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Animal sentience research: Synthesis and proposals

Response to Commentary on [Crump et al.](#) on *Decapod Sentience*

Andrew Crump

Centre for Philosophy of Natural and Social Science, London School of Economics and Political Science

Heather Browning

Department of Philosophy, University of Southampton

Alexandra K. Schnell

Department of Psychology, University of Cambridge

Charlotte Burn

Animal Welfare Science and Ethics, Royal Veterinary College

Jonathan Birch

Centre for Philosophy of Natural and Social Science, London School of Economics and Political Science

Abstract: Most commentaries on our target article broadly support our approach to evaluating evidence of animal sentience. In this Response, we clarify the framework's purpose and address criticisms of our criteria. A recurring theme is that a framework to synthesise current evidence of sentience is not the same as an agenda for future directions in animal sentience research. Although future directions are valuable, our framework aims to evaluate existing evidence and inform animal welfare legislation.



[Andrew Crump](#), Research Officer, LSE, works on the Foundations of Animal Sentience project, specializing in invertebrate sentience and animal welfare. He previously completed a PhD in Biological Sciences at Queen's University Belfast. [Website](#)

Lecturer, Philosophy, University of Southampton, [Heather Browning](#) specializes in animal welfare. Alongside her academic career, Browning has worked as a zookeeper and animal welfare officer. [Website](#)



[Alexandra Schnell](#), Research Fellow, Darwin College, University of Cambridge, focuses on comparing cognitive abilities, such as learning and memory, in diverse taxa including cephalopods and corvids. [Website](#)

Associate Professor at Royal Veterinary College, [Charlotte Burn](#), Deputy Head of Animal Welfare Science and Ethics, specializes in the mechanisms and motivations behind animal behaviour and perception and in concrete improvements to animal welfare. [Website](#)



[Jonathan Birch](#), Associate Professor, LSE, is the Principal Investigator on the Foundations of Animal Sentience project, a five-year Horizon 2020 project investigating animal sentience. [Website](#)

We thank all our commentators for their insightful feedback on our target article (Crump et al. 2022a). Although several excellent commentaries addressed decapod sentience specifically (**Abramson & Calvo 2022, Comstock 2022, Elwood 2022, Walters 2022, Tye 2022**), most responded to our proposed general framework for evaluating evidence, and our responses will focus on this.

Our responses will be organized by theme. We will first consider general issues concerning the framework's purpose, highlighting that our aim is to synthesize existing evidence without claiming that this evidence conclusively settles the issues or delivers certainty (Section 1). We then turn to how our criteria relate to sentience (Section 2) and to each other (Section 3). After that, we address criticisms of specific criteria (Section 4), before zooming out again to the question of whether our framework needs additional criteria (Section 5). We acknowledge the importance of studying feelings other than pain, while also explaining why we think a framework for synthesizing existing evidence of pain has a distinctive role in ethics and policy (Section 6). Finally, we clarify some points about how we communicate uncertainty (Section 7), consider other possible applications of our general framework (Section 8), and reflect on our work's wider ethical and political implications (Section 9).

A recurring theme is that a framework for synthesizing *existing* evidence of sentience, with a view to informing animal welfare laws and regulations, is not the same as an agenda for *future* research into animal sentience. Many commentaries sketch exciting lines of inquiry aimed at finding new, additional kinds of evidence. Many also stress the need for animal sentience research to move beyond its traditional focus on pain. We often agree with these commentaries, but our aim was not to lay out a roadmap of future directions. Our goal was to develop a framework that effectively synthesizes the main types of evidence that can shift probabilities of sentience *now*, and that can be put to work *immediately*, despite ongoing debate and uncertainty about the fundamental nature of sentience. We see the commentaries, taken together, as broadly supporting the idea that our framework achieves that goal.

1. What is our framework for?

As **Andrews (2022)** points out, our focus on confidence “transforms the animal sentience question from ‘are decapods sentient?’ to ‘how confident can we be that decapods are sentient?’” (p.1). **Andrews** argues that we need a more ‘secure’ theory of sentience to make progress on the former question – a theory not yet in place. We agree with this assessment. While our framework was built from what we take to be the current best theories of sentience, we remain open to changing it as more evidence or new theories emerge.

Briffa (2022) similarly observes that our framework does not *conclusively* answer whether decapods (or any other taxa) are sentient. Rather, we are synthesising evidence that can inform animal welfare policy in our current state of uncertainty. There is no tension between looking for more and better evidence while simultaneously making policy decisions using the evidence we have.

Our aim, however, is more ambitious than **Briffa** suggests. He infers that we are merely looking for evidence compatible with the *possibility* of sentience. But we are also synthesizing existing evidence that can raise or lower the *probability* of sentience (including evidence that we think can significantly raise it). One can accept that the

probability has been shifted significantly upwards, yet consider that more would be evidence valuable.

As **Briffa** points out, there are various ways of understanding sentience. His preferred definition, following Broom's (2007) proposal, includes additional properties beyond just having feelings. We did not want our definition of sentience to cover mere detection and response to stimuli, as **Briffa** has interpreted us as saying: Detection and response need to be *experienced*, to be *felt*; our criteria would thus rule out some cases that concern him. Our criteria are set up to identify more complex detection and response, mediated through a valenced *felt experience*.

Briffa describes his preferred method for assessing the possibility of sentience: establishing a definition of sentience, deriving some predicted indicators ("behavioral or other biological properties, for which feelings or higher levels of awareness would be the simplest valid explanation" (p.2)), and then to look for evidence of their presence in the taxon of interest. This describes the method we have developed and applied here. Naturally, broad agreement about high-level strategy allows for disagreements about the definition and indicators of sentience.

Elwood is concerned that "scientists might be less inclined to propose and use novel methods if those methods fail to match one of [our eight] criteria" (p. 1). The framework is certainly not intended to constrain future research in that way. As **Elwood's** own work exemplifies, scientists can bring new lines of evidence into view by devising new experimental approaches (e.g., Appel & Elwood 2009, Elwood & Appel 2009) Frameworks for synthesizing evidence (such as ours) can then be amended and expanded where necessary.

Like the lists that **Elwood** and others have proposed (e.g., Sneddon et al. 2014), our framework aims to organise pre-existing evidence using well-accepted indicators. Building on those lists, the framework includes confidence levels (to assess the strength of evidence) and an approximate grading scheme (to facilitate cross-species comparisons and hypothesis-based evaluations of the evidence). We are very open to amending the framework as and when new sentience indicators are developed.

2. The relationship between our criteria and sentience

For **Dawkins (2022)**, our target article "dismiss[es] a growing volume of evidence that many highly complex processes not only could, but actually do, occur without sentience." (p. 1; see also **Key & Brown 2022**). The term "dismiss" is inaccurate, because evidence about what humans can and cannot do unconsciously has informed our proposals in various ways. We have not found evidence that humans can unconsciously trade-off risk of injury against opportunity for reward (Criterion 5), direct centrally controlled wound-tending behaviours flexibly towards an injury site (Criterion 6), succeed at associative learning tasks beyond classical conditioning (Criterion 7), or value analgesia in sophisticated ways (Criterion 8). **Dawkins** suggests that "many animals could still be like us, but like us when we are in unconscious mode." If animals were like us in unconscious mode, we would not expect them to display a range of cognitive and behavioural abilities that humans have never demonstrated unconsciously.

Plenty of complications do deserve debate here. For example, the question of *which* forms of associative learning sentience facilitates in humans remains a target of ongoing inquiry. This is a serious challenge when formulating Criterion 7 (see Crump et

al. 2022a, pp. 7-8). One might have imagined that instrumental conditioning could occur entirely unconsciously, and some studies seem to point that way (e.g., Pessiglione et al. 2007), but recent work suggests the opposite (Skora et al. 2021), indicating that instrumental conditioning is impossible for subliminal stimuli. Thus, ignoring evidence of instrumental conditioning as sentience-irrelevant would have been a mistake. The human evidential picture is changing all the time, and animal sentience researchers must be sensitive to recent developments.

We need to be careful, though, to avoid the fallacious inference: “because some forms of associative learning can be performed unconsciously, no form of associative learning can raise the probability of sentience in any animal.” Some types of learning do shift probabilities. Let us by all means debate which ones and why (cf. Ginsburg & Jablonka 2019, Birch et al. 2020, 2022, Birch 2022).

There is also a challenges from **Dawkins** to our approximate grading scheme:

“On page 8, a grade of “very high confidence” is defined as “when the weight of scientific evidence leaves no scope for reasonable doubt” that an animal satisfies or fails one of their criteria for sentience. However, on page 9, high or very high confidence is stated to be when there is very strong evidence for sentience itself” (**Dawkins**, p. 3).

Our confidence levels qualify claims about whether a criterion is satisfied or failed. In our view, high or very high confidence that 7+ criteria are satisfied amounts to “very strong evidence for sentience”. This is because, as more lines of evidence point towards sentience, we believe it becomes legitimate to describe the overall case as very strong.

For **Dawkins**, “the criteria themselves are highly uncertain indicators of sentience so even 100% compliance with all of them would not guarantee certainty of sentience.” (p. 3). We agree that satisfying all eight criteria does not *guarantee* sentience. To quote the target article: “Our criteria are not unreasonably demanding—they do not require certainty.” (p. 8). Indeed, if we did claim that our criteria delivered certainty, there would be no need for confidence levels to communicate our uncertainty (see Section 7 of this response for more on confidence levels).

Butlin (2022) and **Key & Brown** object that our criteria are only linked to sentience in humans, so it is plausible that they have no relationship to sentience in other animals. This is why we believe sentience frameworks should include more than a few items, drawing from diverse scientific disciplines (although our criteria are not completely independent of each other; see Section 3). For any single cognitive ability that humans only perform consciously, it is plausible that nonconscious animals could have evolved a mechanism to perform it unconsciously (Browning & Veit 2020). But, as the number of lines of evidence multiply, the idea that this whole functional profile could be achieved without sentience becomes less likely.

Irvine (2022) contends that our criteria do not clearly differentiate between nociception and pain. Using the nematode *Caenorhabditis elegans* as an example, she argues that our grading scheme suggests there is “substantial evidence” of sentience in nematodes because they satisfy three criteria. However, **Irvine** asserts that nematode sentience is unlikely because they fail to meet other criteria. **Andrews** has a strikingly opposite reaction to **Irvine**: she takes nematodes’ ability to satisfy some of our criteria as evidence they may be sentient.

This is not the place to fully review the nematode evidence, so we will limit ourselves to clarifying our framework. It aims to synthesize evidence in a way that

facilitates arguments about which criteria are more important and why. The approximate grading scheme is a rule of thumb, establishing a *default* norm for phrases like “very strong evidence of sentience”. It is not something to be followed religiously. The idea is rather that departures from the default require a rationale. **Irvine** gives a possible rationale for regarding the evidence of sentience in nematodes as less than substantial, namely, that they fail several other criteria. To us, this illustrates the utility of our criteria, rather than undermining them.

A common theme among sceptical responses is that some criteria could potentially be satisfied without sentience. **Ng (2022)** argues that this ‘no-need-for-sentience’ claim is irrelevant. For him, the probability of each possible explanation is what matters: where it is *conceivable* but *highly unlikely* that a given behaviour is performed unconsciously, this possibility can be safely ignored. Indeed, he points out that behaviours complex enough to meet our criteria (or his own preferred marker of flexible/plastic behaviour) are far less likely to be possible in non-sentient animals. **Ng’s** emphasis on probability rather than certainty is welcome. That said, we cannot say, for any of our markers, that the probability of their being performed unconsciously is so low that it can be safely ignored. Rather, we see these criteria, taken together, as effective ways to shift the probability of sentience in one direction or the other.

3. Interrelations between the criteria

3.1. Redundancy. Several commentators highlight redundancies in our criteria, in that some criteria imply others, at least in practice (**Irvine, Jablonka & Ginsburg 2022, Walters**). We think a good framework should cover basic necessary conditions for pain (e.g., Criterion 1: Nociceptors) as well as behavioural indicators of pain (e.g., Criteria 5-7). This makes it very likely that some later criteria will imply earlier criteria. The criteria are not all fully independent. There is a trade-off here: the more criteria one has, the harder it is to ensure their independence. We nonetheless prefer a substantial and diverse list of markers to betting on very few.

For this reason, we disagree with shortened lists of criteria (e.g., **Jablonka & Ginsburg, Walters**), which put all their confidence in one or a few indicators. From a theoretical standpoint, there is no consensus about which indicators provide the best evidence for sentience. From a practical standpoint, our framework was designed to evaluate existing evidence for sentience in understudied taxa. Admitting different lines of evidence increases the likelihood that some criteria have actually been studied in the species under assessment.

Moreover, as **Mallatt & Feinberg (2022)** point out, our eight criteria “match the categories of published studies: nociceptor studies, studies on integrative neural networks, neurotransmitter studies, trade-off studies, associative-learning studies, analgesic-administering studies, etc. Combining the criteria could make these studies more difficult to find in the literature, hampering efforts to answer questions about animal sentience.” (p. 3).

3.2. Weighting. **C. Brown (2022)** and **Jablonka & Ginsburg** suggest numerically weighting the criteria. As our target article highlighted, not all the criteria provide equally strong evidence for sentience. For example, Criterion 1 (Nociceptors) is less compelling than criteria that attempt to distinguish nociception from pain. We are not against weightings in principle. The trouble arises when we try to decide on precise weightings. As the commentaries on our target article illustrate, there is no consensus on which

criteria offer the strongest evidence for sentience. Nervous system organisation (**Key & Brown**)? Flexible or plastic behaviours (**C. Brown, Ng**)? Learning abilities (**Jablonka & Ginsburg**)? Analgesia preference (**Walters**)? Without this consensus, we cannot develop a weighting system that would command widespread support.

Moreover, weightings introduce an element of arbitrariness. Even if we accept that, say, Criterion 8 (Analgesia preference) is stronger evidence for sentience than Criterion 1 (Nociceptors), we still need to decide how much stronger. This question cannot be answered quantitatively, at least with our existing knowledge of sentience. Our framework is intended to have a degree of humility: it does not try to settle questions we do not know how to settle. We hope the framework facilitates extensive (if qualitative!) discussion of the strength of different lines of evidence. We appreciate **Mallatt & Feinberg's** remark that our approach "yields a good middle ground between making quantitative decisions that are too rigid and making qualitative decisions that are too uncertain." (p. 3).

4. Specific criteria

4.1. Criterion 1: Nociception. It is suggested by **Jablonka & Ginsburg** (p. 1-2) "that criterion 1 (Nociception) should not be included in the list because the question asked is whether nociception or the feeling of pain (which necessarily involves nociception) can explain the behavior and internal state of the animals." (For similar criticisms, see **Briffa, C. Brown, Comstock, Elwood, Irvine, Walters**). However, our main question is: *Can the animal feel pain?* We therefore consider it appropriate to assess whether the animal has the basic neural architecture for pain. Establishing the presence of nociception is an important, though clearly inconclusive, part of that case. This lays the foundations for subsequent criteria to distinguish pain from nociception. We do agree, however, that nociceptors *alone* provide weak evidence for pain.

4.2. Criterion 4: Analgesia. Criterion 4 (analgesia) has been criticized for adding little to Criterion 1 (nociception), which is already weak evidence by itself. Several commentators (**Jablonka & Ginsburg, Key & Brown, Irvine, Walters**) express versions of the following thought: If there is nociception, there will be neurotransmitters that inhibit nociception. Such effects will tend to be "consistent" with the hypothesis that these compounds attenuate the experience of pain, but mere consistency is a low bar. **Irvine** points out that opiates modulate nociceptive responses in *C. elegans*, which have fewer than 400 neurons.

As **Comstock** notes, the criterion also raises potential confounds. Analgesics and anaesthetics often reduce general activity, even in the absence of noxious stimulation. For an animal to satisfy Criterion 4 with high confidence, we must control for this effect (see also Gibbons et al. 2022). This issue is discussed in Section 4.4 of the target article, in relation to several experiments.

A small part of a larger case is not nothing, and evidence need not be conclusive to be relevant. In principle, we could have solely found evidence of reductions in general activity levels and/or reduced responsiveness in the peripheral nervous system. This pattern of results would be hard to interpret as consistent with the hypothesis that the compounds alleviate aversive feelings. In fact, however, we found more specific and interesting effects, pointing to complex, centrally mediated mechanisms (e.g. Fossat et al. 2014 on "anxiety-like" states in crayfish). That is relevant evidence. Indeed, describing

these effects as “consistent” with aversive feelings may be too modest. What we mean is that this evidence raises the probability of aversive experiences in crayfish, relative to where it was before, without settling the issue.

4.3. Criterion 5: Motivational trade-offs. Criterion 5 (Motivational trade-offs) draws inspiration from Cabanac's (1992) proposal that pleasure serves as a common currency for decision-making in a range of animals, and from Balasko & Cabanac's (1998a, b) experiments designed around this idea. The proposal was later extended to pain (not just pleasure), especially in trade-off experiments on hermit crabs (Appel & Elwood 2009, Elwood & Appel 2009). **S. Brown's (2022)** thoughtful commentary highlights Hayden and Niv's (2021) recent critique of the “common currency” concept. **S. Brown** offers an alternative function: “Pain may command our attention by *inhibiting* attention to competing needs, desires and potential actions, with more intense pains inhibiting more competing activity.”

S. Brown does not express any view about the most likely explanation of the hermit crab trade-off experiments. It seems these results could be reconciled with either view about the function of pain. In other words, the results do not discriminate between Cabanac's “common currency” idea and the “attentional exclusion” idea. Turning up the shock voltage could increase the weight an internal decision-making system gives to the need to escape. It could also gradually exclude attention to everything else except the need to escape. On this second explanation, the higher quality *Littorina* shell competes more strongly for the hermit crab's attention. But, within both theoretical perspectives, trade-off behaviour offers relevant evidence, by showing that the nociceptive response goes beyond a reflex and involves centralized, integrative processing. This naturally leads to debate about what the centralized, integrative processing involves, and more evidence to choose between “common currency” and “attentional exclusion” would be welcome.

4.4. Criterion 7: Associative learning. Several commentators criticised Criterion 7's inclusion of all associative learning, including simple classical conditioning (**Gibbons & Chittka 2022, Jablonka & Ginsburg, Mallatt & Feinberg, Woodruff 2022**). As these authors highlight, and as our target article acknowledged, humans can probably perform simple classical conditioning unconsciously (Greenwald & De Houwer 2017, LeDoux et al. 2017). By contrast, other forms of associative learning have been linked to consciousness in humans, with varying degrees of empirical support (Birch 2022). Examples include instrumental learning (Skora et al. 2021), rapid reversal learning (Travers et al. 2018), and learning across time gaps (“trace conditioning”; Clark & Squire 1998, 1999).

Our original rationale for accepting all associative learning was that the link between consciousness and different forms of associative learning remains controversial, and so the criterion should be formulated in a relatively open way to avoid missing relevant evidence. However, our commentators have convinced us to reopen this issue.

In the box below is a possible amendment:

Criterion 7 (amended): Associative Learning. The animal shows **forms of associative learning** in which noxious stimuli become associated with neutral stimuli, or in which novel ways of avoiding noxious stimuli are learned through reinforcement. **These forms of associative learning go beyond classical conditioning in which a single conditioned stimulus overlaps temporally with an unconditioned stimulus.**

Note: Forms of associative learning that are linked, at least tentatively, to sentience in humans (such as instrumental learning, reversal learning, and trace conditioning) provide stronger evidence than other forms.

This amendment complicates the criterion but perhaps signals more clearly our engagement with the ongoing debate about which forms of associative learning are sentience-linked and why (although, as **Abramson & Calvo** note, distinguishing between different forms of learning can prove difficult). We welcome feedback: *Is this amendment an improvement?* Given the strong evidence for operant conditioning in decapod crustaceans (**Mallatt & Feinberg**), it would not materially change our evaluation of the decapod evidence.

We would reject other ways of making Criterion 7 more demanding. Recall that we aim to synthesize existing evidence; our aim is not to provide conclusive evidence or certainty. For example, we could amend the criterion to require the full package of **Jablonka & Ginsburg's** "Unlimited Associative Learning", but very little work has ever looked for that package (Birch 2020). Let's not conflate a promising direction for future research with a framework for synthesizing existing research.

Butlin's conscious/unconscious contrast in learning raises a similar objection. Very recent work is beginning to explore this contrast in invertebrates (see Giurfa & Macri 2022, Grover et al. 2022)., This is welcome, but we should not write this promising future direction into our framework now. These recommendations are more valuable as proposed future research than as criteria for synthesizing the existing literature.

Expanding on the argument that simple classical conditioning does not need sentience, **Woodruff** asks whether understanding the neural mechanisms underpinning a behaviour eliminates the need for sentience as an explanation. He does not, however, clarify what sort of mechanism he is considering. If very simple neural mechanisms underpinned one of our behavioural criteria (e.g., it only involved the peripheral nervous system), this would plausibly undermine a potential role for sentience. But, if the mechanism were analogous to brain structures that may underlie sentience in humans, this would strengthen the link to sentience (Crump & Birch 2022).

More broadly, sentient behaviours must have some neural mechanism. For example, neuroscientists are beginning to understand the circuits underlying certain human emotions, but that doesn't eliminate the feeling component of those emotions. Mechanism and sentience are not either/or. By including neurobiological criteria, our framework explicitly recognises this.

5. Additional criteria

In agreement with some of our own work (Birch 2022, Crump & Birch 2022), **Butlin** proposes searching for a behavioural distinction between conscious and unconscious states in animals. As an example, some human studies suggest that conscious awareness

is necessary for trace conditioning (Clark & Squire 1998, 1999). To test whether trace conditioning also requires consciousness in animals, we could mask the stimuli or use a distracting task to divert the animal's attention (Birch 2022, Droege et al. 2021). For conscious animals, we would expect trace conditioning (or any other cognition and behaviour linked to consciousness) to be present in the putatively conscious condition, but "switched off" in the putatively unconscious condition (when the stimuli are masked, or the animal is distracted).

We agree with **Butlin** that this pattern of results would provide compelling evidence for invertebrate sentience. But, as already emphasized in the discussion of Criterion 7, we need to distinguish between a framework that helps us synthesize the most relevant kinds of existing evidence (which is our goal) and a programme of future research. The programme **Butlin** envisions would indeed be a valuable research agenda going forward.

The same can be said of **Key & Brown's** proposed "observer networks" criterion. This is another interesting avenue for future research. However, since the presence or absence of observer networks has never been investigated in invertebrates, it would be inappropriate to incorporate this into a framework that aims to assess the existing evidence for sentience.

Veit (2022) advocates adding "life-history complexity" to our list of criteria, where "life-history complexity" is to be "operationalized in terms of the number of parameters and constraints in the evolutionary optimization problem that animals face". We have emphasized criteria that can be assessed using established experimental strategies. Veit's criterion does not seem to be like this. It is very unclear how to count the number of "parameters and constraints" in the "evolutionary optimization problem" that an animal faces, and it is questionable whether the variables are well-defined (especially since the literature on "niche construction" challenges the idea that biological species face fixed "optimization problems"; Laland et al. 2016). Veit's claim that this criterion would provide a "firm evolutionary basis" for assessments of sentience seems premature.

Elwood regrets our exclusion of some existing lines of evidence, namely, physiological responses to noxious stimuli. We addressed "physiological markers of pain" in the target article, judging that sentience is neither necessary nor sufficient for physiological changes to occur. Whilst such changes may tell us something about the causes of pain in animals that we already regard as sentient, we suggest that they are not good evidence of sentience itself.

Elwood highlights another line of evidence: "behavioural responses that could not be part of a nociceptive reflex because they could only occur some time after the noxious stimulus had stopped" (p. 1). Such behavioural changes may, in the right circumstances, offer evidence for pain. However, **Elwood's** formulation covers any and all behaviours that reliably occur after the cessation of a noxious stimulus. This includes moving, sleeping, courting, fighting, and so on. Even if noxious stimulation caused or changed such behaviours over long timescales, that would not do much to raise the probability of pain. We have focussed our attention on the markers we see as genuinely probability-raising.

Solms (2022) proposes an alternative set of criteria that he takes to be sufficient for determining whether an organism is sentient (rather than for identifying the presence of any specific feeling), grounded in his theory of the function of sentience. We think some of these criteria (being alive, having multiple survival needs) are too inclusive to really

help identify sentient organisms that can experience good or bad feelings, but others (capacity to satisfy multiple needs in novel situations, capacity to learn from these experiences), quite closely resemble some of our behavioural criteria.

6. Feelings other than pain

Several commentators have criticised our framework's restriction to pain (**Andrews, De Waal 2022, Solms, Souza Valente 2022, Woodruff**; although **Gibbons & Chittka** take the opposite view). We see two main reasons for the traditional focus on pain in animal sentience research (which our article continues). One is that pain has special ethical significance, leading to a special role in animal welfare law. For example, the UK's Animal Welfare Act 2006 can be extended to invertebrates if they are shown to be "capable of experiencing pain or suffering". The other reason is that pain has received more research than any other feeling. An attempt to survey *existing* evidence on other feelings would run into very large evidence gaps. Our choice was not intended to imply that all sentient animals must experience pain.

We agree that exploring other feelings could help not only identify which taxa are sentient, but also better understand the dimensions or features of their experience and their welfare needs. Once again, we return to the theme of synthesizing existing evidence vs. setting out future directions. Escaping the traditional focus on pain is a crucial future direction for animal sentience research.

7. Cases where evidence is lacking

Several commentators argued that our framework should not conflate situations in which there is evidence against sentience (through failing a criterion) and situations in which there is no evidence one way or the other (**C. Brown, Comstock, Mallatt & Feinberg, Woodruff**).

We have not really conflated these situations, but the presentation in the target article may have given that impression. In practice, in our reviews of the current evidence (covering cephalopods and decapods in Birch et al. 2021, and now insects in Gibbons et al. 2022), we have not found a single instance in which the evidence leans towards a taxon failing a criterion. This could reflect an element of publication bias (i.e., the difficulty of publishing negative results). However, it is also expected if these animals are in fact sentient and if our criteria are suitable and informative.

The upshot is that our tables, so far, have conspicuously lacked boxes in shades of red, indicating "low", "medium", "high" and "very high confidence" that a criterion is failed (Figure 1). That is just how things turned out. Our framework can express degrees of confidence that a taxon fails a criterion. This is conceptually distinct from a situation where there is no evidence, allowing very low confidence one way or the other (represented in our tables by a grey box).

In the review of insect evidence, Gibbons et al. (2022) used the term "no research found" when absence of evidence explained "very low confidence" levels. We will continue this practice going forward. If we had found abundant evidence against a criterion being satisfied, we would have expressed that with confidence ratings from "very low" to "very high" for the negative evidence.

Confidence that a criterion is failed

Confidence that criterion is satisfied



Figure 1. The full set of possible confidence levels. As it turned out, we found no reason to use the left-hand side for the taxa we considered.

8. Other applications of our framework

Several commentators have proposed applying our framework to other taxa or beings. We welcome this, as our criteria were not chosen for decapods specifically, but rather for their potential application to various types of beings. That said, as several commentators have pointed out, the limiting factor is the amount of information available across different species, particularly the diverse range of invertebrates. As our target article shows, even for decapods, there was little to no research for some criteria.

This is not a cause for pessimism, but rather a call for ongoing and expanded research programs into the relevant characteristics covering a wider range of taxa. We have already assessed cephalopod molluscs in our report for the UK government (Birch et al. 2021), and now have also reviewed the evidence in insects (Gibbons et al. 2022). Further taxa for investigation may include other molluscs (**Kakrada & Colombo 2022**), other arthropods (**Gorman 2022**), nematodes (**Andrews, Irvine**) and annelids (**Burrell 2022**).

Levin (2022) suggests expanding a framework like ours to other types of less familiar beings: artificial intelligence (AI) systems and extra-terrestrial species. He points out that, with the expansion of robotic agents and AI systems, the question of our moral responsibilities towards them looms large, and this requires new and creative methods of assessing sentience. We welcome the wide application of our framework, though caution that use beyond evolved biological systems may undermine the reasons for our choice of criteria, and the background assumptions that we take to justify their use. While our criteria may provide a useful starting point for artificial systems, this application necessitates an in-depth assessment of each criterion's appropriateness, with replacement or modification where necessary.

Although part of our aim in the construction of our framework, was to relax the criteria so they were less mammal-centric, several commentators questioned whether they were still too narrow; in particular, whether they might be too 'neural centric'. **Briffa** challenges the need for integrative brain regions (see also **Burrell 2022**). He argues that a single brain structure is unnecessary for the sort of integration sentience requires, with more decentralised nerve nets potentially serving an integrative function. This is an intriguing future direction, and research correlating decentralised integrative processing with our behavioural markers may justify altering the criterion to allow for more diverse types of integrative processing.

Kakrada & Colombo propose a change in perspective when assessing evidence for invertebrate sentience. Calling on Macphail's (1985) Null Hypothesis regarding lack of qualitative differences in intelligence between vertebrate species, they argue for its extension to the experience of pain in invertebrates. It is worth noting that our framework does not involve taking any particular "null hypothesis". We are simply

evaluating the strength of evidence for and against sentience. It's unclear why a null hypothesis (of any kind) is advantageous in this context.

In a similar vein, **Andrews** proposes a "working hypothesis" that "all animals are sentient". A lot depends here on what "working hypothesis" means. We should absolutely remain *open-minded* about the possibility that many invertebrates are sentient, including intuitively unlikely candidates. Meanwhile, we should absolutely not *assume* this to be the case, since that would not be open-minded at all. If the "working hypothesis" idea is to broadly support researchers investigating sentience in taxa where it has historically been dismissed, we naturally agree.

Reber et al. (2022) take our target article as an opportunity to promote their "cellular basis of consciousness" theory, on which "all living organisms are sentient". Many theories of sentience and consciousness are on the market, and they vary enormously in their implications. Because our framework aims to inform better animal welfare policy decisions, it was important not to rest that framework on a speculative theory. Sound public policy decisions should not involve betting the house on any particular speculation but should instead look for consensus. Accordingly, our target article took an empirical, "theory-light" approach. We aimed to find indicators that can be accepted as relevant (i.e., probability-raising if present) by people of many theoretical persuasions, provided they can agree that experiences of pain have a role in centralized, flexible responses to injury that go beyond mere reflexes.

It's not clear whether **Reber et al.** would agree that their "cellular" theory is speculative. The tone of their commentary suggests that they see it as robustly supported. If that is the claim, then it is false. There is no high-quality evidence of sentience in unicellular organisms. The sort of behavioural and cognitive evidence that we and many others find probability-raising for invertebrates is absent for single cells.

We reject **Reber and colleagues'** claim that "if references to neural traits and neurotransmitters are deleted and 'animal' is replaced by 'organism,' prokaryotes fit the criteria very nicely". They take their earlier work to support this claim, but this work has not made a convincing case. Two examples may explain why. First, the only evidence Reber & Baluška (2021) cite in support of unicellular organisms performing avoidance learning is Jennings' (1906) anecdotal observations of the ciliate *Stentor roeseli*. This is extremely low quality evidence (Birch 2017). Even if there were high quality evidence of avoidance learning in ciliates, it would be unreasonable to generalize to prokaryotes such as bacteria. Second, in a section called "decision making", Reber & Baluška cite a magazine article reporting a study of stochastic gene expression in *E. coli* (Kondev 2014). The author playfully suggested that *E. coli* have "free will", clearly not using the term in its philosophical sense. Reber & Baluska cite this article as evidence that *E. coli* literally has free will – the *only* paper they cite under the heading of "decision making".

The bedrock of our framework is careful attention to the quality of evidence. We have often criticized experiments for lacking robust experimental design (e.g., commenting on sample sizes, controls, or sources of bias) and using inappropriate statistical analyses. Our conclusions are based on high quality research, rather than non-replicable anecdotal reports. If we do not insist on high methodological standards, we risk permitting speculations to be passed off as supported by evidence, with disruptive and possibly harmful consequences for animal welfare policy.

9. Ethical and policy implications

Gorman and **Woodruff** question whether work like ours will change how society treats animals that the scientific community (generally) agrees are sentient. For **Woodruff**, decapod crustaceans fail a “cuddliness criterion for consciousness” (Pribram 1976), which trumps scientific evidence in determining whether animals are protected (see also Mikhalevich & Powell 2020).

It does not always work that way. The scientific evidence presented in our target article led directly to the UK government amending its Animal Welfare (Sentience) Bill to include decapod crustaceans (as described in **Cooper et al. 2022**, Crump 2022). As **Gorman** and **Cooper et al.** caution, it is uncertain whether and how this new law will protect decapods from harmful practices (see Crump et al. 2022b). Even so, it is the first time they have been covered under any UK animal welfare law.

There is nonetheless more to do and, as both **Gorman** and **Woodruff** highlight, effective advocacy and political engagement (informed by social science) can unleash animal sentience research's potential for societal transformation. Part of the context for our report was a coordinated campaign from dozens of animal advocacy organizations calling for UK law to recognize animal sentience (see also the target article of Rowan et al. 2021 and the open peer commentary it has elicited in this journal).

Montemayor (2022) agrees that sentience should lead to moral standing. He breaks down what types of protection may be most appropriate given the different cognitive and affective capacities of different animals. We agree that our criteria are not all equal in this regard; also relevant here are the different dimensions of consciousness that animals may have (Birch et al. 2020). Further discussion on the different types of moral or legal status, and their grounds, is welcome.

10. Corrections

We thank **Walters** for noting an error: our target article incorrectly stated that TRPV1 has been found in decapods. This should have stated that TRPV subfamily ion channels (but not TRPV1) have been found (see Kozma et al. 2020).

Our target article stated that Abramson and Feinman (1988) presumed carapace vibrations to be neutral. They weren't so presumed; as **Abramson & Calvo** point out, the authors obtained evidence that the carapace vibrations were not aversive.

Conflict of Interest: Heather Browning (an author) is the partner of Walter Veit (a commentator).

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