it may be important to know how much of the trait’s variance is likely to respond to natural selection in a given population, what one is trying to establish. If the question is how strongly a trait responds to selection, then review what is known about the heritability of some cognitive traits and their associated brain areas, and come to the conclusion that a lot of work remains to be done. I can only agree with their recommendation (Houle 1992; Kruuk et al. 2000). The 2 measures can lead to very different conclusions (Kruuk et al. 2000), so careful consideration of the outcomes is needed.

WHICH TRAIT IS ACTUALLY HERITABLE?

For both behavioral and neural aspects of cognition, the final outcome measurement depends on many factors. For example, the outcome of a spatial memory task depends both on the spatial memory abilities of the animals (if they are challenged enough) and on their motivation (Rowe and Healy 2014). Memory ability may well be a combination of traits (as mentioned by Croston et al.; see also Smulders et al. 2010), whereas motivation may be both positive (e.g., hunger) and negative (e.g., neophobia). Any additive genetic variation detected in task performance may therefore be due to any or all of these underlying traits. Similarly, significantly nonzero additive genetic variance in (for example) the number of neurons in the hippocampus of food-hoarding birds may be due to genetic variance in the hippocampal developmental program, but it is also possible that what is actually heritable is the motivation to hoard food, which could in turn stimulate the development of the hippocampus.

There is no easy solution to the problem of how to interpret heritability of complex traits such as brain structures and performance on cognitive tasks. Like in the estimates of cognitive abilities themselves, the (by no means simple) solution might be to measure the presumed cognitive abilities and/or confounding factors in a battery of carefully designed tasks (Kamil 1988; Rowe and Healy 2014). This might allow us to separate the different sources of variance.

In conclusion, Croston et al. (2015) set the field a challenging, but not impossible, task. I look forward to seeing some well-designed and carefully interpreted studies in this field in the (hopefully) not-too-distant future.

FUNDING

During the writing of this comment, TVS was funded by the Biotechnology and Biological Sciences Research Council of the UK, grant number BB/K003534/1.

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Received 8 July 2015; accepted 8 July 2015; Advance Access publication 24 July 2015.

doi:10.1093/beheco/arv120

Editor-in-Chief: Leigh Simmons

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More data required: a comment on Croston et al.

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For those of us interested in the cognitive abilities of real animals in the real world, the review by Croston et al. (2015) on the heritability of cognitive traits is most welcome. Not only are they enthusiastic about encouraging more effort to be put into investigating the role of natural selection in shaping cognitive abilities, they also provide some clear pointers for suitable directions to take.

It is abundantly clear from Croston et al. (2015), however, that considerable challenges lie ahead in estimating the heritability of cognitive abilities and of the underlying neural structures and that the picture is unlikely to be clear or complete any time soon. The research program they suggest will require multiple components to be in place before we can confirm heritability of a cognitive trait and that the variation in the cognitive trait and the brain region involved result in variation in fitness (i.e., variation in number of grand-offspring). These components are: 1) identification of the cognitive trait(s) underlying the behavior of interest; 2) appropriate quantification of the variation in the cognitive trait(s) within and among individuals; 3) identification of the relevant brain regions, which may require precise functional description; 4) confirmation that variation in the cognitive trait correlates with variation in the brain structure; and 5) mapping variation in the cognitive trait(s) and associated brain regions to the measure(s) of fitness. Furthermore, this schema becomes multiplicatively more complex should the interest be in determining the evolution of suites of cognitive traits and brain regions.

The amount of work inherent in this endeavor is apparent from Croston et al.’s consideration of the status of perhaps 3 of the best-worked systems, none of which are yet well enough described or appropriately quantified to enable heritability analyses (spatial memory involved in food storing, centered on the hippocampus, song learning, centered on the Higher Vocal Center, and fear conditioning, centered on the amygdala). Perhaps now is the time therefore to take stock of these systems and to consider whether we need modify our approach. Although there is great enthusiasm to investigate cognitive abilities in an increasingly diversity of species, which is providing a steadily richer natural history of cognitive abilities (e.g., Benson-Amram et al. 2011; Davis et al. 2014; Garland and Low 2014; Samuels et al. 2014), it is still rare to integrate these data with the relevant neural data. But now seems a good time for a concerted push to link brain, behavior, and evolution in each system.

In the short term, one way to achieve a lot of data would be for behavioral ecologists to consider taking advantage of the depth to which one can understand both the evolution and mechanistic basis of traits through the use of model systems, such as Drosophila and honey bees to investigate learning (e.g., Mery 2013; Giurfa 2015), and zebra finches to understand the neurobiology of song (e.g., Mello and Clayton 2015). By focusing on a single system in a single species, the combined efforts of multiple research groups with skills and interests that both overlap and differ should facilitate the more rapid collection and synthesis of a lot of data on both cognitive abilities and their neural substrates.

Either through a diversity of study organisms or a focus on a model species, a combination of the current enthusiasm for investigating the adaptive significance cognition and the eagerness with which behavioral ecologists typically embrace interdisciplinary research means that the future looks bright for the evolution of cognition.

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Received 22 August 2015; accepted 29 August 2015. Advance Access publication 24 September 2015.

doi:10.1093/beheco/arv157

Editor-in-Chief: Leigh Simmons

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