This paper addresses the important goal of disentangling flexible behavior and underlying cognitive processes within the broad ecological context of range expansion. Novel aspects are the combined use of experimental and observational protocols, the attempt to measure flexibility across a range of behavioral contexts, and the explicit separation of seemingly flexible behaviors and underlying cognitive processes. A particular strength is that the main hypotheses tested were pre-registered, which constrained and directed the analyses, averting the high potential in this kind of research for post-hoc pattern-seeking. However, to their credit, the authors were sufficiently agile to also test modified hypotheses as suggested by the study results. I have a few recommendations for improvement.

My primary recommendation is that the paper is simplified. As is, it reads more like a thesis than a scientific paper, and I suspect that few readers will persevere sufficiently to get something out of the study. Perhaps the most obvious option for shortening and simplifying is to present only a brief summary of the preregistered hypotheses and associated updates in the body text and move the long and detailed descriptions to supplementary material.

A second concern is that underlying the methodical, seemingly objective, scientific aspects, is a morass of definitional and philosophical complexity around such issues as cognition and behavioral flexibility, and the associated interpretations and assumptions upon which the hypothesis tests and their interpretation are based. This applies even to the fundamental assumption that the experimental measures of "flexibility" do in fact reflect cognitive flexibility as defined in the paper and in the 2017 Mikhalevich paper, rather than some more basic mechanism such as a rule of thumb of the sort "if expected outcome b doesn't follow behaviour B, then switch to behaviour A". In fairness, this partly reflects the status quo in complex fields at the interface of psychology and ecology, such as cognitive ecology and cognitive ethology, and it is difficult to recommend that relevant terms and assumptions are more fully discussed, especially in a paper that is already dense and long. I do, however, recommend that the language is changed to more closely reflect the relationships between observed outcomes and what was actually manipulated/measured (e.g., reversal learning/multiaccess switching) rather than the inferred meaning of these manipulations/measures. This could be complemented in the discussion by more critically examining how these assumptions impact on the interpretation of the results.