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When should we ascribe sentience to animals? A commentary on “Hermit crabs, shells and sentience” (Elwood 2022)

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Abstract

In a new review article, experiments on hermit crab behaviour are discussed in the context of possible animal sentience. Sentience can be defined as the ability to experience feelings such as pleasure or pain but there are also broader definitions that include elements of awareness. Here I suggest that of the different levels of awareness described as components of sentience, only the higher levels (assessment and executive awareness) seem distinct from the basic non-sentient cognitive tasks of gathering, processing and storing information, which are demonstrated by most animals. Studies that attempt to differentiate between basic cognitive functions and higher levels of awareness are rare for most animal taxa, including hermit crabs. Therefore, while results such as those obtained from studies of hermit crab behaviour are compatible with sentience they cannot yet be distinguished from simpler explanations based on basic cognitive functions, which we should prefer for the time-being. Nevertheless, hermit crabs are promising model systems for investigating awareness in animals.

Keywords: Hermit-crab, sentience, awareness, feelings, parsimony, decision-making

What is sentience and do non-human animals show signs of it? This is the topic of Elwood's (2022) review, which uses a body of experimental evidence on hermit crab behaviour to consider these questions. Nearly six decades of research into hermit crab behaviour shows that they make complex decisions, due to their obligate use of empty snail shells. The new review provides a timely and thought-provoking update to the seminal work on this topic, "*Assessments and Decisions: A study of information gathering by hermit crabs*" (Elwood & Neil 1992). Elwood & Neil (1992) considered hermit crab decision-making within the framework of potential rules that integrate information across multiple variables. They favoured a control-based model (Simbolotti et al. 1987) as the most parsimonious but they did not consider how those rules are actually implemented, i.e. the proximate machinery involved in decision-making. Where Elwood and Neil (1992) were agnostic about how animals integrate disparate information sources, Elwood (2022) explores the extent to which sentience might underlie decision-making in hermit crabs. Here I expand on Elwood's review by discussing the meaning of sentience, and its relation to basic cognitive functions. I consider whether we need sentience, as generally understood, to explain some examples of hermit crab behaviour. Finally, I suggest that future research focussing on awareness could offer further progress towards understanding sentience in hermit crabs and other animals.

Defining sentience

Cognition refers to the ways in which animals acquire, process and store information and, ultimately, use it to make decisions (Shettleworth 2001). Sentience might intersect with cognition but it must also refer to something additional; otherwise a different word would not be needed. Cognition begins when energy or chemicals interact with various types of receptor cell, typically leading to changes in membrane polarity, which in turn influences the activity of nearby neurons, thereby converting the initial interaction into information. Basic processing of this information in interneurons involves transporting, filtering and categorising, and storage may also occur. The output of cognition is

decision-making, defined as making a choice between two or more courses of action . Behavioural neuroscience can provide direct insights into how the cognitive machinery operates but we can also make some inferences about cognition by studying behaviour, which is the outwardly observable result of decision-making. Moreover, we can ask whether observed behaviour correlates with external environments that we know animals have been exposed to, and to a lesser extent internal environments, for example if fasting has been imposed. This linking of the inputs (information likely to have been acquired) and outputs (behaviour likely to reflect decisions) of cognition arguably comprises the bulk of experimental work in animal behaviour. Elwood (2022) asks whether these types of studies on hermit crabs, taken as a whole, can also provide evidence for sentience in terms of both awareness and subjective experiences arising from this awareness (feelings). Although these aspects of sentience could supplement cognition, cognition is not necessarily dependent on sentience (Shettleworth 2001).

We can recognise components of sentience but the concept itself is stubbornly resistant to pinning down with a single and broadly agreed on definition (much like cognition; Shettleworth 2001), at least when discussed by scientists. As good a place to start as any is to look at the everyday dictionary definition of sentience, which is “the quality of being able to experience feelings” (Cambridge English Dictionary), derived from the Latin *sentire*, to feel or perceive. Some scientific definitions include only the feelings aspect (e.g. the ability to experience pain or pleasure; see Birch *et al.* 2021) but Broom (2007) offered a more expansive definition to include other components that align with the second interpretation of the original Latin, which Broom refers to as awareness. Treated in this way, sentience is an umbrella term that encompasses a set of related concepts, and as such seems unamenable to a single definition. Rather, Broom (2007) provides descriptions and examples of how we expect sentient animals to behave. Given the extensive range of experiments on information use in hermit crabs, Elwood (2022) uses these as a ‘check list’ against which to consider sentience.

Broom's criteria

Broom's (2007) criteria for sentience are: "Some ability to evaluate the actions of others in relation to itself and third parties, to remember *some* of its own actions and their consequences, to assess risk, to have *some* feelings, and to have *some* degree of awareness" (my italics). It is clear that Broom views sentience as a continuum rather than a binary distinction. Of the criteria listed, awareness seems fundamental, because some elements of awareness are distinct from components already included in the definition of cognition (see below), and without any awareness of captured information it would be impossible to then have subjective experiences of it, i.e. feelings. Furthermore, awareness has undergone a degree of conceptual development whereby Broom (2007) identifies different points along a continuum of increasing awareness as follows:

- Unaware
- Perceptual awareness
- Cognitive awareness
- Assessment awareness
- Executive awareness

From examples of each of the above provided by Broom (2007), we can derive the following definitions: Perceptual awareness means that an animal can receive information, potentially via a range of channels, and that information will elicit decisions. This type of awareness is characteristic of all metazoans capable of non-reflex behaviour and at very fundamental levels can be highly conserved, as in the case of light-sensitive opsins for example (Feuda *et al.* 2012). Cognitive awareness means that behavioural responses result from both new information and stored information. It is not clear whether memory is ubiquitous in animals but it does seem to be widespread (e.g. cnidarians lack a central nervous system but nevertheless can learn and therefore must store information; see Cheng 2021). Assessment awareness means that in addition to current and stored information, decision-making is also influenced by insight into the relevance of that information. Finally, executive

awareness adds in the ability to form hypotheses about the future and for these hypotheses to influence decisions, resulting in forward-planning. In this view, perceptual and cognitive awareness are already included as basic components of cognition as defined by Shettleworth (2001) but assessment and executive awareness exceed these. Furthermore, other aspects of sentience in Broom's list (e.g. evaluating actions and their consequences) seem dependent on or emergent from awareness. Therefore, the two higher levels of awareness seem to represent capacities that could define sentience as distinct from basic cognitive functions.

In comparison with Broom's (2007) broader description, this is quite a restrictive view of sentience. However, it seems justified because perceptual awareness is a property of any animal that can gather information and respond to it beyond a reflex. Cognitive awareness is probably a property of the vast majority of animals as well. If sentience then extends to all metazoans, the concept becomes less useful in terms of defining capacities that exceed basic cognition. In addition, a more expansive definition that includes any level of awareness above unaware probably contradicts what most laypeople and scientists understand sentience to mean, as illustrated by Broom (2007):

"Such animals have an elaborate motivational system that allows them to *think* about the impacts of that environment and then take appropriate decisions." (my italics).

Intuitively, it is easy to assume that other animals must think because thinking forms part of our own decision-making. This makes it difficult for us to conceive of decision-making in the absence of thought. Notwithstanding the possibility that we will never know what thinking, if present, could really mean for a hermit crab (Nagel 1974), it at least seems reasonable to say that thinking is more aligned with insight (assessment awareness), forward planning (executive awareness) and feelings as opposed to the basic functions of acquiring and processing (perceptual awareness) and storing (cognitive awareness) information.

Using Lloyd Morgan's Canon to decide whether ascribing sentience is necessary

If we accept that it extends beyond feelings, studies of sentience in animals should evaluate their level of awareness. Specifically, we can ask whether we need to invoke assessment awareness and executive awareness to explain behavioural data or, alternatively, whether the data can be explained by lower levels of awareness that fall within the bounds of basic cognitive functions. If we cannot experimentally distinguish between sentience and basic cognition, we should then favour the simpler explanation as the more likely one. This parsimony rule, specific to animal behaviour, is called Lloyd Morgan's canon and states that:

"In no case is an animal's activity to be interpreted as the outcome of the exercise of a higher psychological faculty, if it can be fairly interpreted as the outcome of the exercise of one which stands lower in the psychological scale." (Morgan 1894, p. 59).

It would be impossible for the higher levels of awareness to be present in the absence of the lower ones – e.g. insight could not occur in the absence of any information to have insights about. Thus, sentience represents a higher psychological processes that if present must have evolved after the basic cognitive functions defined by Shettleworth (2001). **Awareness in hermit crabs**

Elwood (2022) describes hermit crab behaviour that could clearly reflect underlying sentient capacities. Following Lloyd Morgan we should also consider whether their behaviour can be explained in the absence of such capacities. Elwood (2022) reviews a large number of individual studies concerning different species of hermit crab. Here I will discuss one of them to consider whether we need assessment awareness and executive awareness to explain the results and then outline how the same logic can be applied to other examples.

Briffa et al. (2009) investigated shell choice in relation to small intertidal specimens of the common European hermit crab *Pagurus bernhardus*, which occupy shells of the smooth periwinkle *Littorina obtusata*. These snails exhibit a stable colour polymorphism and the majority of their shells

are either dark brown (*dark reticulata*) or bright yellow (*citrina*). We found that crabs would generally decide to swap their current shell for one of lower contrast against the substrate and furthermore that the chemical presence of a predator, the shore crab *Carcinus maenas*, would change that decision, with fewer crabs choosing to swap when the predator cues were present. In a follow up study on startle response durations across different combinations of shell and substrate colour (Briffa & Twyman 2011), we concluded that hermit crabs are aware of their own conspicuousness. We did not specify which level of awareness we meant in these studies but we can consider that question here. Clearly the hermit crabs on average were at least perceptually aware of the shade of their current shell, of the empty shell they could potentially swap into, and of the substrate, and also of the chemical presence or absence of a predator. There is also the possibility that they are cognitively aware, if we assume that they need to remember the shade of their current shell in order to decide whether to abandon it in favour of a new one. However, a simpler explanation is that due to their mobile eyestalks they can continuously gather information on their current shell colour. Testing between these two possibilities should actually be quite straightforward but until we have performed that test, we should favour the simpler explanation that perceptual awareness is enough. Regardless of whether they need to draw on stored information of their current shell or not, the ability of hermit crabs to make decisions based on four (that we know of, I would not be surprised if there are more!) sources of information seems impressive. But it does not need any explanation beyond perceptual awareness. Insight, or understanding the relevance of their decisions, if present would at least mean the hermit crabs know that by swapping shells they can reduce their risk of being detected by a predator. Furthermore, they might make hypotheses about the future consequences of being spotted by a predator. The data are certainly compatible with these ideas but they can also be explained without recourse to them. We should expect natural selection to favour individuals that choose less conspicuous shells regardless of whether they understand the reasons for doing so, or the consequences of not doing so. Similarly, crabs that avoid changing shells (exposing their vulnerable abdomen) when a predator is present would be selected for irrespective of whether they know this

would reduce their risk of being preyed on. In other words, behaviour that maximises their survival should be selected for irrespective of whether insight has also been selected for.

Similar interpretations are possible for all of the examples discussed in Elwood (2022). When terrestrial hermit crabs, *Coenobita rugosus*, with artificially extended shells could still navigate around obstacles (Senoda et al. 2012) this could indicate that they are aware of the need for efficient locomotion. But we should also expect natural selection to favour individuals that avoid scraping their bodies (or extended bodies) on external objects, regardless of whether they understand that that this would improve the efficiency of locomotion or reduce the risk of damage. Although manoeuvring an artificially extended shell past obstacles is perhaps a complex task (in the sense that it requires the use of several information sources), it could still be accomplished through perceptual awareness of collisions, of the size of their extended shell and position of obstacles, all based on information gathered through a combination of mechanoreception and vision. Similarly, Krieger et al. (2020) placed *Coenobita compressus* in small enclosures that could only be exited via a single aperture in the enclosure wall. When the aperture was small, passing through it was only possible by swapping from a large shell into a smaller one, less adequate in terms of protection. But when the aperture was large, exiting was possible without changing into a less favourable shell. Such sub-optimally small shells are usually avoided but more crabs in the small aperture treatment changed shell. Furthermore, crabs in the small aperture treatment would even swap more frequently into small shells that contained internal spikes, which presumably are even less optimal than a small shell with a smooth internal surface. These results could be explained by insight into the consequences of not changing into a smaller shell, i.e. prolonged entrapment. But they could also be explained without insight, by trial-and-error learning as suggested by Krieger *et al.* (2020). Additionally, some hermit crabs that did not need to swap shells in order to escape nevertheless moved into smaller shells, which might be a residual consequence of the general tendency for hermit crabs to investigate any empty shells they encounter. The chance of such investigations and subsequent exchanges occurring might increase as a function of time in proximity to those smaller shells, which could be greater in crabs that could not

exit before swapping shells. A tendency to swap into a smaller shell when trapped next to one in a constrained space might even provide an adaptive explanation that does not rely on sentience; selection should favour individuals that behave in ways that reduce entrapment time regardless of whether they have any insight of what they need to do to escape their predicament. As a final brief example, the decision to join a vacancy chain, would still be adaptive even if the crabs cannot predict the benefits of doing so, as would the decision to quit a fight on the basis of a cost threshold rather than a pain threshold (although nociception might provide information that correlates with cost). All of these examples involve the integration of multiple information sources but this in itself does not require an explanation beyond perceptual and cognitive awareness, even though they might also be compatible with assessment awareness and executive awareness.

Nociception in hermit crabs

The possibility that animals might experience feelings is important because it impacts on our ethical decisions about how to treat them. Birch et al. (2021) reviewed the evidence for pain in decapods and cephalopods, comparing results against a checklist of physiological prerequisites for pain (e.g. presence of nociceptors) and behavioural signatures compatible with pain (Smith & Boyd, 1991). Drawing on some of the same work reviewed by Elwood (2022) they found strong evidence that hermit crabs possess nociceptors, receptors that detect damaging or potentially damaging (noxious) events, and very strong evidence that they possess brain centres capable of integrating different information channels. They also found strong evidence that hermit crabs respond to noxious stimuli in ways analogous to human pain responses. While these conclusions are compatible with pain experience, they are also compatible with simpler explanations based on nociception in the absence of pain, even when responses to noxious stimuli are modified by information gathered via other sensory channels (Elwood 2019; Birch et al. 2021). An interesting aside is that computer programmes, which probably do not experience feelings, can still produce analogues of the kinds of output that we associate with

feelings (Adamo 2018). For these reasons, studies of nociception in hermit crabs and other decapods are careful to conclude that they *might*, rather than *do*, experience pain. Typically they reach conclusions of behaviour ‘consistent with the idea of pain’ (Elwood 2019), rather than concluding that ‘hermit crabs experience pain’. This language acknowledges the inductive reasoning that underlies all studies of potential pain in non-human animals, expressed in general terms as follows: When communicative humans experience pain they behave in certain ways; non-human animals behave in similar ways; therefore non-human animals experience pain. This type of reasoning is useful as a basis of the precautionary principle for the ethical treatment of animals, but pain researchers are usually careful to clarify its distinction from the types of reasoning used outside of applied issues such as animal welfare.

From a purely scientific point of view, the primary aim is not to influence how society treats animals but to satisfy our curiosity about their lives. In this context, we need a higher level of evidence than that used as a threshold for invoking the precautionary principle (Birch et al. 2021; also see Adamo’s 2018 argument that there can be societal downsides of employing the precautionary principle too readily). We do not know whether hermit crabs and other animals actually experience feelings such as pain, as currently defined (see Elwood 2019 for a discussion) and generally understood. Notwithstanding the consensus that this question could remain open indefinitely (e.g. Adamo 2018, Birch et al. 2021, Elwood 2022, Sneddon et al. 2018), we should apply Lloyd Morgan’s canon and prefer explanations for how hermit crabs respond to noxious stimuli based on simpler cognitive processes that do not rely on assumptions that they also experience feelings.

If not sentience then what?

If adaptive decision-making is not resultant of assessment awareness, executive awareness, or feelings, one might reasonably ask what other proximate mechanisms could be in place. To an extent this misses the point of the current discussion, which is that the data available thus far only indicate

the presence of perceptual (and perhaps cognitive) awareness. Asking this question also risks defaulting to the inductive reasoning outlined above in respect of pain perception. Just because humans seem to use insight, guesses about the future and feelings (i.e. thinking) to reach decisions does not mean that we should assume other animals must reach decisions by the same means. It is still worth briefly considering alternatives to the assessment and executive awareness components of sentience. Elwood (2022) discusses hard-wired decision-making, which means that rules are directly encoded in the animal's nervous system ('innate') and will operate to produce decisions (expressed outwardly as behaviour) independently of sentience. Details will vary greatly between species but the basic principle is that selection has favoured close yet plastic associations among neurones, often concentrated in specific regions, which interact in influencing one another's activity, inhibiting or exciting their action potential. Interestingly, in humans awareness of decision-making might only arise sometime after the neural machinery involved has already completed its task (Soon *et al.* 2008). This demonstrates that although the neural mechanisms involved do not preclude the possibility that sentience is also present (or emergent from it), their outputs may not be dependent on sentience.

Limits to Lloyd Morgan's canon?

Sentience, if present, should of course be a consequence of selection as much as hard-wired decisions would be. There are interesting debates about whether higher levels of awareness (if viewed as being synonymous with consciousness, as is sometimes the case, see discussion in Elwood 2022) could be a direct consequence of selection, or whether it would be best viewed as a spandrel, emergent from adaptive cognition (Robinson *et al.* 2015). Nevertheless, there is an argument that Lloyd Morgan's canon may have its limits with respect to animal sentience. As discussed above, Lloyd Morgan's canon is a parsimony argument based on preferring simpler explanations for behaviour (e.g. basic cognition) over more complex ones (e.g. sentience) where the two possibilities cannot otherwise be distinguished. A more general parsimony rule is Occam's razor (e.g. see Epstein 1984), where

explanations with fewer components should be preferred over those with more components if they can't otherwise be distinguished. Taking into account all of the hermit crab work reviewed in Elwood (2022), one could argue that Lloyd Morgan's cannon and Occam's razor come into conflict because a large collection of innate heuristics seems to contain more components than a capacity for domain-general flexibility. On the other hand, it seems that we don't at present know much about the relative biological complexities that would be required to produce a large set of heuristics versus an overarching capacity for insight and forward planning. For the time being I think we remain on safer ground by sticking with Lloyd Morgan's canon and judging each set of behavioural results by its own merits.

Conclusion

Are hermit crabs sentient? It is likely that forthcoming legislation in the UK concerning all decapods and cephalopods will confer this status on them, so as far as the law is concerned the answer will be yes. It will be interesting over the coming years to see how this feeds through to the regulations for handling decapods (see recommendations in Birch et al. 2021) and whether comparable levels of protection will be afforded across different sectors (e.g. the shellfish industry, scientific research). The scientific answer depends on which definition we use. If sentience is restricted to feelings, the question is largely settled – we will probably never know for sure whether hermit crabs experience pain (or other feelings) but should assume they might for the purposes of how we treat them. If we use the wider definition that encompasses awareness as well, the answer depends in the first instance on where we draw the line for sentience. In the foregoing I have suggested that sentience should be restricted to those higher levels of awareness that exceed the basic cognitive functions that are properties of most if not all metazoans, and which are continuously demonstrated in the majority of animal behaviour experiments. The more interesting question is whether hermit crabs (and other animals) do indeed possess the higher levels of awareness among those outlined by Broom (2007).

Differentiating between these in hermit crabs will no doubt require careful consideration of appropriate questions and experimental designs. See for example discussions around the evidence for forward planning in corvids, versus the cognitively simpler process of associative learning (Suddendorf & Corballis 2007). Work on forward planning in corvids also shows that we need to be careful about generalising results among even relatively closely related species. Canada jays don't forward plan (Martin *et al.* 2021) whereas Californian scrub jays do (Raby *et al.* 2007). On the other hand, the diversity of hermit crab species amenable to study provides the opportunity for comparative cognitive studies amongst the Anomura.

The hermit crab experiments reviewed by Elwood (2022) showcase the often surprising ways in which they demonstrate perceptual and possibly cognitive awareness. However, we have yet to see any results that could be explained only by higher levels of awareness. Therefore, we should favour the simpler explanations for behaviour in hermit crabs for the time being. This is not to say that the higher levels of awareness that I have equated with sentience will never be demonstrated in hermit crabs (e.g. see Tinbergen 1951, p.4), and I agree with Elwood (2022) that the results of numerous hermit crab studies are compatible with that possibility. Elwood (2022) also shows how the various species of commonly studied hermit crabs are excellent models for probing the extent of awareness in animals. I suggest two considerations for future experiments on hermit crabs and other animals that would be useful in further resolving the question of animal sentience. First, experimental designs should include treatment groups that focus specifically on differentiating across the different levels of awareness, particularly between perceptual or cognitive on the one hand against assessment and executive on the other. Second, in addition to data that allows comparison of behavioural outcomes across treatments, we should collect detailed ethological data allowing analysis of the sequencing of behavioural events across treatments. This is because it seems difficult to distinguish between levels of awareness on the basis of outcomes alone (see discussion of hermit crab experiments above). In contrast, the same outcome could be reached via different sequences of information-gathering activities depending on the level of awareness involved. Such approaches could contribute to the

challenge of devising experiments that can differentiate assessment and executive awareness from simpler levels of awareness that are already included within the basic cognitive functions of gathering, processing and storing information. In my view, this will be essential for further resolving the fascinating question of sentience in non-human animals.

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