

ANIMAL SENTIENCE

AN INTERDISCIPLINARY JOURNAL ON ANIMAL FEELING

Elwood, Robert W. (2022) [Pros and cons of a framework for evaluating potential pain in decapods](#). *Animal Sentience* 32(29)

DOI: 10.51291/2377-7478.1766

Date of submission: 2022-01-01

Date of acceptance: 2022-11-30



This article has appeared in the journal *Animal Sentience*, a peer-reviewed journal on animal cognition and feeling. It has been made open access, free for all, by WellBeing International and deposited in the WBI Studies Repository. For more information, please contact wbisr-info@wellbeingintl.org.

Pros and cons of a framework for evaluating potential pain in decapods

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

Robert W Elwood

Queen's University, Belfast

Abstract: The rigorous framework for research into potential pain in decapods was successful in allowing legislators in the United Kingdom to evaluate a complex scientific issue. However, it might produce problems for research. I discuss doubts about the usefulness of the eight criteria. Some have yet to receive any investigation and others do not allow much inference about pain. In addition, some existing studies are not covered in the framework. Most worrying, however, is the potential for stifling future research of novel areas that are excluded from the framework.

[Robert W. Elwood](#) is Emeritus Professor of Animal Behaviour, Queen's University, Belfast, UK. He works on pain, information-gathering, motivation, and aggression.



[Website](#)

Introduction. Crump et al. (2022) assess whether pain might occur in decapod crustaceans by creating a framework of eight criteria and a scoring system. Some commentaries on their target article suggest that this is a good idea because it provides a rigorous approach (e.g. Brown 2022; Levin 2022), which may be easily understood by a wide audience, including those with a limited scientific background. If persuaded by the evidence, this audience might then influence legislation on protecting these animals from ill treatment and possible suffering. To that end it has been remarkably successful. The approach was devised initially for a report on possible sentience in decapods and cephalopods, commissioned by the UK government (Birch et al. 2021). The review of the evidence for pain within the framework caused the UK government to recognize sentience in both taxonomic groups. Although that has not resulted in any immediate change in the treatment of these animals, their sentient status must be considered should any new laws concerning these animals be proposed.

Neglected approaches. Crump et al. (2022) suggest that their framework should be applied when evaluating evidence on other taxa, for example insects, gastropods and spiders. However, that would also shape future research on potential pain, and I suggest that this goes too far. A key reason for this is that rather than encouraging new research it might well have a negative impact. Scientists might be less inclined to propose and use novel methods if those methods fail to match one of the criteria. This is not an alarmist view, because a previous method from my laboratory has been ignored even though it showed great promise, presumably because it did not fit the framework. The method was described in two papers (Elwood and Appel 2009; Appel and Elwood 2009a). Whilst these are cited in the Crump et al. target article, and minor side results are described, no mention is made of the key approach and associated results. The two studies ask if behaviour may be altered by a noxious stimulus

in the medium to long-term (e.g. Sneddon et al. 2014). They involved behavioural responses that could not be part of a nociceptive reflex because they could only occur some time after the noxious stimulus had stopped. The technique involved giving small electric shocks onto the abdomen of hermit crabs while they were in their shells. A previous study had established the voltage of the shocks required to cause hermit crabs to evacuate their shells (Appel and Elwood 2009b), but the aim of Elwood and Appel (2009) was to shock crabs at a sufficiently low level to not induce many to evacuate. Other crabs were in similarly wired shells, but no shock was applied. We then asked if receiving a shock in a shell would alter their motivation to retain that shell when they were subsequently offered the chance to move into a new shell. We hypothesised that being shocked within the shell would reduce the crab's perception of the value of the shell and thus the crab would become more motivated to change to a new shell when it had the opportunity. The new shell was made available 20 secs after the last of ten short shocks or at an equivalent time for those that were not shocked. The two groups behaved in very different ways when offered new shells. Shocked crabs were more likely to approach and contact the new shell and were more likely to move into the new shell than were those that were not shocked. Further, when just those crabs that moved into the shell were examined it was found that shocked crabs contacted the shell more quickly, spent a shorter time investigating the new shell and used fewer probes with their claws (chelipeds) to evaluate the new shell. That is, they behaved as if they had an elevated motivation to acquire a new shell. Crabs in inadequate shells (less preferred species or too small) also show a high motivation to obtain a new shell and do so with minimal investigation (Elwood and Stewart 1985, Elwood 1995, Jackson and Elwood 1990). That is, the shocks had induced a change in behaviour 20 seconds after cessation of the stimulus; this cannot be regarded as a reflex response.

Appel and Elwood (2009a) extended the interval between the cessation of shock and offering a new shell to 5 min, 30 min, 120 min or 24hrs. We found that shocked crabs contacted those shells in a shorter time and fewer cheliped probes were used to assess the new shell. Further, there was an indication that the increased motivation to obtain a new shell, caused by the noxious stimulus, persisted for at least 24 hours. That is, these data are consistent with an expectation of a pain-induced, long-term shift in behaviour. However, the approach does not fit into the target article's framework. For example, the data cannot be considered within criterion 7, associative learning, because there is no suggestion that the changes in motivation were influenced by reinforcement. Nevertheless, it seems that the crabs have a memory of the noxious stimulus and that has altered the crab's assessment of shell quality, from adequate to very poor and thus might be a form of learning (Elwood 2011).

A second neglected aspect is "anxiety", which is another relatively long-term change in behaviour noted in crayfish (Fossat et al. 2014). Crayfish normally explore a cross maze with two light and two dark arms and there is a slight preference for the dark arms. After repeated shock, however, there is a marked shift to a strong preference for the dark arms. Light areas are expected to be more dangerous than dark conditions for crayfish because they are more likely to be detected by potential predators. The increased avoidance of light after shock is thus consistent with the idea that noxious stimuli cause a shift to risk aversion. This is consistent with a key prediction of pain in that we should see a change in behaviour that minimises the risk of further damage (Sneddon et al. 2014). Whilst this study and that of Fossat et al. (2015) are noted in the Crump et al.'s review, the focus is not on the behavioural change but on the physiological basis of that change. Somewhat confusingly, that is discussed

within the criterion of “Analgesia”. In terms of the function of potential pain; yet it is the relatively long-term change in behaviour that is important, so I would have expected that to be a criterion.

A further exclusion from the framework concerns physiological markers of pain, albeit with some caveats (and some further discussion in other categories). I have previously suggested that there is a need for more studies on physiological responses to noxious stimuli (Elwood 2011). We know that stress responses occur when decapods are wounded (Patterson et al. 2007) or given electric shock (Elwood and Adams 2015). However, because stress may occur in situations unlikely to induce pain (e.g., just handling causes stress responses in shore crabs; Wilson et al. 2021), the target article rejects the use of stress as a criterion for pain. This misses an opportunity to use stress responses as a means of investigating how the animal copes with the noxious stimulus. If a noxious stimulus fails to produce a stress response it could be assumed that the stimulus was of little importance. If it did have an effect, the intensity of the stimulus could be varied to determine whether the stress response also varies.

However, we need to get around the problem that a noxious stimulus often causes vigorous behavioural responses, and the behaviour might cause physiological change. Thus, Elwood and Adams (2015) compared the stress responses of crabs that received electric shock, or not, but only compared animals that engaged in similar behaviour, that is, walking in the test arena. We excluded animals that remained still or showed vigorous escape attempts or threat displays. Animals that had been shocked showed considerably higher levels of stress markers indicating that it was the stimulus that had a major negative impact on the animal. That finding is consistent with the idea of pain. A further approach could examine possible physiological stress following avoidance learning. The animal might be trained to avoid a noxious stimulus that is preceded by a conditioned stimulus (Elwood 2011). If stress responses occur when only the conditioned stimulus is presented, but without the possibility of performing the normal avoidance, then it would demonstrate that a memory of the noxious stimulus is associated with the previously neutral stimulus, and that the memory is stressful. This would demonstrate something akin to anxiety and would be consistent with the idea of pain having lasting effects on the animal.

These examples indicate that Crump et al.’s proposed framework is too restrictive. It largely excludes long-term shifts in responsiveness, other than those due to associative learning, and physiological change (other than in different criteria), which might indicate that pain induces stress. The framework has the potential to stifle novel approaches to the study of pain.

1. **Nociception**
 2. **Sensory integration**
 3. **Integrated nociception**
 4. **Analgesia:** (a) endogenous (b) exogenous
 5. **Motivational trade-offs**
 6. **Flexible self-protection**
 7. **Associative Learning**
 8. **Analgesia preference:** (a) self-administer (b) location (c) prioritised
- Crump et al.’s eight criteria**

Comments on Crump et al.'s eight criteria. Having suggested that the framework is too restrictive, I now consider whether all the eight criteria are of equal usefulness, and/or whether some might be redundant. I reflect on the use of these approaches, where appropriate, within my own laboratory.

1. **Nociception:** Because of the wide taxonomic occurrence of nociceptors, demonstrating their presence adds little to deciding whether pain might be experienced (Elwood 2011). This is also the conclusion of several other commentaries (e.g. Briffa 2022; Irvine 2022; Jablonka & Ginsburg 2022; Walters 2022). The target article accepts the very limited usefulness of the first criterion, nociception, but still argues for its inclusion. Yet Crump et al. reject another possible criterion concerning the animal moving away from the noxious stimulus, because that might just be due to a nociceptive reflex. However, if an animal avoids stimuli such as heat, acid or electric shock it must have a system to perceive those stimuli, i.e., nociceptors. Whilst I agree that moving away fails to indicate pain, it seems contradictory to mark a species down because nociceptors have not been demonstrated but refuse to consider moving away from noxious stimuli as an indicator of those receptors.
2. **Sensory integration:** I previously concluded that investigations of the central nervous system provide limited clues of what is, or is not, required for pain experience (Elwood 2011). However, studies have since been published that provide considerably more information about the morphology of decapod brains (e.g., Strausfeld et al. 2020). This study demonstrates that different taxonomic groups of decapods show marked variation in the degree to which hemiellipsoid bodies and accessory lobes are developed. Whilst the former are suggested to be areas involved in integration of information, their underdeveloped state in lobsters and crayfish leads to the suggestion that those groups might use the accessory lobes for that function. Whilst this might be true, or indeed both brain areas might integrate information, there has been no demonstration that they are involved in a pain experience. Thus, I have not altered my view about the limited usefulness of brain structures in assessing whether those animals might experience pain. These views are shared by some of the commentators (e.g., Jablonka & Ginsburg 2022). However, there is no doubt that decapods can integrate information from numerous sources (Elwood 2022). Hermit crabs work to gather information about numerous aspects of their current shell and of an alternative shell to enable a final decision about which to occupy (Elwood 1995). Hermit crabs fighting for ownership of shells integrate even more sources of information in reaching decisions (Briffa & Elwood 2000, 2001). Thus we know they have these abilities even though we are not certain about which brain areas are involved.
3. **Integrated nociception:** This is suggested to be an important evidential gap because there is little known of links between the nociceptors and the integrative brain regions and thus little evidence of whether they occur. However, as others note (e.g. Jablonka & Ginsburg 2022), because we know that nociceptive input is integrated with other motivational requirements (i.e., trade-offs, see below), and that if sensory integration occurs, then then these links must be present.

A general comment about brain pathways is that a demonstration of their occurrence, and their activation when responding to a noxious stimulus, does not prove that they are involved in a pain experience. It would simply show that the area is active at a particular time. However, information on brain structure is important for the understanding the broader biology of decapods. That might give insights into possible use in pain experience, but proof of that connection will be difficult to establish.

4. **Analgesia:** Work in my laboratory has demonstrated that glass prawns respond to the initial application of benzocaine to an antenna as if it were aversive, with far more prawns showing tail-flick during the application of benzocaine than to the application of seawater. There was no change in subsequent general activity but there was a subsequent increase in grooming directed at the treated antenna; however, there was no increase in rubbing the antenna on the side of the tank. This initial aversive response is presumably due to the acidic nature of the medium in which the local anaesthetic is dissolved (Elwood 2019). When noxious chemicals were applied 5-6 minutes after the first treatment, the responses of the prawns were markedly reduced by the benzocaine. Prawns receiving this local anaesthetic showed less grooming and rubbing of the antenna when subsequently treated with noxious chemicals but, importantly, there was no change in general activity. This is consistent with the idea that the firing of nociceptors is disrupted by the local anaesthetic and hence the complex and prolonged grooming and rubbing (not easily described as reflexes) did not occur. Benzocaine thus appears to have an effect similar to that seen in mammals.

The target article considers studies in which crabs treated with opioids subsequently showed a reduction in responses to noxious stimuli but also to apparent danger (e.g. Lozada et al. 1988). Barr and Elwood (2011) also tested crabs with opioids but used a paradigm in which an increase in responses would be expected if morphine reduced a pain-like experience. We offered crabs an escape from bright light if they entered a dark shelter. However, some crabs received electric shock within the shelter; the idea was that they should be more likely to enter if the effect of shock was reduced by the morphine. This was not found, however; the crabs just became limp and unresponsive to all stimuli. The conclusion was that morphine did not have a specific analgesic effect.

We are at an early stage in understanding analgesics for use in decapods. Local anaesthetics are effective and act on the nociceptive inputs. Those that might act centrally, however, require considerable research and only then might they be of use in helping to clarify whether these animals are sentient.

5. **Motivational trade-offs:** The idea of using motivational trade-offs to investigate potential pain in decapods was that if those trade-offs occurred it would support the idea that there was central decision-making with respect to responses to noxious stimuli (Appel & Elwood 2009a). However, should trade-offs not be shown, those responses might be described as nociceptive reflexes rather than pain (Appel & Elwood 2009a). The first study examined whether hermit crabs, in good quality shells, would resist leaving those shells more than would those in poor quality shells following electric shock. There was a clear hypothesis that, should a trade-off occur, those in good shells would endure higher voltage than would those in poor shells, (Appel & Elwood 2009b). This was found when using a one-tailed test. That test is

appropriate when only one direction of difference is being considered as supporting the hypothesis and thus, the result is valid.

A second study was not intended to examine trade-offs (Elwood & Appel 2009) but still used good and poor shells. Crabs were more likely to leave poor shells after shock than to leave good shells. Thus, there was a trade-off between getting out of the shell and shell quality.

A third study used a predator odour and electric shock with the hypothesis that hermit crabs should be less likely to get out of the shell if there were cues about a potential predator (Magee & Elwood 2016a). Controls were odour of a non-predator (mussels) and seawater without added odours. Odours were obtained by maintaining shore crabs (N = 5) with a wet weight of 634.51 g, or mussels (N = 41) with a wet weight of 635.6 g, in 6 l seawater for 24 hours. This would create a massive concentration of odour compared to natural conditions in which there will be a much greater volume of water coupled with flow. The ability to respond to low concentrations is important because that would enable the hermit crab to detect a predator before it makes contact. However, we did not know what that concentration would be, so we used two concentrations. In one (undiluted) we added 1 ml of the tank water to the test arena whereas in the second that 1 ml was diluted with 99 ml of seawater and 1ml of that added to the test arena. Hermit crabs in normal seawater were the most likely to evacuate their shells following shock (95.4%) and crabs with the dilute predator odour were the least likely (40.9%). Those with dilute mussel odour (80%) did not differ from those in seawater but did from the dilute predator odour. Those with the non-dilute predator odour (47.3%) were like those in the dilute predator odour. However, those in the non-dilute mussel odour were intermediate in their tendency to evacuate (57.9%). They did not differ significantly from the dilute mussel odour, but neither did they differ from either of the two predator odours.

Thus, the result was difficult to evaluate, and this has been used to cast doubt on the trade-off that was clearly shown with the dilute odours. However, because the dilute concentration of a predator odour could be detected by the hermit crab that concentration probably better reflects the situation in the field than does the higher concentration. At the low concentration the data show a clear, significant, trade-off between avoiding shock and avoiding predation with both controls being different from the predator odour. With high concentration, the trade-off is significant when responses to predator odour and normal sea water are compared.

In conclusion, we have three experiments that show trade-offs between avoidance of shock and other motivational requirements. These could not be explained by a reflex; rather, they show that there is some means of prioritising motivations in these animals so that effective decisions may be made. These trade-offs are consistent with the idea of pain because they exclude the possibility of nociceptive reflexes (Elwood 2019).

6. **Flexible self-protection:** Crump et al. (2022) list several studies on various decapods that provide clear evidence of behaviour directed at the specific site of a wound or application of a novel stimulus. My own laboratory has shown that noxious chemicals applied to one antenna cause repeated grooming of that specific antenna and rubbing of that antenna against the side of the tank (Barr et al. 2008). We have observed grooming and rubbing of mouth parts of shore crabs when acetic acid was applied and

if acid was placed on one eye that specific eye was retracted for longer than was the alternative eye to which non-noxious stimuli were applied (Elwood et al. 2017). We have seen hermit crabs directly grooming their abdomen when they evacuated a shell in which electric shock had been applied, but we have never seen this in crabs removed from shells by cracking the shell in a bench-vise (Appel & Elwood 2009b). Further, crabs that had a cheliped removed by breaking (as seen in fishery practice) direct behaviour towards the site of the wound (McCambridge et al. 2016). Thus, there is an ability to localise the site of the wound or stimulus and to tend to that area in a protective manner. This does not appear to be a reflex response because it is prolonged and occurs long after the stimulus has been applied. These observations are consistent with the idea of pain.

7. **Associative learning:** A key function of pain is that it should alter future behaviour in ways that would minimise the possibility of further wounding. There are different ways this might be achieved, but learning is especially expected if that leads to avoidance of the situation that resulted in pain (Elwood 2011). Speed of learning is important in this context. The learning should result in rapid reduction of further damage if it is to improve the fitness of the animal.

We have used two approaches to examine avoidance learning in shore crabs, each using the natural aversion of crabs to bright light. Magee and Elwood (2013) placed crabs in the centre of a brightly lit arena that had a dark shelter at either end. Crabs were randomly selected to be shocked or not in the shelter they first entered, and in subsequent trials that shelter resulted in the same shock or not. If the crab entered a non-shock shelter it was allowed to remain for 2 min. If the shock shelter was entered the crab received a shock every 5 sec it remained in the shelter for a maximum of 2 min. If it got out of the shelter the shocks stopped but were given again if the crab re-entered that shelter. However, if it went to the non-shock shelter it was allowed to remain in that shelter for 2 min. At the end of each of the ten trials the crab was removed from the enclosure for 2 min before the next trial.

Crabs in trial 2 showed a strong preference to return to the first shelter irrespective of whether it was the shock or non-shock shelter. We found that in trial 3 those crabs that had selected the shock shelter in the previous trial were significantly more likely to switch their choice to the non-shock shelter and that crabs would begin to use that shelter in subsequent trials. Many crabs exited the shock (but not the non-shock) shelter and the proportion of crabs that did so increased over the ten trials. Some then went back to the shock shelter but the majority went to the alternative shelter, although that was only significant during later trials (6, 8, 9 and 10). Some crabs failed to enter either shelter during a trial; that was more common if they had received shock in the preceding trial. This suggests that these are choosing to avoid the shock by remaining in the normally avoided light.

We used a final trial that did not involve shock in either shelter. However, some crabs were oriented in a different direction such that if they had walked to the left to reach the previously safe shelter they now had to walk to the right. In addition, distinctive visual cues above the shelter were switched for some crabs. This demonstrated that the crabs had not used the visual cues but had instead used the direction (left or right) of movement to avoid the shock. That is, the crabs showed swift avoidance learning

(following just two trials of experience). This swift learning is impressive because they had shown a strong preference for the first chosen shelter; hence that preference had to be overcome in order to avoid the shock.

Our second experiment used a different paradigm, in which a partition was placed in the middle of the tank and the crab was placed on one side and then the other in alternate trials so that only one shelter could be accessed on each trial (Magee & Elwood 2016b). This sequential exposure to shelters did not result in avoidance learning when a choice of shelters was offered without the partition. Sequential presentation of stimuli in learning studies typically produces poorer learning (Dyer & Neumeyer 2005). However, although crabs did not discriminate between the shelters, they did appear to be learning how to reduce the number of shocks. First, the proportion of crabs that left the shock shelter increased over the five trials in which shock was given. Second, the time taken to leave the shock shelter was significantly shorter in the final trial compared to the first.

A recent study on crayfish has demonstrated swift learning of an association between visual cues and electric shock (Okada et al. 2021), so there is little doubt that noxious stimuli alter later behaviour via associative learning. That is clearly consistent with the idea of pain.

8. **Analgesia preference:** Studies of vertebrates exposed to a long-term noxious stimulus demonstrate an increased intake of food containing pain killer. These provide strong evidence of pain (e.g., Colpaert 1980). Thus, similar findings in decapods would provide strong indications of pain-like states in this taxon. I agree with Crump et al. that it is unfortunate that such studies have not been attempted in decapods. I also agree that the methods used by Datta et al. (2018), by which drugs could be administered into freely moving crayfish, should be appropriate when combined with a good experimental design. This approach should be added to a list of potential studies that might provide considerable insights into the affective states of decapods.

Conclusions. These eight criteria clearly differ in their usefulness in indicating pain in decapods or any taxon. However, they do not encompass all methods that might be useful in pain studies. This is a major problem if current knowledge is ignored -- or even worse, if future researchers fail to consider novel approaches because they do not fit into the framework. Some authors have produced lists, rather than frameworks, of approaches that might help in evaluating whether pain might occur. Sometimes these are primarily for vertebrates (e.g. Bateson 1991), sometimes specifically for invertebrates (e.g. Elwood 2011, 2019) or for both (Sneddon et al 2014). These lists have been offered as suggestions, or merely to organise reviews of current knowledge about different taxa (Sneddon et al 2014), or to suggest approaches that might prove useful (Elwood 2011, 2019). Sneddon et al. (2014) produced a checklist for how different approaches had matched to different taxa. These reviews, and that of the target article, conclude that there is substantial evidence consistent with the idea of pain in decapods. However, there is a need of further study, even for those approaches that might not be particularly convincing about pain rather than mere nociception. It is important to gather as much information about the potential for pain and suffering so that sound decisions can be made in various jurisdictions in which little or no protection is currently given.

References

- Appel, Mirjam; and Elwood, Robert W. (2009a). [Gender differences, responsiveness and memory of a potentially painful event in hermit crabs](#). *Animal Behaviour*. 78(6), 1373-1379.
- Appel, Mirjam; and Elwood, Robert W. (2009b). [Motivational trade-offs and potential pain experience in hermit crabs](#). *Applied Animal Behaviour Science*. 119(1-2): 120-124.
- Barr, Stuart; and Elwood, Robert W. (2011). [No evidence of morphine analgesia to noxious shock in the shore crab, *Carcinus maenas*](#). *Behavioural Processes*. 86(3): 340-344.
- Barr, Stuart; Laming, Peter R.; Dick, Jaimie T. A.; and Elwood, Robert W. (2008). [Nociception or pain in a decapod crustacean?](#) *Animal Behaviour*. 75(3): 745- 751.
- Bateson, Patrick (1991). [Assessment of pain in animals](#). *Animal Behaviour*. 42(5): 827- 839.
- Birch, Jonathan; Burn, Charlotte; Schnell, Alexandra, K.; Browning, Heather; and Crump, Andrew (2021). [Review of the Evidence of Sentience in Cephalopod Molluscs and Decapod Crustaceans](#). Department for Environment, Food & Rural Affairs (Defra).
- Briffa, Mark (2022). [Sentience in decapods: an open question](#). *Animal Sentience* 32(19)
- Briffa, Mark; and Elwood, Robert W. (2000). [The power of rapping influences eviction during hermit crab shell fights](#). *Behavioral Ecology*. 11: 288-293.
- Briffa, Mark; and Elwood, Robert W. (2001). [Decision rules, energy metabolism and vigour in hermit crab fights](#). *Proceedings of the Royal Society B* 268: 1841-1847
- Brown, Culum (2022). [Fine-tuning the criteria for inferring sentience](#). *Animal Sentience* 32(7)
- Colpaert, F. C.; De Witte, P.; Marole, A. N.; Awouters, F.; Niemegeers, E.; and Janssen, P. A. J. (1980). [Self-administration of the analgesic suprofen in arthritis rats: *Mycobacterium butyricum*-induced arthritis as an experiment model of chronic pain](#). *Life Sciences*, 27, 921e928.
- Crump, Andrew; Browning, Heather; Schnell, Alex; Burn, Charlotte; and Birch, Jonathan (2022). [Sentience in decapod crustaceans: A general framework and review of the evidence](#). *Animal Sentience*. 32(1)
- Datta, Udit; Van Staaden, Moira; and Huber, Robert (2018). [Crayfish self-administer amphetamine in a spatially contingent task](#). *Frontiers in Physiology*. 9: 433.
- Dyer, Adrian G.; and Neumeyer, Christa (2005). [Simultaneous and successive colour discrimination in the honeybee \(*Apis mellifera*\)](#). *Journal of Comparative Physiology A*. 191(6): 547-557.
- Elwood, Robert W. (1995). [Motivational change during resource assessment by hermit crabs](#). *Journal of Experimental Marine Biology & Ecology*. 193(1-2): 41-55.
- Elwood Robert W. (2011). [Pain and suffering in invertebrates?](#) *ILAR Journal*. 52: 175-184.
- Elwood, Robert W. (2019). [Discrimination between nociceptive reflexes and more complex responses consistent with pain in crustaceans](#). *Philosophical Transactions of the Royal Society of London B*. 374(1785): 20190368.
- Elwood, Robert W. (2022). [Hermit crabs, shells, and sentience](#). *Animal Cognition*. 1-17.
- Elwood, Robert W.; and Adams, L. (2015). [Electric shock causes physiological stress responses in shore crabs, consistent with prediction of pain](#). *Biology Letters*. 11(11): 20150800.
- Elwood, Robert W.; and Appel, Mirjam (2009). [Pain experience in hermit crabs?](#) *Animal Behaviour*. 77(5): 1243-1246.
- Elwood, Robert W.; Dalton, Natasha; and Riddell, Gillian (2017). [Aversive responses by shore crabs to acetic acid but not to capsaicin](#). *Behavioural Processes*. 140: 1-5.
- Elwood, Robert W.; and Stewart Anne (1985). [The timing of decisions during shell investigation by the hermit crab, *Pagurus bernhardus*](#). *Animal Behaviour* 33: 620-627.

- Fossat, Pascal; Bacqué-Cazenave, Julien; De Deurwaerdère, Philippe; Delbecque, Jean Paul; and Cattaert, Daniel (2014). [Anxiety-like behavior in crayfish is controlled by serotonin](#). *Science*. 344(6189): 1293-1297.
- Fossat, Pascal; Bacqué-Cazenave, Julien; De Deurwaerdère, Philippe; Cattaert, Daniel; and Delbecque, Jean-Paul (2015). [Serotonin, but not dopamine, controls the stress response and anxiety-like behavior in the crayfish *Procambarus clarkii*](#). *Journal of Experimental Biology*. 218(17): 2745-2752.
- Irvine, Elizabeth (2022). [Independence, weight and priority of evidence for sentience](#). *Animal Sentience* 32(10)
- Jablonka, Eva and Ginsburg, Simona (2022). [Pain sentience criteria and their grading](#). *Animal Sentience* 32(4)
- Jackson Nicholas W.; and Elwood, Robert W. (1989). [How animals make assessments: information gathering by the hermit crab, *Pagurus bernhardus*](#). *Animal Behaviour*. 38: 951-957.
- Levin, Michael (2022). [Generalizing frameworks for sentience beyond natural species](#). *Animal Sentience*. 32(15)
- Lozada, Mariana; Romano, Arturo; and Maldonado, Hector (1988). [Effect of morphine and naloxone on a defensive response of the crab *Chasmagnathus granulatus*](#). *Pharmacology Biochemistry & Behavior*. 30(3): 635-640.
- Magee, Barry; and Elwood, Robert W. (2013). [Shock avoidance by discrimination learning in the shore crab \(*Carcinus maenas*\) is consistent with a key criterion for pain](#). *Journal of Experimental Biology*. 216(3): 353-358.
- Magee, Barry; and Elwood, Robert W. (2016a). [Trade-offs between predator avoidance and electric shock avoidance in hermit crabs demonstrate a non-reflexive response to noxious stimuli consistent with prediction of pain](#). *Behavioural Processes*. 130: 31-35.
- Magee, Barry; and Elwood, Robert W. (2016b). [No discrimination shock avoidance with sequential presentation of stimuli but shore crabs still reduce shock exposure](#). *Biology Open*. 5(7): 883-888.
- McCambridge, Claire; Dick, Jaimie T. A.; and Elwood, Robert W. (2016). [Effects of autotomy compared to manual declawing on contests between males for females in the edible crab *Cancer pagurus*: implications for fishery practice and animal welfare](#). *Journal of Shellfish Research*. 35(4): 1037-1044.
- Okada, Shione; Hirano, Natsumi; Abe, Toshiki; and Nagayama, Toshiki (2021). [Aversive operant conditioning alters the phototactic orientation of the marbled crayfish](#). *Journal of Experimental Biology*. 224,
- Patterson, Lynsey; Dick, Jaimie, T.A.; and Elwood, Robert W. (2007). [Physiological stress responses in the edible crab *Cancer pagurus* to the fishery practice of de-clawing](#). *Marine Biology*. 152: 265-272
- Sneddon, Lynne U.; Elwood, Robert W.; Adamo, Shelley A.; and Leach, Matthew C. (2014). [Defining and assessing animal pain](#). *Animal Behaviour*. 97: 201-212.
- Strausfeld, Nicholas James; Wolff, Gabriella Hanna; and Sayre, Marcel Ethan (2020). [Mushroom body evolution demonstrates homology and divergence across Pancrustacea](#). *eLife*. 9: e52411.
- Walters, Edgar T (2022) [Strong inferences about pain in invertebrates require stronger evidence](#). *Animal Sentience* 32(14)
- Wilson, Charlotte H.; Nancollas, Sarah J.; Rivers, Molly L.; Spicer, John I. and McGaw Iain J. (2021). [Effects of handling during experimental procedures on stress indices in the green shore crab, *Carcinus maenas* \(L\)](#). *Marine and Freshwater Behaviour and Physiology*. 54:2, 65-86.