether insects can feel pain (Tiffin, 2016). However, recent studies that utilise a framework formulated by Birch et al. (2021) found evidence for the capacity to feel pain in six insect orders, including (adult) Diptera (Gibbons, Crump, et al., 2022).

Similarly, several "exceptional" or "advanced" invertebrate species, in particular cephalopods, have recently been included into Directive 2010/63/EU (Sykes et al., 2012). This means that, when used for experimentation or other scientific purposes, these animals ought to be treated as sentient creatures, and are subject to legal protection (Berry *et al*., 2015). This inclusion follows findings indicating that these animals are likely to have "the ability to experience and express pain, suffering, distress and lasting harm" (ibid., p. 268). This is in line with a growing amount of literature suggesting that various invertebrates possess the capacities required to ascribe sentience (e.g. Elwood & Appel, 2009; Elwood, 2011; Mather, 2001).

Based on these findings, the Dutch Council for Animal Affairs has stated, with regards to the emerging insect industry, that "(.) based on the existing evidence, the most recent scientific reviews and reports give invertebrates the benefit of the doubt when it comes to pain and well-being" (2018, p. 30). At the same time, however, it also remarked that "even modern scientific methods cannot determine animals' subjective states with certainty" (2018, p. 29). The latter statement relates to the "explanatory gap" (Levine, 1983) and the so-called "hard problem of consciousness" (Chalmers, 1995), and defines sentience with the capacity to *feel* (akin to Broom, 2019), which is often referred to as "phenomenal consciousness" in philosophy of mind and the cognitive sciences. Descriptions of this kind of consciousness are often phrased in terms of "what it is like" (Nagel, 1974). That is, what it is like for a human or an animal (a bat in Nagel's famous example) to undergo particular mental states (for example, a percept, sensation, belief, desire, intention) from a "first-person perspective". As these "raw feelings" or experiential descriptions cannot be formulated in functional terms, some argue that it is impossible to explain this aspect of consciousness in terms of reductive physicalism (2015). Hence, Pali-Schöll et al. (2019, p. 2767) state that "we are, most likely, never going to conclusively determine whether or not insects are sentient".

Contrary to this kind of mystification, there are several theories of consciousness that do attempt to bridge the explanatory gap by means of (neuro)reductionism – empirical evidence alone cannot provide us with conclusions about sentience. These theories, however, draw different conclusions as to whether insects are capable of having subjective experiences, i.e. whether an insect actually *feels* pain when presented with noxious stimuli. First-order theorists, for example, such as Dretske (1995) and Tye (1995) explain phenomenal consciousness in terms of world-directed (i.e. first-order) intentional states, and, support that insects possess phenomenal consciousness (Tye, 2016). Barron and Klein (2016) concur, albeit on different theoretical considerations; based on the information-integration theory of consciousness (Tononi, 2004, 2008). Carruthers (2004b, 2007, 2019), however, has criticised these positions, and argues on the basis of global workspace theory (Baars, 1988, 1997), that different arthropods (i.e. jumping spiders and honeybees) possess certain (so-called "access") conscious states (see Block, 1995), but not phenomenal ones. While Carruthers denies sentience in insects, he has argued that insects and other invertebrates can still warrant moral concern (Carruthers, 2004a) and urges us to think about welfare without consciousness – a view also expressed by Dawkins (2017).

Determining whether insects are capable of subjective experiences becomes even more complicated when we take into consideration that insects are tremendously diverse (Stork, 2018). We conclude, therefore, that there currently is no consensus among scientists and philosophers on whether insects are sentient. Within this vast diversity of species, there are undoubtedly all kinds of differences in behaviour, cognition, as well as experiential abilities. Hence insects do not seem good candidates for justified generalisations and extrapolation. Here, we propose – despite uncertainty about insect sentience and thus as a matter of precaution – to further study and develop species-specific guidelines for insect welfare for insects that are farmed for food, feed, or other human economic enterprises. We believe that the evidence that insects might possess emotional states, even if the associated research is still scarce (see Perry & Baciadonna, 2017), as well as the precautionary principle regarding insect welfare, should be adequate motives. What is more, the large numbers of insects maintained for food and feed production in mass rearing conditions (Rowe, 2020), urge us to suggest that insect welfare research and relevant animal welfare regulations are necessary.

3. Insect welfare: A pragmatic approach

Following the current discussion on animal welfare requirements (see Box), we wish to review the relevant research which has been done to insects. Our approach aims at combining what could be harmful to insects, but also what would constitute an environment contributing to positive welfare and promotion of animal agency. In the same spirit, we approach the assessment of welfare not only through the discussion of health, behaviour and physiology, but also through the expression of preference or motivation (Appleby et al., 2018) (Figure 1).

3.1. Nutrition

Hunger, thirst and malnutrition can be safeguarded by providing ready access to good quality water and food, in accordance with the insect natural diet requirements. In reality, artificial or semi-artificial diets may have different results in insect physiology, while certain ingredients may lead to digestive stress (Francuski & Beukeboom, 2020; Pisa et al., 2022). In the case of housefly larvae, for example, various types of manure had a different effect on their fitness (Ganda et al., 2022; Khan et al., 2012), whereas in the case of the black soldier fly, various waste stream combinations from agriculture and brewing industry had different effects on their overall performance (Chia et al., 2018; Scala et al., 2020). Developmental durations for the insect life stages from egg to adult eclosion, fecundity and survival served in both cases as significant parameters for the assessment of suitability of the various substrates.

A recent study showed that black soldier fly larvae prefer manure to an artificial diet and that the older the larvae the stronger their preference grew (Parodi et al., 2020). In reality, organic left over streams, like manure, are not used in the insect feed industry, because they have not been legislatively licenced yet. This restraint on the part of legislators is explained by uncertainties about how the use of manure and other "waste streams" will affect animal welfare and food safety, given the possible contamination by, for example, mycotoxins, which can have adverse effects on human and animal health (Niermans et al., 2021; Zain, 2011). However, this is a direction the sector may be allowed to follow in the future, to achieve circular use of resources.

Yet, another challenge the sector would face is that "waste streams" might be deficient of certain essential nutritional elements. Therefore, they should be mixed with artificial media based on wheat bran or other grains, which have been shown to be appropriate for health development both for the housefly and the black soldier fly (Barragan-Fonseca et al., 2017; Kökdener et al., 2021; Leyo et al., 2022). In general, minimum contents of 10% protein and 2% fat can sustain sufficient larval growth with the prerequisite of sufficient carbohydrates, while a protein-to-carbohydrate ratio of 17:55 has been shown to support high larval and adult performance with high larval protein and intermediate fat content (Barragan Fonseca et al., 2019). Similarly, house fly larvae have been successfully reared on different types of manure with a protein and fat content of 15,3–23,3% and 1,2%, respectively (Hussein et al., 2017).

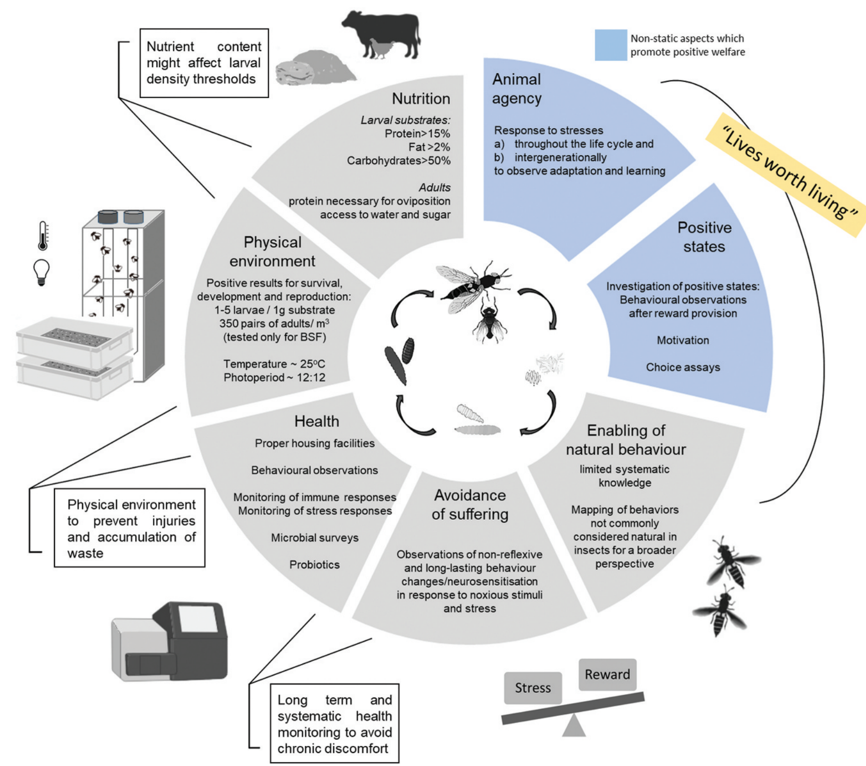

Figure 1. A pragmatic approach to insect welfare focusing on the black soldier fly and the house fly, combining traditional animal welfare criteria with positive welfare and animal agency.

Furthermore, we should take into account that different developmental stages of insects may have different nutritional requirements. Animal manure may be an excellent developmental substrate for housefly larvae, for example, but housefly adults live longer when they have access to sugar (Lysyk, 1991). At the same time, adult female flies need access to protein to oviposit, with manure alone not being adequate (Pastor et al., 2011). In the case of black soldier flies, it was a common belief that the fly does not eat. A recent study showed that the adult has a functional digestive system and that food administration affects the adult fly's longevity (Bruno et al., 2019).

3.2. Physical environment

The issue of proper physical environment and avoidance of physical discomfort was originally raised for vertebrate animals which were not provided sufficient space and suitable abiotic conditions (see Box). For insects, research is required to set the appropriate densities for each developmental stage, as discomfort cannot be monitored and evaluated as easily as in the case of vertebrate animals, especially if one considers the high natural larval densities of certain insect species. On the one hand, high larval densities could promote social digestion and protect against low environmental temperatures, but on the other hand, they could result in accumulation of waste products or competition for resources (Barragan-Fonseca et al., 2017; Green & Popa, 2012).

Studies on the black soldier fly have shown that larval survival was negatively correlated with the tested rearing densities, with the lower density set at 5 larvae per 1 g of substrate in one case (Dzepe et al., 2020) and 1 larva/cm^3 or 2 larvae per 1 g of substrate in another (Opare et al., 2021). Larval developmental time, on the other hand, correlated positively (Barragan-Fonseca et al., 2017; Dzepe et al., 2020). Similarly, housefly larvae, reared in cups with 1 larvae/1 g of substrate ratio showed higher survival, compared to higher densities, regardless of the diet used (Kökdener et al., 2021).

For adults, insect density should be such that injuries are avoided. Adult population density in combination with the levels of flight activity can lead to overcrowded environments leading to injury. Data from a recent study showed that damaging of house fly wings occurs on average after 6 hours of flight and depends on housing conditions (Wehmann et al., 2022). More specifically, flies living in more cramped conditions suffered 20 times more the damage that insects in spacious cages did in a free-flight experiment. For that, flight activity and space should be in such ratio that such situations are prevented. On the other hand, it should be dense enough for successful reproduction to happen (Čičková et al., 2012). A study showed successful reproduction in black soldier flies in cages from a density of 350 pairs/m^3 (Nakamura et al., 2016). Egg production was higher in higher densities but adult survival was lower (Liu et al., 2022). Also, factors affecting the activity of adults in a given density, like temperature and photoperiod, should be monitored. In the case of the housefly, for example, the combination of population density and temperature has been shown to result in different levels of flight activity (Schou et al., 2013). A photoperiod of 12:12 light/dark ratio and temperatures around 25°C have been associated with fast development both for black soldier fly (Harnden & Tomberlin, 2016) and housefly larvae, for which the developmental rate rose significantly for temperature ranges from 16°C to 25°C, and less fast for ranges from 28°C to 34°C (Wang et al., 2018).

3.3. Health

Studies on insects have investigated short-term and long-term pain (Sherwin, 2001), yet the difference between the invertebrate and the vertebrate brain does not always allow the drawing of safe conclusions of how pain is experienced by insects or the rejection of explanations of pain which exclude the notion of suffering (Adamo, 2016). However, behavioural and physiological responses to noxious stimuli or analgesic substances can indicate the existence of pain (Elwood, 2011; Sherwin, 2001). In defiance of the latter, treatment of insects in the industry is not always transparent (Erens et al., 2012). One would expect that at least the killing methods would be regulated; however, this is not the case. To our knowledge, there is no systematic research or clear consensus on which method could be more "humane". Insect producers have dealt with the issue, taking into account both what would be less painful for the insect and also what method would be more acceptable by the consumers (Bear, 2019). Freezing of insects is a common practice because ectotherms become lethargic at low temperatures, however there is no evidence on the absence of pain (Cooper, 2011).

In the same spirit of recognising the indications of pain existence in insects, injury and diseases should be prevented or rapidly diagnosed and treated. In connection with the avoidance of discomfort, as discussed in the previous sub-section, overcrowding should be prevented or limited to those levels which do not lead to injuries. Furthermore, potentially harmful microbes should be easily monitored. In literature it is implied that insect health and fitness are so easily affected by pathogenic microbes that it is unrealistic to propose complete safeguarding of insect health (De Goede et al., 2013; Maciel-Vergara et al., 2021). However, infection prevention by designing of proper housing facilities and rapid diagnosis are not impossible. An example could be the monitoring of immunity genes expression which has been identified to function as defensive mechanisms against microbial infections (M. Vogel et al., 2022; Sackton et al., 2017).

Although automatic health monitoring in mass insect rearing conditions is currently lacking, we believe that research on insect immunity and microbiome can help to ensure and evaluate insect health in large-scale cultures. Insect immunity can be affected by various factors which can be regulated in mass rearing settings (M. Vogel et al., 2022). Temperature, for instance, can affect physiology and metabolic rates, disrupting homoeostasis (Wojda, 2017). Furthermore, the effect of artificial diets on immunity should be investigated. In *Drosophila* and black soldier flies, the nutritional composition of the diet plays a role in immunity (Ayres et al., 2009; H. Vogel et al., 2018). A recent study suggested that the inclusion of catering waste in the diet of black soldier flies positively affected the species' immune system (Candian et al., 2023). Modulating the expression of antimicrobial peptides (AMPs) through the diet could be a tool in managing insect health in mass rearings.

Moreover, another research target should be the diverse repertoire of immunity genes that are up-regulated after microbial infection (M. Vogel et al., 2022; Sackton et al., 2017). Measuring the expression of AMPs and other stress response genes provides a tool to detect infections that challenge insect health, even well before they lead to externally visible effects. Also, the study of insect-associated beneficial microbes that contribute significantly to the insect fitness and health (De Smet et al., 2018; Engel & Moran, 2013; M. Vogel et al., 2022) is needed to define these conditions (e.g. temperature, diet) which will not compromise the healthy insect-microbiota in mass rearing facilities. The use of probiotic bacteria in insect rearing could also be promising for the safeguarding of insect health (Jordan & Tomberlin, 2021).

3.4. Avoidance of suffering

Biological markers which have been often used to evaluate stress in animals cannot serve as direct signals for negative states in the case of insects. The European Food and Safety Authority, for example, categorised non-social insects included in scientific experiments as not able to experience pain and distress (Dzepe et al. 2005). Theoretically, we know that stressful situations can be avoided by ensuring conditions preventing chronic suffering; however, chronic suffering is not easily diagnosed in insects. Research on mammals has quantified the experience of pain by observing non-reflexive and long-lasting behaviour changes, which are mediated by descending controls (Sadler et al., 2022). In the same way, examples of insects showing such behaviours could support the idea of pain in insects (Gibbons, Sarlak, et al., 2022). For that, we would need systematic testing for various potential stressors. A recent review on cognition and sentience of insects gathered evidence that many insects, across a broad taxonomic range, possess cognitive abilities, and what is more, can experience emotional states such as stress (Lambert et al., 2021).

For example, research on *Drosophila* has shown that nerve injury leads to chronic neuropathic sensitisation (Khuong et al., 2019). Similarly, other studies on *Drosophila* flies have tested fear, anxiety and aversion responses against stresses such as simulations of predator attack and have found evidence for persistent states of defensive behaviour or learned helplessness (Batsching et al., 2016; Gibson et al., 2015; Mohammad et al., 2016; Yang et al., 2013). *Drosophila* flies have served as a model to investigate the molecular mechanisms of nociception even for humans, particularly with respect to the developed *Drosophila* "pain" paradigms (Milinkeviciute et al., 2012).

3.5. Enabling of natural behaviour

To avoid limitation of the insects' natural behaviour, further research is needed to evaluate what could be considered as natural behaviour for insects. The fact that we cannot draw conclusions on the insect experience by observing facial expressions or body postures, like we are able to do with vertebrate animals to a certain extent, is definitely an obstacle in behavioural studies. Avoidance of fear, for example, which we discussed in the previous paragraph, is a challenge when discussing insects as production animals. We believe that this challenge has less to do with our lack of knowledge on whether insects can experience emotions and more with the limited systematic knowledge of their natural behaviour (McKellar & Wyttenbach, 2017).

As knowledge on the biology of production insects expands, we should focus on the description of their natural behaviour to assess the quality of their experience (Wemelsfelder, 2007). Systematic observations under different conditions can identify other responses which might be recurrent in rewarding or stressful circumstances (e.g. food reward or starvation) (see Cassill et al., 2016; Kortsmit et al., 2022). We believe that investigation of behaviours not commonly considered natural in insects (e.g. playing, defined as engaging in interactions with conspecifics for gaining positive welfare) would broaden our perspective on what should be considered "natural behaviour".

3.6. Investigation of positive states in insects

The definition of negative and positive states is a challenging issue in the case of insects. However, as difficult as the understanding of the insects' perception may be, the relative simplicity of their neural system could also be an asset in investigating aspects of their experience (Perry & Baciadonna, 2017). For example, researchers conducting experiments with *Drosophila* flies have managed to map neurons involved in many behavioural observations

(Dickson, 2008; Donlea et al., 2014; Iliadi, 2009). What is more, research on emotional phenomena in the brains of animals has contributed to our understanding of functions in the human brain (LeDoux, 2012). Although largely lacking, there is research showing very interesting findings with regard to emotional states of insects. Honeybees and bumblebees have been included in studies of judgement bias (optimism/pessimism) by adapting experimental protocols applied in tests of vertebrate animals (Bateson et al., 2011; Perry et al., 2016; Schlüns et al., 2017). Therefore, we support that such behavioural studies in insects will give us more tools in approaching the animal perception.

3.7. *Promotion of animal agency*

In relation to sections 3.5. and 3.6., safeguarding the ability to exhibit natural behaviour emphasises that animals need positive experiences to promote biological functioning. For that, we should attend to determining whether the animal's behaviour allows it to meet the demands of its environmental circumstances. There are conditions which can be characterised as natural stresses, for instance temperature changes or food scarcity, that are eliminated in controlled rearing conditions. According to Hoffmann and Ross (2018), this could lead to insect lines susceptible to stresses in comparison to natural populations. We support that research on the insects' response to various stresses could help us observe whether these challenges promote learning in insects (see Alem et al., 2016; Giurfa, 2013). Thus, we could study how and if certain challenges might help the species of interest to cope more efficiently with its environment through generations.

4. Conclusions

Large-scale insect farming aimed at feed production will inevitably result in mass insect rearing. The subsequent intensive and industrial conditions raise the question of how to design farming facilities that respect insect welfare. Insects as "mini-livestock" is not an entirely new phenomenon, but rather, rearing insects is a practice that seemingly has largely escaped ethical reflection. We discussed that, although the common concepts of welfare can serve as a baseline for designing rearing systems, they only define welfare as a static concept of avoiding harmful situations and are only partially applicable to insects such as flies, since they were originally developed for animals that are traditionally kept as livestock. Our approach wants to combine the knowledge on what could be harmful to specific insect species, but also to discuss what would constitute an environment which would promote positive welfare and animal agency. After reviewing the relevant literature about the black soldier fly and the housefly, we found that although certain welfare regulations can already be drawn with the use of existing scientific knowledge, much more research is needed to address aspects of welfare, such as the enabling of natural behaviour, states of positive welfare or animal agency.

More specifically, as far as nutrition is concerned, studies have indicated which are the optimal protein, fat, and carbohydrate contents of larval substrates that promote high survival and fitness. Also, the nutritional demands of adult flies have been studied. Although some criteria which have been used are more relevant to the commercial value of insects (e.g. protein content in larvae), there are others which are closely associated with welfare, such as survival, fitness and reproduction efficiency. Furthermore, the physical environment of the two species has been investigated in order to find which population densities and abiotic conditions promote their welfare. For larvae, the challenge is to allow aggregations which aid in social digestion and regulation of their micro-environment, but also to prevent accumulation of waste products and competition for resources. For adults, on the other hand, insect density should meet a balance so that injuries are avoided, but successful reproduction is plausible. The effect of the environmental temperature and the photoperiod have also been tested. Finally, in line with the insect farming sector development, there is a growing discussion on the proper and hygiene insect housing conditions. We propose that frequent microbial surveys and monitoring of the antimicrobial peptide gene and stress response gene expression in insects can serve rapid disease diagnosis and prevention. We believe that more focus should be given to insect-associated beneficial microbes and the use of probiotics.

On the other hand, general behavioural observations and research on the capacity of insects to feel are way more limited. Systematic research on insect behaviour has been done with regard to responses to abiotic factors or with regard to courtship. We propose that studying behaviours not commonly considered natural in insects (e.g. playing) would broaden our perspective on what should be considered "natural". Furthermore, studies on whether insects can suffer or feel pain have been limited mostly to *Drosophila* flies and certain Hymenoptera, indicating that it is possible for insects to be in states of chronic discomfort or sensitisation. Even though these studies are valuable, we strongly suggest that the inclusion of insect species used in insect farming enterprises is necessary. Such experiments should include observations of reflexive and non-reflexive reactions as well as long-lasting behaviour changes, in response to noxious stimuli and stresses (e.g. starvation, amputation, heat shock). Behavioural changes in response to reward (e.g. food reward), would also help us to understand how to perceive positive welfare in insects. We believe that both behavioural observations and health monitoring should happen throughout the animal's life cycle and also intergenerationally, to study the insect's capacity to bounce back from harmful situations and/or learn how to avoid them.

In conclusion, we believe that a new concept of animal welfare is needed, taking into consideration specific cases of insects kept as mini-livestock, while going beyond the mystification of subjective experience. In order to adapt general assumptions of animal welfare to insects, biological disciplines can help to interpret behaviour and physiology in terms of animal perceptions, while acknowledging the species-specific needs. The need for ethical and philosophical reflection on the nature of consciousness and its moral relevance remains, and should be addressed in tandem with these biological questions. The identification of topics for future research, e.g. cognition, behaviour, emotion, responses to noxious and analgesic stimuli, the relation between the (innate) immune system and the central nervous system, can provide more certainty concerning the question of how a particular insect species should be treated.

Acknowledgments

We would like to thank all members of the Insect Feed consortium who provided their feedback on the manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

Our research has been supported by the Dutch Research Council (NWO; NWA programme, InsectFeed project, NWA.1160.18.144).

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