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Keeping invertebrate research ethical in a landscape of shifting public opinion

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Abstract

Invertebrate study systems are cornerstones of biological and biomedical research, providing key insights into fields from genetics to behavioural ecology. Despite the widespread use of invertebrates in research there are very few ethical guidelines surrounding their use.

Focussing on two ethical considerations faced during invertebrate studies – collecting methods and euthanasia - we make recommendations for integrating principles of vertebrate research into invertebrate research practice.

We argue, given emerging research on invertebrate cognition and shifting public perception on the use of invertebrates in research, it is vital that the scientific community revisits the ethics of invertebrate use in research.

Without careful consideration and development of the ethics surrounding the use of invertebrates by the scientific community, there is a danger of losing public support. It is imperative that the public understand the significance of research that uses invertebrates and that scientists demonstrate their ethical treatment of their experimental subjects.

Keywords: Ethics, invertebrates, public perception, animal welfare

Introduction

Ethics in research shift constantly, and ethical standards are neither universal or immutable (Ferdowsian & Beck, 2011). Dramatic shifts in perception and attitudes towards ethics in vertebrate research in just the last century demonstrate just how far and how fast ethical standards can move. When, in 1982, Rollin presented a review to the US Congress of the available literature on providing analgesics for laboratory animals, the Library of Congress had only two papers (Rollin, 2006) on this subject. In 2011 there were over 11,000 relevant papers in the same library (Rollin, 2011). As well as an increased appreciation for the importance of controlling pain in animals in research, there have been shifts in scientific protocol with the development of the three R's principles (reduction, refinement and replacement), as set out in the book "The Principles of Humane Experimental Technique" (Russell & Burch, 1959). Despite the initially slow reception of the book (Balls, 2009), these principles are now key to modern research practices, having been adopted and promoted across the international research community (Farnaud, 2009; Lindsjö, Fahlman, & Törnqvist, 2016). Examples of bodies which now oversee the implementation the three Rs, as well as other aspects of animal welfare, include the Australian and New Zealand Council for the Care of Animals in Research and Teaching (established in 1987)(University of Adelaide, 2018), the Canadian Council on Animal Care (established 1968)(CCAC, 2019), and the National Centre for the Replacement, Refinement and Reduction of Animals in Research in the UK (established 2004)(N3Rs, 2019).

Historical shifts in ethical stances towards vertebrate experimentation highlight how rapidly ethical norms have moved to stay in line with scientific understanding of animal suffering. Keeping ethical frameworks current with our understanding of the systems that we are working on is critical to ensuring that our work is carried out with the highest levels ethical and moral integrity.

Moral obligations of researchers and effects of previous shifts in ethical frameworks

Shifting views of the public and scientific community, and the legislation that have followed these shifts in the past have provided hugely important improvements in animal welfare by today's standards. A key example of this is the British Act of 1876 (Cruelty to Animals Act), in no little part sparked by the public reaction (and similarly outraged reaction from a section of the scientific community (Dewsbury, 1990)) to the highly publicised rise in anatomical studies being carried out in France at the time (Rollin, 2006). Infamous examples of these studies included cases like the public dissection of a dog carried out in the UK lasting two days without anaesthetic, leaving the animal without pain relief on the dissecting table overnight (Franco, 2013). Cases like this highlight how important shifts in ethical views from the public and scientific community are to push through legislation preventing studies which by today's standards are inexcusably cruel.

Changes in attitudes to ethics, particularly within the use of animals in research, have also provoked concerns over the costs to the development of science that restricting practices may cause. Even the British Act of 1876 (Cruelty to Animals Act) was subject to concerns

and criticisms surrounding its possible impact on science (Dewsbury, 1990). Similar fears are voiced today over contemporary ethical issues. One recent case study includes concerns that unease over the use of human cells being included in chimeras could halt the progress of chimera research, and the potential loss of medical advances that could be gained from their study (Hyun, 2016; Inoue, Shineha, & Yashiro, 2016).

Potential concerns from the scientific community about calls to consider invertebrate ethics

We expect that, similarly to times of change in vertebrate ethics (Cohen, 1986; Dewsbury, 1990), suggestions of change within the ethics of invertebrate research will be met with concern from some branches of science about potential limits to research progress. We would like to make clear that we are not arguing against using invertebrates in research, nor against euthanising invertebrates during research. Rather, we are arguing for careful consideration and discussion surrounding which methods are most appropriate for use on any given system, particularly in terms of ensuring ethical euthanasia of study organisms, and during collection of wild invertebrates.

For vertebrates, there is already a well-established field investigating the appropriateness of different methods for procedures that have welfare implications, such as euthanasia (van Rijn, Krijnen, Menting-Hermeling, & Coenen, 2011; Shine et al., 2015; Valentim et al., 2016). These studies allow researchers to make informed decisions on the appropriateness of different methods. However, in invertebrates, this research is lacking in many systems, with gaps in research into even simple metrics like comparing the time different euthanasia methods take to work. These types of study would be highly valuable, allowing researchers to make informed decisions on how appropriate a method may be for their study species. Many researchers already aim to do this (Cooper, 2011; Lewbart & Mosley, 2012), and we hope that this article will encourage further discussion, research and debate around this topic.

Risks of mismatched ethical expectations between the scientific community and the public

Continual reassessment and consideration of ethical frameworks has the secondary function of not only ensuring the highest level of care for study subjects, but also of protecting scientists and the research they do from unexpected backlash from the public. While the motivations behind developing ethical frameworks to protect scientists, and developing frameworks to protect their study subjects may come from different places, they converge towards the same results and both should be considered in the debate surrounding invertebrate ethics.

When considering the role of ethical frameworks in protecting researchers from public backlash, the historical literature is littered with examples showing how mismatched expectations in ethics can have severe negative consequences for researchers and the research they conduct (Knaiz, 1995; Pettite, 2017). In recent history, examples can be taken from the 1970s and 1980s with the rise of the animal

liberation movement, where polarised opinions surrounding animal ethics resulted in some factions turning to violent acts like arson, letter bombs and harassment, as well as protest (Knaiz, 1995; Wilson, 2004).

One case from study the animal liberation movement described in detail by Pettite (2017), is the public protests against the “great cat mutilation” in the 1970s, the aftermath of which involved the retirement of the scientist, Lester Aronson, and the dissolution of the American Museum of Natural History’s Department of Animal Behaviour (AMNH). It was claimed that Aronson’s work at the AMNH on cat sexuality complied with existing regulation and was accepted within the scientific community (Pettite, 2017); however, in 1970s New York perceptions towards cats were shifting from pests to pets with the ability to feel. Protests broke out outside the museum, arguing against the ethics of the research and attacking Aronson’s morals personally (Pettite, 2017). We do not believe that currently shifting perceptions in invertebrates would result in a repeat of the ethical struggles of the 1970, but use this as an extreme example to demonstrate how important preserving public trust in the ethical frameworks used in laboratories is to maintaining links and open discourse with the public.

Today, given the prevalence of social media, and ease of organising online campaigns, researchers are more vulnerable than ever to rapid public outrage to perceived ethical transgressions. Recent examples of the campaigns against Christine Lattin and Christopher Filardi demonstrate how both established and junior researchers can be targeted in online animal rights campaigns despite their work being carried out within ethical guidelines set by the scientific community as well as government legislation. In the case of Lattin, a viral video about her work on birds was circulated by PETA and helped to fuel a campaign of harassment at her place of work and home (Grimm, 2017). In the case of Filardi, petitions circulated demanding him to be fired and jailed reached thousands of signatures, after he took a single specimen of rare bird for a museum collection (Filardi, 2015; Johnson, 2018). In both cases the ethical guidelines from the scientific community and government legislation did not match with the public perception of what ethical standards within science were expected to be. These mismatches in ethical perception, and the negative consequences resulting from them, highlight how important both up-to-date ethical frameworks are, as well as public education about current ethical norms are to protecting researchers from public backlash.

In these cases, there was an ethical gap in viewpoints despite the ethical frameworks centred on vertebrates, which have already been considered and developed in detail. So far, the ethics surrounding invertebrate experimentation has received far less attention. Recent developments in our understanding of invertebrate consciousness (Mendl, Paul, & Chittka, 2011; Klein & Barron, 2016) and recent concern from the charity sector about the ethics of experiments on invertebrates (Knapton, 2017; Barkham, 2017), point to a need to revisit the ethics of invertebrates in science, to prevent the development of an ethical gap between researchers and the public.

Current state of ethics for invertebrates

Invertebrates are key experimental models in a diverse range of research fields from medical biology (Sanz et al., 2017; Rittschof & Schirmeier, 2018) to behavioural ecology (Kralj-Fišer & Schuett, 2014; Hollis & Guillet, 2015; Barron & Klein, 2016). However, despite the importance and widespread use of invertebrates in research there are few ethical guidelines governing their use in science. Legal protection of invertebrates in research is inconsistent between countries: for example, regulation of crustaceans euthanasia in New Zealand (Ministry for Primary Industry, 2017), but not in the UK. Currently, what ethical guidance there is comes from guidelines on invertebrate use recommended by scientific societies like the Association for the Society for Animal Behaviour (ASAB, 2018). These society guidelines are used as a reference by editors considering papers for publication in journals associated with the society, however outside decisions on society journal publications and small society research grants, these guidelines are not widely enforced. While existing legislation and journal-led guidelines are clearly important, we would argue that more can be done to standardise and encourage consideration of invertebrate ethics in research.

Ethical exceptions among invertebrates

Among invertebrates, crustaceans and cephalopods are granted some ethical protection which aims to reduce suffering. For crustaceans the protection does not extend to research but covers transport and euthanasia in certain countries. These include New Zealand where crabs, rock lobsters and crayfish have to be insensible before death (Ministry for Primary Industry, 2017), as well as Switzerland which requires crustaceans to be stunned before death, and where crustaceans cannot be transported in ice or ice water. The regulations in banning transport of crustaceans in ice has also been recently adopted by Italy (Italian Supreme Court, 2017).

Cephalopods on the other hand, have greater legislative protection. Recently the EU introduced extensive regulation, with legislation covering an estimated 700 species cephalopods (Fiorito et al., 2014) during research under Directive 2010/63/EU (Berry, Vitale, Carere, & Alleva, 2015). This was a milestone decision based on the recommendations of a scientific panel who concluded there was evidence for pain perception in cephalopods; this decision was not uncontroversial, however, with concerns voiced over the impact this new status may have on science (Fiorito et al., 2014). Following the changes to EU legislation, the UK then changed its own legislation bringing it more in line with the EU with the regulation of all living cephalopods (except cephalopod embryos) in research (Animals (Scientific Procedures) Act 1986, Act Amendment regulations, 2012). Outside Europe, the status of ethical regulation of the use of cephalopods is less clear. In Canada the legality of animal research is outside federal control due to the Constitution Act 1867, but instead is controlled at a provincial level. However, to gain federal funding institutional certification is needed from the Canadian Council on Animal Care (CCAC, 1993) (CCAC). The CCAC suggests that “cephalopods and some other higher invertebrates”, have complex nervous systems and may be eligible for inclusion under certain ethical frameworks (CCAC, 1993).

The consideration of cephalopods, and more recently the limited inclusion of crustaceans,

in legislative frameworks (see Table 1) to reduce suffering sets a precedent for including invertebrates in the conversation surrounding standards of care for animals used in research. In cases where these invertebrates have been included under ethical legislation, inclusion has been largely due to the perception these animals show advanced cognition and the ability to experience pain or suffering (Fiorito et al., 2015; Rowe, 2018). It could be the case that these are “exceptional” invertebrates, different to all other invertebrates in their cognitive abilities and ability to experience pain, or it may be the case that future research demonstrates similar capabilities in other species, and that these are the first of many which will be afforded regulation as further understanding of invertebrate cognition is gained.

Recent advances in understanding invertebrate cognition

Understanding cognition in invertebrates is crucial to invertebrate ethics, as perception that a species or group has the cognitive capacity to experience pain or suffering has been key to the development of existing legislation protecting first vertebrates, and now certain invertebrates (Fiorito et al., 2015; Rowe, 2018). The capacity and complexity of invertebrate brains and their resultant cognitive abilities is an area of considerable contemporary study and debate (Chittka & Niven, 2009; Barron & Klein, 2016; Klein & Barron, 2016; Perry, Barron, & Chittka, 2017). While it was once assumed that large brains were needed for cognitive complexity, it is now appreciated that that brain size has less of a role in determining cognitive capacity than once supposed (Chittka & Niven, 2009; Perry et al., 2017). Instead, structural features of brain architecture like modularity and interconnectivity have a greater role (Chittka & Niven, 2009). Findings that the structure of the brain is more important than brain size challenges previous assumptions that because many invertebrates have small brains they have little cognitive complexity, and raises the possibility of more cognitive complexity in invertebrates than previously assumed (Chittka & Niven, 2009). Further evidence for the role of brain architecture in dictating cognitive capacity comes from the study of complex behaviours now known to occur in invertebrate systems. Invertebrates display many behaviours once thought to be exclusive to larger-brained organisms, including ability to complete complex social learning tasks, recognise multiple individuals of the same species and even use tools (Perry et al., 2017). However, it is still not understood whether invertebrate cognition extends to pain, defined as “a subjective experience of discomfort, despair and other negative affective states” (Adamo, 2016) and consciousness, defined as “marked by the presence of subjective experience” (Barron & Klein, 2016).

Recent behavioural and physiological work has gone so far as to suggest that there is some evidence for consciousness in invertebrates. Behaviourally, bees which were subject to a simulated dangerous environment went on to show “pessimistic” cognitive bias, suggesting capacity for subjective experiences (Mendl et al., 2011), while bees which have been injured will self-administer analgesic (Groening, Venini, & Srinivasan, 2017). With regard to physiology, analogous structures found in the invertebrate and vertebrate brain have been used to suggest that similarities in capacity for consciousness may exist (Barron & Klein, 2016; Klein & Barron, 2016).

Table 1: Summary of important changes to invertebrate ethical legislation			
Date	Summary of action	Country	Legislation
2010	Regulation on the treatment of an estimated 700 species of cephalopods in research	EU wide	Directive 2010/63/EU (Berry et al., 2015)
2012	Use of all living cephalopods (except cephalopod embryos) in research is regulated.	UK	(The Animals (Scientific Procedures) Act 1986, Act Amendment regulations 2012.
2017	Crabs, rock lobsters and crayfish must be insensible before death.	New Zealand	(Ministry for Primary Industry, 2017)
2017	Transport of crustaceans in ice banned.	Italy	(Italian Supreme Court, 2017)
2018	Crustaceans to be stunned before death, and where crustaceans cannot be transported in ice or ice water.	Switzerland	(Schweizerische Eidgenossenschaft, 2018)

Changing attitudes to invertebrates

Given the long-term appreciation of cephalopod cognition, it is perhaps unsurprising that dialogue surrounding ethical concerns about improving invertebrate ethics often hinges on cephalopods. Current concerns about their care can be seen in recent petitions on banning live consumption of octopus in US restaurants, one of which gained over 47,000 signatures (Wolverton, 2019).

However, in light of research on lobster pain perception (Barr, Laming, Dick, & Elwood, 2008; Elwood, 2012), there has also been a flurry of petitions in multiple countries, demanding a range of tighter ethical controls over treatment of crustaceans. In the UK, a recent petition demanding the British Government include lobsters and crabs under the Animal Welfare Act, exceeded 41,000 signatures (Crustacean Compassion, 2018). In the USA, PETA has started campaigns against the current practices used for killing lobsters for supermarket consumption (Toliver, 2018). Other countries who have already taken steps to improve crustacean welfare are summarised in table 1.

Addressing invertebrates more broadly, animal rights organisations (PETA, 2017; Peta2, 2018), and individuals on social activism websites (Geer, 2015) have voiced concerns about the ethical treatment of invertebrates. While there has been less uptake from the wider public on these issues from a purely ethical angle; there is increasing real public concern about the plight and decline of pollinators, with over 99,000 people signing a petitioning against neonicotinoids to the UK government (Petitions, 2015) after concerns were raised about the impact of these pesticides on pollinators (Whitehorn, O'Connor, Wackers, & Goulson, 2012; Van der Sluijs et al., 2013; Rundlöf et al., 2015).

The current interest and concern about declining pollinators may appear to be outside the scope of considering invertebrate ethics in research, but in fact it highlights the importance of strong public education about the practices involved in studying invertebrates in the field. In many cases the critical research to investigate invertebrate declines, including pollinators, requires the killing of thousands of invertebrate specimens. An example of public concerns about the ethics of conducting research that involves invertebrate mortality, given the decline in pollinators, is the 2017 Great Wasp Survey (Knaption, 2017). The Great Wasp Survey was designed as a public science project with public recorders building and setting up wasp traps, collecting the trapped wasps, and sending them to scientists to be identified. Although the project was intended to understand wasp species distribution across the country, and to provide data to support conservation, the project was aggressively criticized for killing pollinators (Barkham, 2017). In fact, the project captured no queens, had a very limited by-catch and just two weeks of citizen engagement resulted in data comparable to four decades of expert sampling (Sumner, Bevan, Hart, & Isaac, 2019).

Public perception of invertebrate studies is important to multiple aspects of carrying out work on invertebrates. Large scale citizen science projects, publicly funded projects, or work which relies on volunteer recorders, all depend on a positive public response to the work being done, and the view that the work is ethically justified. It is therefore important that projects with ecological sampling, and public participation be ethically transparent and that steps are taken to mitigate potential ethical concerns.

Conservation concerns

Most of the public concerns about studies which take specimens from the wild (both vertebrate and invertebrate), centre on the conservation issues this may cause (Knapton, 2017; Barkham, 2017; Johnson, 2018). These types of concern should be taken seriously when considering invertebrate ethics. While the impact of long-term sampling on invertebrates has not been well studied, among the studies which have been done, conservation concerns have been raised over a few very specific forms of sampling. These include examples like destructive sampling of bromeliads to investigate invertebrate communities which live within them (Jocque, Kernahan, Nobes, Willians, & Field, 2010), the off-target effects of formalin use for earthworm sampling on environmental microbial communities (Čoja, Zehetner, Bruckner, Watzinger, & Meyer, 2008) and lethal sampling being used to monitor rare or translocated invertebrates (Bowle & Frampton, 1998; Bowie, Hodge, Banks, & Vink, 2006). In each of these examples, less destructive alternatives to these sampling methods have been investigated (Bowle & Frampton, 1998; Čoja et al., 2008; Jocque et al., 2010). Outside these very specific examples, there is little evidence to suggest that the most collecting carried out as part of scientific studies poses any serious conservation threat to invertebrates. However, this is an area which would benefit from more systematic and data-driven assessment of sampling impacts.

Despite the lack of evidence for scientific collection impacting invertebrate communities, many research centres and individual studies already apply a principle of reducing possible impacts as far as possible. One example of a research centre applying these principles is the Nouragues Research Centre in French Guiana which prohibits the use of non-selective sampling methods like light traps or fogging (Centre national de la recherche scientifique, 2019) in order to reduce the impact of studies on bycatch species. Another example, this time from an individual study, is the previously discussed Big Wasp Survey, which aimed to reduce the impact that wasp collecting may have by ensuring collection only took place late in the summer, so most collected wasps would be nearing the end of their reproductive lives (Big Wasp Survey, 2017).

Overall, there is already some progress within the scientific community to mitigate impact that studies involving invertebrate collection may have, particularly in cases where the species are rare (Bowle & Frampton, 1998), or where sampling methods are damaging to the local environment (Čoja et al., 2008; Jocque et al., 2010). We argue that ethically, and in line with public opinion, this should be encouraged. However, there also needs to be space for well justified studies which use non-selective trapping throughout the year as these can be the only way to collect critically important data with important conservation outcomes (Hallmann et al., 2017; Lister & Garcia, 2018). In the cases of large scale non-selective trapping however, public engagement and education may also be important to communicate the justifications for the work, and to ensure a gap in ethical perspectives between the public and scientific communities does not emerge.

Suggestions for improving ethical practices around invertebrates

Mounting evidence for increased public awareness of and concern for invertebrates in research, particularly those collected from the wild, plus a developing understanding of the potential capacity for at least some invertebrate species to experience pain or to suffer,

suggests a need for invertebrate ethics to be revisited by the research community, and discussion opened with the public. Addressing these concerns will be important, not only to ensuring an appropriate standard of the welfare the invertebrate study systems, but also to maintaining public support for invertebrate-based research.

Here we present a set of five suggestions to improve invertebrate research ethics. In this paper we focus on case studies of euthanasia and wild collecting methods. These areas have been chosen as there are cases of each of these being the recent focus of public concern (Knapton, 2017), or legislative change (Rowe, 2018). We hope that exploring these areas will spark discussions about the other ethical questions surrounding invertebrate use in research.

1) Power analysis

Power analysis is a useful tool to determine the smallest number of individuals that can be used in an experiment while still providing appropriate statistical power, a practice long encouraged in work on vertebrates (Festing et al., 1998; Shaw, Festing, Peers, & Furlong, 2002), and used in many invertebrate studies already (Arnqvist & Henriksson, 1997; Evans, Clinton, Allen, & Frampton, 2003; Brereton, Cruickshanks, Risely, Noble, & Roy, 2011). Adoption of pre-study power analysis as standard practice among those who research invertebrates, and acceptance by journals of lower samples sizes (given appropriate justification of power), could be an effective way of reducing the numbers of invertebrates used in trials.

2) Selection of specific trapping methods to reduce bycatch

During sampling work, in addition to lethal sampling of focal species, with many trapping methods bycatch of non-target species is inevitable. The limited evidence available on target species suggests sampling for research has little effect on study populations (Gezon, Wyman, Ascher, Inouye, & Irwin, 2015), but very little work has been done on the impacts of trapping on non-target species. Even without population-level impacts of bycatch, if we were to apply similar ethical principles to invertebrate systems as are applied to vertebrate systems with the importance of reduction, refinement and replacement, reducing the amount of off-target mortality should be encouraged (Russell & Burch, 1959). In many cases these principles are already in place, driven by practical benefits of reduced specimen processing and sorting times (Cha et al., 2015).

3) Selection of specific trapping methods to reduce bycatch

Certain adaptations of trapping methods are employed to reduce non-target bycatch and can have an important role in changing which species are likely to be caught, hence reducing the impact of trapping on non-target species. Examples include altering the funnel structure of pheromone traps (Martín et al., 2013), changing the size of pitfall traps (Brennan, Majer, & Reygaert, 1999) or even changing the colour of traps (Clare et al., 2000). Many important studies on this area have already been carried out (Brennan et al., 1999; Pendola & New,

2007; Cha et al., 2015). Further research into methods of reducing off-target species capture could be effective in maintaining public support, particularly in large field studies, or studies with public involvement.

4) Make bycatch available for further use

In many cases reducing bycatch entirely may not be possible. In these cases, there may be real benefits to making bycatch available, accessible and advertised for study by other researchers (Buchholz, Kreuels, Kronshage, Terlutter, & Finch, 2011), and making the associated data open access. This would not be feasible for all bycatch, but high-quality or well-preserved bycatch, particularly if carried out as part of a large or long-term trial could contain a plethora of important information about a system that was not the focus of the study (Skvarla & Holland, 2011). In some cases, bycatch is already being used in other studies: one example is a project monitoring cerambycid diversity being conducted using the bycatch of a project specifically monitoring Asian Longhorn beetles (*Anoplophora glabripennis*)(DiGirolomo & Dodds, 2014). Making more bycatch available for study could provide important insights into the sampled systems and, in some cases, reduce the need for sampling similar areas a second time, reducing invertebrate mortality, as well as reducing the costs of these studies. Methods developed to enable collaboration among ecologists (Buchholz et al., 2011) could be beneficially adopted more widely.

5) Where possible minimising invertebrate suffering

Minimising animal suffering is key to the development of ethical guidelines for vertebrate studies, as well as for the small number of invertebrates which currently have ethical protection. It is likely to also be an important area of focus of invertebrate ethics. The main challenge for developing protocols to minimise invertebrate suffering stems from difficulties in determining whether or not an invertebrate is suffering, particularly when the perception of pain and suffering in invertebrates is not fully understood (Adamo, 2016). While more research is undoubtedly needed to investigate pain perception in invertebrates, in the short term it may be possible to look to the vertebrate for proxies of suffering.

A variety of proxies has been adopted to tackle the challenge of assessing pain in vertebrates (Flecknell & Roughan, 2004), these include changes in movement, changes in food consumption, change in behaviour in response to a noxious stimuli (Flecknell & Roughan, 2004), or even reduction in response to noxious stimuli when analgesic is applied (Sneddon, 2003). Similar proxies, like retraction from a noxious stimuli have been used in invertebrates to assess potential suffering during procedures like euthanasia (Gilbertson & Wyatt, 2016). These authors argue that while a behaviour like retraction in response to a stimuli could be a reflex, if there is a choice of methods with no significant disadvantages, it could be ethical to choose the method with in which the animal shows a less marked behavioural reaction to the stimuli, until it has been shown definitively that the response is a reflex rather than an indication of suffering (Gilbertson & Wyatt, 2016).

Conclusion

The current state of invertebrate ethics, and communication of these ethical standards need to be re- explored in light of our developing understanding of invertebrate cognition and pain perception and public perception of invertebrate studies. While invertebrate research ethics develops, the literature surrounding the already more developed vertebrate research ethics are rich in guidelines and philosophy which could be adapted to invertebrate use. As well as revisiting the ethics of using invertebrates in research, it is also highly important as a field to engage the public to highlight the need for often lethal invertebrate studies, as well as the ethical measures employed to reduce negative impacts. To ignore the changing public perceptions of invertebrate studies could mean losing public support for invertebrate studies.

Author's contribution statement

ED and EJHR conceived the presented idea; ED, EJHR and AGH advanced the presented idea and developed the theoretical framework. ED wrote the manuscript with input from EJHR and AGH. All authors discussed and contributed to the final manuscript.

Data Accessibility

Not applicable as no original data presented.

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