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Integrating evolution into animal sentience

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Abstract: Like many others, I see Crump et al. (2022) as a milestone for improving upon previous guidelines and for extending their framework to decapod crustaceans. Their proposal would benefit from a firm evolutionary foundation by adding the comparative measurement of life-history complexity as a ninth criterion for attributing sentience to nonhuman animals.

In this target article, as in their previous report (Birch et al. 2021), which influenced the scope of the UK's animal sentience bill, Crump et al. (2022), take a significant step toward a rigorous study of sentience across the Metazoan kingdom. They make the important point that sentience could be instantiated in different ways in species distantly related to us. They suggest that their indicators are related to plausible evolutionary functions of sentience, noting that ion channels connected to nociception are "highly conserved evolutionarily" (p. 12). But there is more to be said on how evolutionary considerations might be helpful in inferring sentience. A firm evolutionary basis may help us understand the feelings of distantly related animals in a less anthropocentric way (Veit 2022a,b,c).

Ethologists included behaviour in the Darwinian revolution, constructing ethograms of the healthy and pathological behaviours of animals in the natural environments in which they evolved (Tinbergen 1951). The twenty-first century equivalent of these ethograms can be found in *life-history theory*, an analytical framework for studying the diversity of strategies that organisms pursue in nature, their "strategic decisions over... [their] lifetime" (McNamara and Houston 1996, p. 215), especially the trade-offs they face (Roff 1992; Veit forthcoming). Life-history theory allows a Darwinian study of the mind along the lines Donald Griffin (1976) called for: a cognitive ethology that investigates what consciousness does for animals in their natural lives.

Many scientists and philosophers (e.g. Griffin 1976; Ginsburg & Jablonka 2019; Godfrey-Smith 2020) who have pondered the evolutionary function of consciousness have suggested that it has something to do with the *complexity* of animals. Such suggestions -- with the exception of Integrated Information Theory (Oizumi, Albantakis, & Tononi 2014) -- have usually been left vague. A biologically neutral measure of complexity such as information integration, however, cannot help us ascertain the adaptive benefit of sentience. Life-history complexity can be operationalized in terms of the number of parameters and constraints in the evolutionary

optimization problem that animals face (Veit forthcoming). If animals have to deal with more trade-offs in their lives -- for example, because they need to deal with a larger number of predators or because they have to choose among a greater diversity of food sources -- their life-history complexity will be higher. Thus, generalists such as the common brushtail possum (*Trichosurus vulpecula*) will have higher life-history complexity than specialists such as the koala (*Phascolarctos cinereus*). This would correlate with their intelligence or cognitive complexity (as in the case of the octopus, Vitti 2013), as well as with personality differences (Wolf et al. 2007)

Crump et al.'s fifth criterion (motivational trade-offs) suggests that sentient animals can trade off the positive and negative valence of different stimuli through a common neural measure of value. Might this be the evolutionary function of sentience (Cabanac 1996; Veit 2022b)? Behavioral ecologists have long argued that a centralized and integrated means of evaluating trade-offs between the competing demands of an animal's life is needed for complex, flexible, and efficient decision-making (McFarland and Sibly 1975; McCleery 1977; McNamara and Houston 1986). A way to test the hypothesis that sentience evolved in order to deal with trade-offs might be to compare the life-history complexity of different animals with the richness of their capacity to engage in motivational trade-offs. Finding high life-history complexity in species can thus strengthen our case for their sentience.

Crump et al. note that because only a tiny proportion of the 15,000 extant decapod species have been assessed in terms of sentience indicators, their framework should not be used to conclude that almost all decapod species lack sentience (i.e., that it is unlikely that they can feel). Instead, inferences from well-studied crustaceans should be generalized to their closely related species. Tests of sentience-related capacities are rare, but there is a much greater wealth of data about animals' life histories. There is so far little animal sentience research in penaeid shrimps (*Penaeidae*), but their life histories are reasonably similar to those of caridean shrimps (*Caridea*), which should strengthen our confidence in their sentience. Relatedness alone should not be the sole factor, because even closely related species can have very different life history strategies. These may well influence whether sentience would be "worth having" as a trait that (presumably) has to pay for itself in requiring special neural circuitry. Species with lower life history complexity for example, insects that have reduced in size from their Cambrian ancestors, may have lost their sentience. Higher or equal life history complexity should be considered as compelling evidence that generalizing sentience is justified.

In conclusion, adding life-history complexity as a ninth addition to Crump et al.'s eight criteria would help in making better-informed evolutionary decisions about which animals to protect. A close examination of the life histories of animals would also bring us closer to integrating the field of animal sentience research with the other biological sciences, allowing us to study animal sentience in a less anthropocentric way.

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