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Invertebrate welfare: an overlooked issue

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Abstract
While invertebrates make up the majority of animal species, their welfare is overlooked compared to the concern shown to vertebrates. This fact is highlighted by the near absence of regulations in animal research, with the exception of cephalopods in the European Union. This is often justified by assumptions that invertebrates do not experience pain and stress while lacking the capacity for higher order cognitive functions. Recent research suggests that invertebrates may be just as capable as vertebrates in experiencing pain and stress, and some species display comparable cognitive capacities. Another obstacle is the negative view of invertebrates by the public, which often regards them as pests with no individual personalities, gastronomic entities, or individuals for scientific experimentation without rules. Increasingly, studies have revealed that invertebrates possess individual profiles comparable to the personalities found in vertebrates. Given the large economic impact of invertebrates, developing certain attitude changes in invertebrate welfare may be beneficial for producers while providing higher welfare conditions for the animals. While the immense number and type of species makes it difficult to suggest that all invertebrates will benefit from increased welfare, in this review we provide evidence that the topic of invertebrate welfare should be revisited, more thoroughly investigated, and in cases where appropriate, formally instituted.

Key words
• invertebrates
• animal welfare
• stress
• pain
• behaviour

INTRODUCTION

Invertebrates are a diverse and influential group that compose more than 90% of the estimated 10 million-plus animal species, mainly arthropods [1]. They are widely used in research, aquaculture, farming, and as displays in aquaria or insectariums [2]. Invertebrates such as shrimps, clams, squids, locusts, termites, grasshoppers, and beetle grubs, as well as honey from bees serve as a major source of human food worldwide [1]. Several species are farmed, while, more recently, some economically relevant species such as lobsters are reared for restocking purposes to replenish over fished areas or areas with habitat degradation [1, 3]. In these cases welfare issues are crucial for farming and restocking success. Invertebrates are also valued for their ability to make luxuries such as silk, pearls, and shells, and the preserved or live bodies of invertebrates like butterflies are used for decorative or artistic purposes [1]. Additionally, the diversity, short generation time, large number of offspring, and availability of invertebrates make them scientifically important [1]. For instance, research utilizing invertebrates includes everything from field research on biodiversity and conservation to use as laboratory models for the biological systems of other animals, including humans [2, 4].

Despite their importance, there is a general lack of concern for the treatment of invertebrates, and compared to vertebrates, they are often maintained with minimal animal care and oversight [5]. The general public tends to express feelings of aversion or fear towards most invertebrates due to concerns of disease and stings from some species, being pests/invasive species that eat people's food, or by being highly unattractive animals, which is the case for octopuses and others [1]. The scientific community even values the minimal ethical concerns for invertebrates which make them easier to use as models for many experiments in place of vertebrate animals, which receive greater ethical considerations [6].

However, this sentiment is beginning to change. There is a growing public concern about the welfare of some invertebrate species. For some, the concern is related to the organism's ecological importance. Environmental

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concerns are substantial given the importance of invertebrate species in maintaining ecosystems and their role in natural food chains. As an example, commercially important aquatic invertebrates must be caught from the wild to meet production demands, because captive breeding programs are unsuccessful [7]. Removing animals from the wild impacts both ecosystem structure and the population of not only the species removed, but also the populations of the other species inhabiting the same environment including endangered and protected vertebrate species [7]. Public concern is also economically motivated. For example, the increased occurrence of colony-collapse disorder in honey bees has led to increased research into bee health and welfare, because of their importance in producing honey and pollinating crops [8]. But the most striking example of the public's increased concern about invertebrate welfare is the growing dialogue on the welfare of decapod crustaceans during live cooking [5, 9].

Currently, most countries do not have ethical guidelines or regulations for the use and handling of invertebrates in research or for other purposes [7]. A major recent exception is directive 2010/63/EU of the European Parliament, which includes cephalopods in animal use protection legislation [10]. Cephalopods are similarly protected in Canada, but protection in Australia and the United States is not national and instead is limited to institution specific guidelines [7]. Drafting legislature for animal welfare involves knowing the specific species' capacity to suffer, understanding the practical considerations for implementing positive welfare for the species, and developing the philosophical reasons for promoting it. In this review, we will question whether invertebrates meet similar criteria for ethical concern as vertebrates for each of these aspects and comment on some of the improvements in invertebrate welfare that could be implemented.

THE CAPACITY TO SUFFER

The European Union raised the minimum standards of care for animals based on scientific evidence that vertebrate animals have a higher capacity to experience pain, suffering, and distress than previously thought. Directive 2010/63/EU of the European Parliament requires that animals experience the minimum amount of pain, suffering, or distress when used for research or other purposes [10]. Additionally, animals with the lowest capacity for pain, suffering, or distress should be selected when the choice is available [10]. However, the directive defines "animals" as non-human vertebrates, independently feeding larval forms of vertebrates, foetal mammals in the last trimester of development, and live cephalopods [10]. Invertebrates, with the exception of cephalopods, are not included in this description arguably due to the belief that they do not experience pain, suffering, or distress. However, similarities in behaviour between invertebrates and vertebrates suggest that pain, stress, cognition, and personality traits are similar between the two groups, including their ability to suffer (*e.g.* crustaceans, [11, 12]).

PAIN

A main challenge to including invertebrates in animal welfare legislation is the debate on whether invertebrates have the capacity for pain and suffering or if they simply exhibit nociception [4]. The International Association for the Study of Pain defines pain as "an unpleasant sensory and emotional experience associated with actual or potential tissue damage, or described in terms of such damage" [13]. On the other hand, nociception refers to the ability to detect and respond to a noxious stimulus and does not require the emotional perception of pain [5, 13]. Nociceptive responses are reflexes that do not change regardless of motivational priorities [5]. Pain, however, involves a negative emotional state that motivates an animal to rapidly learn to avoid a noxious stimulus and thus prevent a second exposure [14]. Consciousness is not always necessary for an animal to avoid noxious stimuli or obtain a motivational state [14].

Many cite the vastly different physiologies of invertebrates as a reason why they do not experience pain. However, the high conservation of nociceptive processes means that molluscs, which have some of the most complex nervous systems among invertebrates, are used as a model for the pathways that may be involved in the human experience of pain. In these studies, the molluscs are exposed to noxious stimuli that would be considered painful in vertebrates [14]. However, some molluscs lack a centralized nervous system, myelinated nerves, and have different synapses than vertebrates, which could cause a difference in experience [14]. However, some physiological differences may not make a difference in the experience of pain. In fact, some invertebrates have the capacity for complex visual processes even with the absence of a centralized visual cortex and if pain mechanisms work similarly, then a centralized nervous system may not be necessary for the perception of pain [14].

Researchers use behavioural indicators to determine whether invertebrates have the capacity for pain, because their nervous systems are so different from that of vertebrates [15]. One type of experiment used is modelled after drug tests for pain medication in vertebrates, where a drug is considered effective at decreasing pain when it changes an animal's behavioural responses to noxious stimuli after administration [6]. Using similar methods to those used with vertebrates, Manev and Dimitrijevic [6] found that *Drosophila* respond similarly to rats both in the ability to have nociception blocked by action against the $GABA_B$ receptor system and in behavioural responses to heat. They also found that effective analgesics in mammals cause anti-nociceptive effects in *Drosophila*. Similarly, other authors [18] found that prawns show nociceptive behaviour when a noxious stimulus is applied to one of their antennae. Benzocaine prior to administration of a noxious stimulus eliminated escape behaviour in prawns and later reduced location specific grooming and rubbing of the treated area [18]. Specific grooming and rubbing may act as a pain coping strategy for prawns and it also suggests that a higher level processing is involved in pain mediation other than simple reflex [18].

Another method of behavioural assessment of a nociceptive reflex against a pain experience is by testing the motivational priorities of an animal against a noxious stimulus. A severe electric shock to the abdomen will cause a hermit crab to evacuate its shell and start grooming the shocked area [15]. Again, directed grooming of an affected area is a consistent indicator of pain. Hermit crabs were more likely to move to a new shell after receiving a shock, and when moving into it, they spent less time examining the new shell, suggesting an increased motivation to leave the shell where they experienced the shock [15]. Exhibiting a motivation to leave their shell and rapidly enter a new one suggests that the hermit crabs experienced a pain-like sensation rather than just a nociceptive reflex [16].

The ability to experience pain increases an individual's ability to survive and reproduce [5]. The sensation of pain predicts tissue damage from noxious stimuli, which could make it a common process with similar mechanisms in varied complex biological systems [17]. However, the only way to prove that an animal exhibits pain, not just nociception, is through subjective experience. This is not possible in invertebrates or any vertebrates other than humans. Instead, responses to drugs, behavioural changes, and motivational changes are used to determine whether animals experience pain. Using these methods for testing pain, the invertebrates mentioned previously and possibly others exhibit similar results to those shown by many vertebrates suggesting that some invertebrates have the capacity for nociception if not also the emotional experience of pain. Regardless of whether invertebrates have the capacity to experience pain and suffer emotional stress, they should receive an analgesic when subjected to any procedure that could cause pain [19]. Invertebrates, just like vertebrates, display withdrawal or escape behaviours when exposed to mechanical, chemical, or electrical stimuli [19]. Anaesthetic and analgesic agents can prevent withdrawal and escape behaviours in invertebrates. For example, anesthetizing *Aplysia* prevents neuronal sensitization, which can then interfere with studies on neuronal plasticity [14]. The types of anaesthetic agents used on invertebrates are similar to those used in vertebrates, but can cause differences in effect due to physiological differences. Carbon dioxide is a controversial anaesthetic agent for both vertebrates and invertebrates; instead, volatile anaesthetic agents such as isoflurane are less controversial and more effective [19]. Diluted lidocaine can act as a post surgery topical analgesic to reduce any postoperative pain or stress [19]. Reducing postoperative pain can potentially increase recovery time, animal welfare, and increase scientific validity.

STRESS AND COPING

Stress acts as an adaptive response to environmental conditions outside an animal's normal physiological range, disease, or threatening stimuli [5]. A stress response in vertebrates involves a coordinated cascade of behavioural, autonomic nervous system (ANS), and neuroendocrine reactions in the hypothalamic-pituitary-adrenal axis [20]. Catecholamines released from the adrenal medulla by the actions of the ANS in vertebrates act as a fast stress response to fight or flight situations [20]. The vertebrate stress response system originates in the invertebrate nervous system [21]. While invertebrates do not possess the same structures as vertebrates, they similarly release biogenic amines in response to acute stressors followed by a neuroendocrine factor [22].

Exposure to chronic stress typically increases basal levels of stress hormones in both vertebrates and invertebrates [22]. A stress response in animals acts as a short term adaptive coping mechanism, but can inhibit normal functions when prolonged [20] Chronic stress decreases feeding, increases weight loss, and increases basal hemolymph in crickets [23]. Scorpions exposed to stress by prolonged desiccation also show a decrease in body mass and an increase in carbohydrate catabolism [24]. Purple sea urchin larvae (*S. purpuratus*) delay metamorphosis when exposed to thermal stress, which potentially promotes their survival in constantly changing intertidal regions [25]. Even sponges (*I. basta*) when exposed to handling stress exhibit tissue regression as a response mechanism [26]. Exposure to acute stressors results in the release of crustacean hyperglycaemic hormone (CHH) and heat shock proteins in the American lobster [27]. CHH works similarly in crustaceans as glucocorticoids work in vertebrates [5]. Catecholamines promote energy mobilization, blood vessel dilation, and increase muscle contractility, cardiac output, and respiratory rate in response to stressors [20], which makes their concentrations a useful indicator of sublethal stress in aquatic invertebrates [28].

Invertebrates exhibit a similar stress response to vertebrates after experiencing pain (see previous section). Morphine and pathways using morphine that limit nervous and immune functions have been found in invertebrate tissues making opiates and opioid signalling a conserved endogenous signalling process [21]. Opioid peptides stimulate immunocyte mobilization in both invertebrates and vertebrates [21]. The sensing receptors *Hm*TLR1 and *Hm*NLR involved in neuroimmune responses in leeches (*H. medicinalis*) have similar activities and distributions as in vertebrate species [29]. Also, adrenocorticotropin controls immunoregulation and some signalling processes, which makes it part of a stress response in organisms with at least 500 million years of divergence in evolution [21].

COGNITION

The public believes that invertebrates are capable of experiencing pain, but do not possess advanced cognitive processes [1]. The exception to this thought is that bees are believed to have a robust and plastic working memory and capacity for decision making [30]. However, it is cephalopods, not bees that have gained legislative protection due to their advanced cognitive abilities. Indeed, cephalopods have the ability to solve complex tasks and puzzles that many vertebrate species are unable to solve. Octopuses have the ability to learn by various methods and benefit from environmental enrichment [31]. For example, *Octopus vulgaris* discriminates between different

Figure 1
Juvenile European lobsters (*Homarus gammarus*) reared in enriched environment (left) approach a shelter sooner than individuals reared in non-enriched environment during a behavioural test of exploration (right). Photo by M. Della Gala

objects and learns through operant conditioning and observational learning [32]. Giant Pacific octopuses discriminate individual humans [33], while *Octopus vulgaris* recognise and remember a familiar conspecific for at least one day [34]. Providing enrichment and increasing the amount of experiences an octopus encounters will increase its ability to cope if released into the wild [35]. It is this apparent cognitive capacity and ability to learn that has led to increased legislative protection for the use of cephalopods in some countries.

Social learning in some vertebrates suggests a higher level of awareness; however, this idea usually does not translate to invertebrates that display similar cognitive capacities [36]. Social learning tends to develop in animals that have parental care, interactions between multiple generations, and frequent interactions with other conspecifics [37] and allows animals to learn about their environment quicker [38]. Adult desert locusts show local enhancement when feeding [37]. Bumblebees also exhibit local enhancement with flower choice by preferring flowers that other conspecifics visit [38]. Fruit flies use social learning to determine which substrate to lay their eggs [39]. Social enhancement may not necessarily require higher cognitive abilities; however these observations suggest that some social invertebrates have the capacity for social learning, which does not exclude more complex forms of social cognition.

An animal that experiences a motivational trade-off must use some form of processing system in which the needs of the animals are weighed against each other [5]. When an animal makes a trade-off between a requirement such as food and an escape response to a noxious stimulus, then it is more likely to involve some sort of central processing rather than being purely a reflex response [16]. In the case of hermit crabs, they choose to remain in a high quality shell even after receiving an electric shock, because the quality of the shell outweighs the pain of the shock [16]. Similarly, hermit crabs evacuate low quality shells at a lower shock threshold. Hermit crabs evacuated a shell when the shock was highly aversive, suggesting they would rather risk a vulnerable, naked state than remain in a protected state with the potential for more electrical shocks [16]. Behavioural observations of some hermit crabs after being shocked suggest an awareness of the site of the problem since they would investigate the shell attempting to remove the adverse stimuli, much as they do when sand is caught inside the shell. The hermit crabs will choose to change their shell even if the opportunity to move into a new shell is delayed suggesting the crabs have a memory of the event [16].

Self-referencing refers to the ability of an individual to match a target individual to themselves [40]. The ability to know oneself from another is needed for survival by allowing an individual to determine whether other individuals are the right species or sex to mate with, thus having self-awareness allows an individual to discriminate between oneself and others [40]. Hermit crabs have the ability to look at another hermit crab and make a decision to enter a competition for the available resources [41]. Information gathered by the crabs prior to contesting resources include assessing internal volume of a competitor's shell based on visual cues such as shell size and shell fit of the other crab and prior experience with the type of shell involved [41]. The hermit crab then compares information about its own shell and information gathered from a competitor's shell and makes a decision on whether to initiate competition for the shell [41]. In this sense, hermit crabs and potentially other invertebrates have the ability to self-reference through their ability to determine information about themselves and other hermit crabs.

Other invertebrates have increasingly been tested in similar manners to vertebrates and cephalopods to determine their capacity for higher order cognition despite the general lack of a centralized nervous system. Honeybees exposed to vigorous shaking show a pessimistic cognitive bias towards an intermediate stimulus [42]. Decapod crustaceans form complex associations between two or more stimuli and respond to these stimuli adaptively while maintaining the memory of association for a long time [12]. Pit building antlions use associative learning as sedentary predators to efficiently detect and capture prey [43]. Associative learning increases the fitness of the antlions by decreasing prey capture time and increasing feeding efficiency, which results in faster growth for the individual [43]. In the previously mentioned study by Barr and colleagues [18], directed grooming and rubbing by prawns after experiencing a noxious stimulus suggests a higher level processing than a simple reflex response. Fruit flies exhibit relief learning when presented with an odour that predicted the end of a traumatic experience [44]. Relief learning helps to show the behavioural consequences an animal experiences in response to a painful or traumatic experience [44]. Fruit flies also learn through operant or classical conditioning to avoid noxious stimuli [17]. The ability to learn and show complex behaviours is used as evidence that *Drosophila* is complex enough to be used in pain research [17]. By these measures, it is clear that many invertebrates show similar levels of cognition as many vertebrate species.

INDIVIDUAL DIFFERENCES AND PERSONALITIES

In animal research, personality refers to behavioural and physiological clusters of traits that characterize individuals of the same species, independent of age and sex, when they are consistent over time. Animal personalities may develop early in life, possess an epigenetically regulated basis, neuroendocrine correlates, and are comparable to human personality traits [11, 45, 46]. Invertebrates may seem unlikely to possess personalities but some species typically exhibit consistent individual differences in behaviour and evidence is accumulating in this respect [47]. Studies have found evidence of the presence of personality in invertebrates such as squid, octopus, spiders, ants, crustaceans, snails, and sea stars [11, 46-48]. Honeybees have shown evidence of not only having individual personalities, but also a collective colony personality [49]. Practical experience handling crustaceans such as crabs reveals differences in individual reactions of the animals towards handlers within a range of hyperactivity or aggression to freezing [11].

Ignoring the effect of personality traits may cause differential results in scientific research and other uses of animals [11]. Individuals react differently to stress and artificial housing conditions, which can lead to differences in the welfare of individuals [45]. One example can be seen in captive breeding programs. Crustaceans raised in a captive breeding program will not be subjected to predation risk making bolder animals more likely to have reproductive success in captivity [11]. When the offspring of these animals are released into the wild, their genetic profile will favour a bold personality, which will also increase their risk of predation resulting in a reduced reproductive success in the wild [11]. Bold individuals tend to have more high-risk foraging strategies that expose them to greater predation risk [48].

Also, the presence of multiple personalities in a population will increase the ability of the species to survive changes to their environment [11]. Bridge spiders show personality polymorphism and behavioural plasticity, and their success in high density groups in urban environments seems due to the presence of a balanced mix of both aggressive and tolerant individuals [50] with a population consisting of high between-individual and low intra-individual variability in behaviour [50]. Black turban snails (*C. funebralis*) and ocher sea stars (*P. ochraceus*) exhibit a predator-prey relationship that alter personality types in both populations between bold or shy prey and active or inactive predators [48]. This predator-prey personality-type feedback can be seen among many predator-prey interactions resulting in multiple personality types in both populations [48].

Personality can change across an individual's development [45]. Personality studies of firebugs across ontogeny suggest that firebugs have more consistent behaviours during adulthood and show more boldness through decreased latencies to explore, more thorough explorations, and greater activity [51]. A study on field crickets showed that bold individuals become shy and shy individuals become bold when exposed to a predator [52]. This suggests that different personality types have different strategies for predator avoidance. However, in a control setting, cricket behaviour was more consistent suggesting that context plays a role in the expression of a bold personality [52].

The ability to see personalities in animals has made them popular with the general public and has increased the public's desire to protect charismatic animals. When octopuses were first displayed in aquaria, they changed public opinion of them from that of a scary monster to one of wonder through their movements and ability to camouflage [53]. Octopuses then became more popular in research due to their dual nature as a "simple" animal capable of performing complex behaviours [53].

PRACTICAL CONSIDERATIONS AND ADVANTAGES FOR PROMOTING INVERTEBRATE WELFARE

The practicality involved in promoting invertebrate welfare is difficult to assess due to the large number of species involved. The lack of information about many species makes efforts to increase the welfare of all invertebrates as a whole difficult. Standard guidelines and methods of euthanasia for invertebrates need to be developed and implemented to ensure humane endpoints [4]. For example, one problem with using anaesthetic agents on cephalopods is that the depth of anaesthesia is difficult to assess [19]. Standardizing guidelines would ensure that invertebrates would receive the most humane care based on the most up to date research available. The amount of invertebrates used in research is not generally recorded due to difficulties in counting certain species such as *Drosophila*, *C. elegans*, or *Artemia* [4]. The methods of husbandry, breeding, disease monitoring and treatment, and transportation vary between the species used in research [4]. Some species of invertebrates are easy to acquire, whereas the methods of acquiring some species may be questionable as to the ethics and environmental impact involved in acquisition [4]. While review of invertebrate research is not required, with the exception of cephalopods in some countries, it should be included as a part of protocols to maintain high standards of research and the three R's (replace, reduce, refine) involved in any animal use [4].

Increasing animal welfare in commercial invertebrate production can provide many benefits. Removing stressors or reducing the effect of stressors will benefit invertebrates in production settings. For example, reducing handling stress in oysters including the use of a rest period will improve the effect of any anaesthetics administered [19]. Mather and Anderson [40] recommend quick and humane euthanization for cephalopods harvested for human consumption for both ethical concerns for the welfare of the animals and to prevent stress from reducing the quality of the meat harvested. Removing farmed abalones (*Haliotis sp.)* from substratum for commercial production requires using mechanical force, which can result in a slow recovering injury or death to the animal [19]. In this instance, the use of a muscle relaxant or anaesthetic agent could prevent both stress and mechanical injuries to the abalones [19]. By preventing stress and injury, the farmed abalone will be more likely to reach the proper size for harvest faster with a lower mortality rate for the whole operation, which could potentially benefit farmers economically.

Restocking captive bred invertebrate populations into the wild highlights the need for increased captive welfare. Restocking of lobster species has occurred in many areas to replenish natural stocks that have been damaged by overfishing [3]. When rearing lobsters for release, it is important that hatchery reared animals have the ability to survive in the wild [3]. They must develop normal feeding, anti-predator, and reproductive behaviours, otherwise restocking efforts will result in economic loss or failure [54]. Higher welfare conditions in captive breeding facilities through methods including enrichment (*e.g.* shelters in young lobsters, *Figure 1*) and exposure to the risk of predation may provide invertebrates with important early experiences that shape the individual behavioural profiles and potentially increase the likelihood of survival when released into the wild [55].

Invertebrates benefit the environment through ecosystem stabilization, energy and nutrient transfer, trophic level maintenance, plant protection, and by providing habitats for other organisms [1]. The diverse interactions between invertebrates and the environment increase ecosystem stability. Invertebrates accelerate the decomposition of waste materials, which, in turn, increases nutrient availability in soil for plant production [1]. Invertebrates are useful indicators of environmental quality and are increasingly used to monitor water pollution and heavy metal contaminations in aquatic ecosystems [1, 56]. Molluscs, for example, are both environmentally and economically important due to their ability to filter water and debris and also act as a source of food, pets, display animals, and research animals [19]. Invertebrates help with plant pollination and seed dispersal, which is essential for most forms of agricultural production [1]. Honeybees, in particular, are important for agriculture by pollinating important food crops as well as providing honey, wax, and other hive products [8]. Due to the essential functions that invertebrates serve, there should be at least some ethical concern about their treatment to maintain the ecosystem services they provide.

CONSIDERATIONS ON CONSCIOUSNESS IN INVERTEBRATES

Arguments including whether invertebrates have minds or consciousness, arguments-by-analogy, and physiological differences are used as ethical dividers to prevent invertebrates from being covered under legislation. Directive 2010/63/EU of the European Parliament states that animals have an intrinsic value and they should be treated as sentient creatures [10]. The presence of a mind would make an animal capable of suffering and worthy of the same sympathy one would show to another human, however, the general public does not believe that invertebrates have minds [57]. Some invertebrates show behaviours consistent with those expressed in having a mind such as navigation in bees and advanced planning in jumping spiders [57]. However, Carruthers [57] argues that feelings of concern are not necessarily required, even though invertebrates may possess similar minds as humans. While Carruthers [57] disagrees that invertebrates require concern, the criteria he uses to justify some invertebrates having minds is consistent with justification used to provide welfare legislation for vertebrates.

Invertebrates are considered substitutes to vertebrates for use in biomedical research such as physiological, genetic, behavioural, ecological, and toxicological studies [2]. Evolutionary conservation of physiological processes is used as a justification for using "lower" animals to study processes that will then be applied in "higher" animals such as humans [14]. However, if evolutionary conservation has made the processes so similar, it would suggest that "lower" animals would experience suffering similarly to the "higher" animals and in this sense, snails, octopuses, mice, and chimpanzees all have the same potential to suffer [14]. Due to its status as a "lower" animal, the fruit fly is used to discover new genes and the systems involved in the genes' behavioural output, which are then used to determine whether a human correlate of the genes exists [58]. There may be some homologous genes and neurotransmission systems between fruit flies and humans, but there are differences in the behaviours of fruit flies and humans [58]. Due to differences between insects and humans, using *Drosophila* as a model for pain would cause some drugs to be ineffective in humans that would be effective in insects and vice versa [17]. For example, anger and aggression in fruit flies and humans may share some basic genetic mechanisms, but the expression of the behaviour is different between the two [58]. These differences would require that any drugs found effective in *Drosophila* would then have to be tested in various vertebrate species anyway before a trial version was available to humans, because, in some cases, compounds may cause the opposite or different effects in vertebrates that occur in invertebrates as is the case with some sexual hormones [59].

Consciousness is believed to be a widespread phenomenon that is unique to every individual animal based on experiences that make that animal what it is [60]. However, no evidence of conscious affective states exists in many invertebrate species [61]. Many invertebrates such as zooplankton or coral polyps most likely do not have a nervous system that would generate conscious emotion or have a lifestyle that would require them to develop any form of it [61]. But, if a human is not able to perceive an environment, for example, in the way that a bat does through sonar, it does not mean that a bat does not have consciousness [60]. While it is impossible to determine whether invertebrates experience emotion, it is likely that emotions evolved, and while invertebrates may not feel anger the same way humans do, it is possible that they experience some form of analogous experience [58]. A consistent use of argument-by-analogy for assessing the capacity of non-human animals to suffer would suggest that invertebrates have the capacity to suffer unless there is strong evidence suggesting otherwise [36]. The experience of pain or nociception may differ in some ways, but as long as it leads to a negative mental state, then suffering still occurs. As Sherwin states, the "absence of evidence is not evidence of absence," and until sufficient evidence of absence exists, invertebrates should be given the same consideration as any other animal species [36].

CONCLUSION

Currently, little concern is shown for the welfare of invertebrates unless there is a need to keep them alive [40]. Even "more advanced" marine animals such as fish face minimal welfare concerns as they die from asphyxiation as they are harvested from the ocean [40, 62]. Evidence suggests that some, if not all, invertebrates have the potential to suffer through current practices that do not take into consideration that invertebrates may experience something like pain and stress and have the capacity for advanced and unexpected cognitive abilities. Further, a recent review highlighted that interest in many aspects of invertebrate cognition such as social recognition systems is just beginning to gain momentum [63]. The negative feelings people have towards invertebrates makes conservation and welfare efforts challenging to introduce [1]. While it is unlikely that humans will develop affinities for many invertebrate species, public understanding of invertebrate science and education depicting the contributions invertebrates make to humans will help reduce negative perceptions of invertebrates [1].

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