Sih A, Del Giudice M. 2012. Linking behavioural syndromes and cognition: a behavioural ecology perspective. Phil Trans R Soc B. 367:2762–2772.
Thornton A, Isden J, Madden JR. 2014. Towards wild psychometrics: linking individual cognitive differences to fitness. Behav Ecol. 25:1299–1301.
Thornton A, Lukas D. 2012. Individual variation in cognitive performance: developmental and evolutionary perspectives. Phil Trans R Soc B. 367:2773–2783.

Towards fruitful interaction between behavioral ecology and cognitive science: a comment on Rowe and Healy

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As noted by Rowe and Healy (2014), researchers in behavioral ecology are becoming increasingly aware of, and interested in, the fact that an animal's fitness is not just determined by its physical and physiological qualities but also by its cognitive abilities: a Rambo may be outsmarted by an Einstein. But although physical and physiological qualities are usually relatively straightforward to measure, an animal's cognitive abilities may require special conditions to be revealed and can only be measured indirectly. Rowe and Healy discuss a number of pitfalls and complications that may hinder the study of such abilities and call for a reflection on what it is that one wants to measure and how this is done. I fully agree and should like to add 3 points to underscore their important message.

PERFORMANCE AND COGNITIVE VARIABILITY

First, in a way, Rowe and Healy are modest in their take-home message. They rightly state that individual variation in performance in cognitive tasks does not necessarily demonstrate variation in cognitive ability. However, I should like to add that *absence* of variability in performance need not demonstrate *absence* of individual variation in the cognitive ability that the test is supposed to measure. If it only shows that the problem can be solved, but not how, then a simple performance measure such as the number of trials to reach criterion, does not reveal much about the cognitive process involved. As an example, in the context of examining whether songbirds have the ability for learning "artificial grammar" rules, we (van Heijningen et al. 2013) asked the question whether zebra finches were able to distinguish sequences of song elements that were artificially arranged according to different rules. Among the birds that managed the task, subsequent tests with a variety of differently structured test stimuli revealed that individuals could differ substantially in how they discriminated the sequences (van Heijningen et al. 2013)—variation unrelated to the number of trials needed to reach the initial discrimination.

PERSONALITIES

My second point concerns the wider relevance of Rowe and Healy's message. Cognition is not the only property of an animal that is made up from a set of different components and which cannot be measured by just a single test. The arguments and reasoning of Rowe and Healy can also be applied to that other area in which behavioral ecologists sometimes use simple tests: that of animal "personalities" or "behavioral syndromes." The exploration in an open field test or the latency to approach a novel object are measures that can indicate something about the "boldness" of individuals, but here also the same types of problems arise: Is individual variation in a novel object test, even when repeated, really due to a difference in "boldness" and indicative of a whole set of other (untested) correlated traits? Or is the response to the specific novel object presented indicative for the response to all types of novel objects or is it due to some other, extraneous, factor linked to that particular object or tested individual? Hence, here also, using a single test is likely to be insufficient or even misleading to reliably characterize differences in "personality" (see also Dall and Griffith 2014). This issue is particularly relevant as the increasing interest in the relation between variation in cognition and variation in personality types (Sih and Del Giudice 2012) requires reliable measurements of both properties.

A BRIGHT FUTURE?

Finally, should behavioral ecologists now be put off by all the complications raised by Rowe and Healy (2014) and above? I hope not. On the contrary: there is an important reason why behavioral ecologists should be encouraged to study cognitive traits. Cognitive science is dominated by research on humans and their cognitive abilities, and many studies of animal cognition are inspired by the question whether or not a certain cognitive trait is present in nonhuman animals and how it compares to human abilities. This is a perfectly legitimate motivation for scientific research and it may reveal a lot about the cognitive abilities that animals may have as well as provide suggestions about the building blocks or evolutionary precursors from which human cognitive complexity may have arisen. However, it may result in a focus on whether a trait is present at the species level, ignoring the variation that may be present among individuals and the question why it is that the species under consideration shows the abilities and variation that it does. With their training and background, behavioral ecologists are particularly well suited to address exactly those questions. For instance, something that studies on personality differences have made clear is that, like differences in cognitive abilities, what is "better" may vary in time, space, and social context (e.g., Dingemanse et al. 2004; Boon et al. 2008). As a consequence, variation in personality can be maintained within or between populations. With a more detailed and rigorous study of the variation in cognitive traits and their fitness benefits, we may anticipate that this also will show that at least part of its variation may be present because what is best depends on the context (see also Sih and Del Giudice 2012). It may raise the awareness among cognitive scientists that an average may obscure meaningful individual differences that may be very informative about the cognitive abilities of a species. Hence, to conclude, although behavioral ecology can benefit from paying more attention to the knowledge, questions, and methods of cognitive science, the same is true the other way around.

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REFERENCES

Boon AK, Réale D, Boutin S. 2008. Personality, habitat use, and their consequences for survival in North American red squirrels Tamiasciurus hudsonicus. Oikos. 117:1321–1328.

Dall SRX, Griffith SC. 2014. An empiricist guide to animal personality variation in ecology and evolution. Front Ecol Evol. doi:10.3389/fevo.2014.00003.

Dingemanse NJ, Both C, Drent PJ, Tinbergen JM. 2004. Fitness consequences of avian personalities in a fluctuating environment. Proc R Soc B. 271:847–852.

Rowe C, Healy SD. 2014. Measuring variation in cognition. Behav Ecol. 25:1287–1292.

Sih A, Del Giudice M. 2012. Linking behavioural syndromes and cognition: a behavioural ecology perspective. Phil Trans R Soc B. 367:2762–2772.

van Heijningen CAA, Chen J, van Laatum I, van der Hulst B, ten Cate C. 2013. Rule learning by zebra finches in an artificial grammar learning task: which rule? Anim Cogn. 16:165–175.

Measuring variation in cognition can be done, but it requires hard empirical work: a comment on Rowe and Healy

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Rowe and Healy (2014) provide an interesting review of the potential pitfalls associated with the study of animal cognition from a behavioral ecology perspective. Their review is peppered with intriguing hypothetical examples of how studies of cognition can generate results that should be interpreted with caution. Apart from flagging up the importance of designing cognitive experiments that limit biases, something that is important for all experimental research, Rowe and Healy are very open in admitting that they cannot provide any cure to the problems with measuring variation in cognition.

Inspired by Rowe and Healy, I argue that there is, if not a cure, at least a "band aid" that can be used to achieve better understanding of how cognitive ability evolves. Unfortunately for us that study these questions empirically, this "band aid" is hard work. I target 2 aspects that this necessary hard work should focus on: 1) designing cognitive tests that are of ecological relevance and 2) broadening the taxonomic scope in the study of cognition.

For the first point, a recent article in *Behavioral Ecology* by Thornton et al. (2014) summarizes how we can use cognitive tests based on ideas from psychology and place these in an ecological context to investigate how cognition can evolve. In fact, placing tests of cognition in an ecologically relevant framework is a direction that our colleagues in psychology have been advocating for some time (e.g., Moll et al. 2005; Spooner and Pachana 2006). Doing this will require that studies go beyond single tests of cognition because these studies require an additional test phase that places the individuals in an ecological context followed by quantification of some fitness-related aspect. Alternatively, one can design tests of cognitive ability that directly assess an ecologically fitness-related aspect of cognition. Such an example was recently provided by Nachev and Winter (2012) that used artificial flowers with different sugar concentrations to quantify variation in the ability of individually marked bats to discriminate between food sources of different quality. Needless to say, also tests with ecological relevance must be designed so that they 1) limit the effects of confounding variables, 2) consider spatial and temporal variation (sensu Rowe and Healy's "what is good in one situation might not be good in another"), and 3) ensure the cognitive abilities under study are linked to demonstrated indirect or direct measures of fitness.

For the second point, much of the work on cognition has been undertaken in few species and mostly in birds and mammals. By examining cognition in a wider range of species, we can gain a better appreciation of the role cognition plays in adapting organisms to their niches and to the circumstances they encounter. Among the vertebrates, fishes form an interesting group in this respect because they display enormous variation both in behavior, neurobiology, and cognitive ability. Fishes were also highlighted as suitable for studies on social cognition in a recent review by Bshary et al. (2014). With regards to other taxa, the insects (outside of the fantastic work that has been done on insect model organisms, such as *Drosophila* and honey bees) are an almost unused source of cognitive variation that can be targeted by future work on the evolution of cognition. The work using artificial selection of cognitive ability in *Drosophila* (e.g., Mery and Kawecki 2002) is an inspiring example for work on species with short generation times. Ideally, the suggested broadening of taxonomic scope should also use a combination of experimental work at the within species level (that can establish causality) and phylogenetic comparative analysis (that can determine general macroevolutionary patterns) to provide general tests of the classic hypotheses concerning cognitive evolution. MacLean et al. (2014) provide an elegant example of how this combinatory approach can be a powerful tool to shed light on the evolutionary processes and mechanisms that generate variation in cognition. These types of projects require the design of comparable tests of cognition for multiple species and their labor intensity often require several research groups joining forces. But MacLean et al.'s study shows that such collaborations, also between psychologists and behavioral ecologists, are indeed possible.

To conclude, we should not back down, and much hard work lies ahead of us before we can achieve a firm understanding of how and why cognitive ability varies at all taxonomic levels. But who said that solving one of the greatest mysteries in biology would be easy?

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