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## **Invited Commentary**

Dissecting how behavior and environment shape spatial personalities: a comment on Stuber et al.

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Animal movement is a prominent behavior that links animals' decisions to their ecological environment. Yet, despite the central interest of behavioral ecologist in animal personalities, the repeatability of movement behavior and space-use has received little attention until recently (Spiegel et al. 2017). Certain personality traits that are often examined, such as "exploratory behavior" or "activity," are inherently linked to movement, but their ecological context is rarely discussed, and whether lab-based measures reflect exploration in natural settings has been recently questioned (Mouchet and Dingemanse 2021). The meta-analysis by Stuber et al (2022) exposes how little we know about the repeatability of spatial behavior and uncovers some of the challenges to studying spatial personalities.

The most interesting finding of Stuber et al.'s (2022) meta-analysis is that spatial behaviors are highly repeatable (R  $\sim$ 0.70) compared with other behaviors (R = 0.37; Bell et al. 2009). The authors highlight this point and suggest that high repeatability in spatial behavior may arise from environmental constraints. We completely agree with this interpretation and would like to expand on it here. When the spatial behavior of an animal is assessed

repeatedly in a natural setting, the animal will face the same spatial constraints on its movement every time it is assessed (e.g., rivers and cliffs). Thus, observed consistent behavioral differences among individuals may reflect, in part, differences in the geographical features or resource distribution, within each individual's home range rather than inherent differences in spatial personality. We echo Stuber et al.'s (2022) insight that our inability to distinguish between environmentally induced and inherent behavioral consistency can delay conceptual progress in studying spatial personalities, and limit our ability to predict the response of wildlife to human-induced environmental changes.

As Stuber et al. (2022) suggest, one way to disentangle the mechanisms that underlie consistent spatial behaviors are experimental manipulations, such as translocations that decouple the individual from its environment. However, not all animals can be translocated, and some might return to the original location (Pinter-Wollman 2009). Other approaches for disentangling the causes of observed consistent differences in spatial behavior include: landscape modification, such as manipulating resource abundance and distribution; playback experiments that alter the perception of conspecific and predator presence; and comparing individuals' spaceuse across different environments. Some animals naturally relocate among different environments throughout their lives, providing natural experiments for uncovering whether consistent spatial behaviors emerge from inherent attributes or environmental features. Interestingly, the rate of natural home-range relocation may represent another aspect of spatial personality.

Another challenge when dissecting the internal causes of spatial personalities is that variation in movement can emerge from either different movement tendencies (e.g., due to physiology) or from individual variation in *preferences* for certain habitat features,

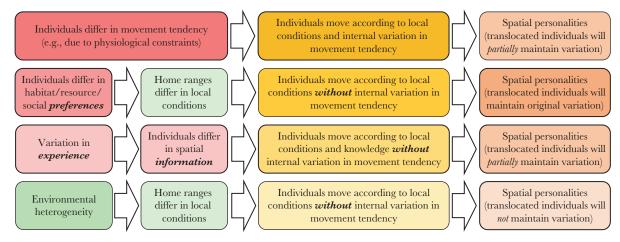


Figure 1 Four (non-mutually) exclusive pathways leading to apparent spatial personalities.

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resources, and/or social interactions (Toscano et al. 2016). Indeed, individuals likely differ consistently in their habitat *preference* (Webber et al. 2020) rather than in their habitat *use.* Thus, for example, if certain individuals prefer a particular type of food, their movements may be consistent even if relocated (Figure 1) because of the distribution of their preferred food, rather than because of an inherent spatial personality. Similarly, preference for certain habitats and/or social interactions may result in observed spatial personalities.

Finally, spatial personalities may emerge from a feedback between spatial behavior and spatial information. An individual's movements determine the amount of spatial information they have (Spiegel and Crofoot 2016). The value of spatial information depends on the rate at which the environment changes, and the interaction between information and environmental change will inform future movement patterns, such as where to settle and forage. For example, in highly variable environments with scarce resources, individual differences in movement patterns could emerge from differences among individuals in spatial information. Thus, the environmental conditions under which animals are observed and the amount of spatial information they possess could influence inferences about the existence and the causes of spatial personalities.

The strong dependencies between environmental conditions and animal movement patterns highlight the challenges awaiting future research on spatial personalities. These challenges will require combining diverse experimental approaches (e.g. natural experiments, translocations, and habitat manipulations) to deepen our understanding of the genetic, physiological, behavioral, social, and ecological mechanisms that underlie consistencies in spatial behaviors and their ecological and evolutionary consequences for wildlife populations in a changing world.

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