The importance of heritability estimates for understanding the evolution of cognition: a response to comments on Croston et al.

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We agree with all 3 sets of commentators (Healy 2015; Smulders 2015; Thornton and Wilson 2015) that the goal we set is challenging, (Croston et al. 2015) and we are well aware of the magnitude of effort involved in such an undertaking. It is notable that 50 years ago, Sydney Brenner wisely chose the simple nematode, *Caenorhabditis elegans*, as a model system for dissecting the links among genes, neurons, and behavior (Brenner 1974), yet hundreds of thousands of published papers and a few Nobel prizes later, there is still no end in sight. Given that *C. elegans* are a relatively simple organism and that cognition in most species is a complex phenotype associated with many genes of small effects, quantitative genetic approaches will likely provide the most useful advances in understanding how natural selection affects cognition. We are happy to hear that there is support for a renewed focus on trait heritability in behavioral ecology research, and we look forward to further insight arising from this effort.

Smulders (2015) reiterates a valid point that it is critical to know which specific traits are heritable, as a trait of interest may be the outcome of multiple and necessarily coincident factors. In such cases, any additive genetic variance detected in that trait may be due to these confounding factors. This problem, however, can often be resolved via conventional experimental approaches aimed at isolating the trait of interest from any potential confounds. For example, Smulders (2015) suggested that heritability estimates of the number of hippocampal neurons might be affected by potentially heritable motivation to hoard food, which is necessarily tied to hoarding behavior. If that were the case, we would expect that animals hoarding less should have fewer neurons. However, for chickadees that spent their entire life in captivity and had little motivation to cache, the total number of hippocampal neurons is similar to that of their wild, highly motivated counterparts (Pravosudov and Roth 2013). In this example, then, it is unlikely that motivation to hoard food directly drives development of the hippocampus. Similar experimental approaches can be employed in careful consideration of what precise trait is being measured, so that heritability estimates are not confounded by other behavioral or cognitive traits.

Thornton and Wilson (2015) caution against what they refer to as an "overemphasis" on studies of trait heritability, on grounds that traits operate in concert and selection does not act on single traits, and that heritability estimates cannot predict selective responses in the presence of any of several phenomena known to affect gene expression. Instead, they suggest a focus on the genetic architecture of traits. We have not suggested the abandonment of any effort to identify specific genes in association with traits of interest. However, because the genetic architecture underlying cognitive traits is typically complex and includes multiple genes with small effects, it may be difficult to identify the individual genes involved (Rockman 2012). Research in fruit flies, however, illustrates that such task, though challenging, is feasible (e.g., Shorter et al. 2015). We suggest that for any effort at understanding trait evolution, including uncovering genetic underpinnings, we must logically begin with the determination that that trait is heritable. It is clear that the nature and extent to which heritability estimates can provide insight into trait evolution depends entirely on the question being asked (e.g., Smulders 2015). Rausher and Delph (2015) point out that evolutionary biologists are often primarily interested in selective pressures driving the evolution of *phenotypes*, and addressing questions about heritability of phenotypes, then, constitutes a complete explanation for evolutionary phenotypic change. Definitive answers to these questions may often be gained without identifying underlying genes (Rausher and Delph 2015).

Although we agree that identifying genetic networks underlying specific traits is important, this approach is subject to the same weaknesses as estimating heritability—many traits change simultaneously, and determining genetic basis for particular traits is a daunting task. As cognitive traits are likely polygenic, involving many genes with likely small allelic effects, quantitative genetics might provide an easier approach to investigate effects of natural selection (Rockman 2012). Although it may be true that heritability estimates cannot provide insight into causal pathways underlying genotype–phenotype associations, quantitative genetic approaches have been successful in investigating the evolution of complex phenotypes. Many cognitive traits are quantitative in nature, meaning that adaptation in these traits likely involves additive effects at many small effect loci, and parallel trait evolution may produce different genetic architecture for polygenic traits, even among different populations within the same species (e.g., Soria-Carrasco et al. 2014; Feldman et al. 2015).

As with any biological inquiry, multiple approaches will be necessary for addressing key questions about the evolutionary biology of cognition. However, the first step is establishing whether a trait can respond to selection. From there, we can move on to test specific predictions about how selective, or nonselective evolutionary drivers, may act on these traits.

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