

communities. The authors highlight the importance of considering variation within populations in individual responses. Intraspecific variation is a topic that has received much attention in recent years and is by now generally accepted as a factor that needs to be considered when investigating responses of populations to environmental change (Sih 2013). Yet, fewer than 10% of the studies identified by Harding et al. consider intraspecific variation in responses to noise. This number has to increase as knowledge about individual variation not only informs us about the possibility of adaptation to new conditions—phenotypic variation is the raw material for natural selection—but also increases our knowledge of the mechanisms behind the impacts of noise on populations. Only when the mechanisms are known can we develop efficient strategies for mitigating the negative effects of noise on populations and communities. An understanding of individual variation can clarify which individuals are most sensitive to noise and which are best able to cope with the disturbance, and how differences in coping ability depend on individual characteristics. This information can then be used to predict how populations will develop under noise and which management strategies are needed to maintain viable populations and diverse species communities. Thus, an increased understanding of individual variation can help us predict how populations on average will adapt to a changing world.

Behavioral ecology has here a central role to play, as it links phenotypes to fitness under specific environmental conditions. It illuminates the interaction between the individual and the environment that underlies intraspecific variation. As Harding et al. point out, both intrinsic and extrinsic factors influence the individual variation, but the distinction between them is also blurred. The extrinsic environment influences intrinsic characteristics (and to some extent vice versa): individuals living in different patches within a habitat, or who are born at different times, are exposed to different environmental conditions and thus develop different characteristics, such as body size, boldness, or stress tolerance, and can, therefore, differ in their responses to noise. Behavioral ecology, especially when combined with genetic studies, can increase our insight into how different individuals respond to environmental change, why they respond as they do, the consequences of the responses for populations and communities, and the management strategies that are needed to mitigate any negative effects on populations and communities (Wong and Candolin 2015).

Exactly how such studies on the impact of intraspecific variation on populations and communities should be performed is still an open question for many species: which individual characteristics and behaviors should be measured, and what is the appropriate time and space scale to consider? To advance the research field, a framework should be constructed that clarifies which factors need to be considered for species with different life histories living under different conditions. Although we are not yet there, the strength of Harding et al.'s review lies in providing suggestions on the design, implementation, and reporting of studies on individual variation in relation to noise, and how the information can be used to mitigate negative effects of noise on populations and communities. Thus, the article has the potential to improve the quality of data collected, as well as enlighten us on how to use of the data in conservation work. The review is thus timely with an important message—the importance of considering individual variation in responses to disturbances—a message that needs to be echoed across studies on anthropogenic disturbances.

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In a noisy world, some animals are more equal than others: a response to comments on Harding et al.

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We are grateful for the positive and thought-provoking commentaries (Blumstein 2019; Candolin 2019; Lehnardt et al. 2019; Pruitt 2019; Shannon 2019) written about our recent review on the causes and consequences of intraspecific variation in animal responses to anthropogenic noise (Harding et al. 2019). All commentators agree on the timeliness of the subject matter, in terms of both the global threat posed by sounds arising from human activities and the value of considering how conspecific individuals may be affected differently as a result of a range of intrinsic characteristics and extrinsic factors. Here, we take the opportunity to emphasize four key points moving forwards.

First, long-term monitoring of both acoustics and animal responses is of crucial importance (Lehnardt et al. 2019; Shannon 2019). Moving beyond short-term studies creates a better understanding of responses to anthropogenic noise in general, but is particularly critical if we are to determine impacts on individual fitness. Ultimately, this will allow us to develop an understanding of likely evolutionary consequences and population-, community-, and ecosystem-level effects. However, there is a real need to consider how such long-term monitoring might be achievable in a cost-effective, widespread fashion. For instance, traditional ocean-based passive-acoustic monitoring programmes use expensive devices located in just a small handful of locations. Whilst such monitoring programmes are undoubtedly valuable, it would be beneficial if

their scope and range could be greatly expanded, potentially through the complementary deployment of relatively inexpensive equipment (e.g., cameras with audio feeds) and the engagement of citizen-science activities that have proved successful in other contexts.

Second, it is important not just to document the effects of noise, but to use the resulting data and information to develop evidence-based mitigation and management plans (Blumstein 2019; Candolin 2019; Shannon 2019). Noise is an anthropogenic disturbance where there are some relatively feasible measures that can be taken to make a positive difference. Unlike chemicals, for example, noise pollution leaves no lingering contamination when its sources are stopped or moved away. Moreover, it is possible to quieten our activities: for instance, through improved engine and propeller design in ships and motorboats, with the use of bubble curtains around pile-driving units, and by building sound barriers alongside terrestrial highways. Rather than just measuring the resulting reductions in noise levels, as is mostly the case now, studies testing the (hopefully beneficial) effects on wildlife are needed.

Third, there is a strong belief that behavioral ecologists are central to achieving these goals (Blumstein 2019; Candolin 2019; Pruitt 2019; Shannon 2019). Behavioral ecology has a well-established tradition of long-term studies, enabling the gradual accumulation of baseline knowledge but also the opportunity to document changes across time in response to environmental events. The behavioral ecology community is also increasingly aware of the importance of initial research documenting how our activities affect animals, alongside deep understanding of the behavior and ecology of species and their interactions with one another, in developing practical conservation solutions. Whilst this link might not always have been as tight as is ideal, there is certainly a rapidly burgeoning connection now.

Finally, whilst we focused our review on anthropogenic noise (Harding et al. 2019), all of its general principles are applicable to a range of other anthropogenic disturbances and stressors (Candolin 2019; Shannon 2019). Wherever humans are causing

changes to the environment—and we are doing so at an unprecedented rate with respect to, for instance, climate change, habitat destruction, chemical and light pollution—the same need for basic research combined with management plans is required; and the same importance should be afforded to the consideration of intraspecific variation. It is intuitive that different species may respond in different ways to any particular challenge; it ought to be equally intuitive that different individuals of the same species may be similarly different in their responses. When it comes to monitoring and managing threats to our wild ecosystems, we must be mindful of the Orwellian trope: “some animals are more equal than others.” Both between and within species, variation is vital; now is the time for that understanding to take center stage as we attempt to maximize the mitigation of our activities.

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