frontiers in Ecology and Evolution

OPINION
published: 25 February 2020
doi: 10.3389/fevo.2020.00039

The Overlooked Influence of Hybridization on Cognition

*Amber M. Rice**†

Department of Biological Sciences, Lehigh University, Bethlehem, PA, United States

Keywords: hybridization, cognition, selection, trade-off, environmentally dependent selection

For many animal species, cognitive traits are important for fitness. Such traits may be especially important in rapidly changing environments, where innovation and learning about new challenges could mean the difference between persistence and extinction (Dukas, 2013; Mery, 2013). One factor that may affect cognitive performance is hybridization. Hybridization occurs when individuals from distinct species mate and produce offspring. It is widespread, with estimates suggesting 1–10% of all animal species hybridize (Mallet, 2005; Schwenk et al., 2008), and is expected to become increasingly common as species distributions shift due to climate change (Chunco, 2014). Yet, the extent to which hybridization affects cognition, and any resulting impacts on hybrid fitness, remain relatively unknown. Recently, Rice and McQuillan (2018) described several mechanisms by which hybridization could directly affect cognitive abilities and negatively influence hybrid fitness. Here, I also consider that hybridization's impacts on cognition could lead to positive fitness consequences, and *indirectly* affect the expression of cognitive traits. I further discuss how the trade-off between investment in cognition and other functions could have important implications for the ultimate evolutionary outcome of hybridization. Currently, little is known about hybridization's effects on the expression of and selection on cognitive traits, and I argue that this is an important area for future research.

OPEN ACCESS

Edited by:
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****Correspondence:***
Amber M. Rice
amr511@lehigh.edu

†ORCID:
Amber M. Rice
orcid.org/0000-0002-5475-8226

Specialty section:
This article was submitted to Behavioral and Evolutionary Ecology, a section of the journal Frontiers in Ecology and Evolution

Received: *15 October 2019*
Accepted: *10 February 2020*
Published: *25 February 2020*

Citation:
Rice AM (2020) The Overlooked Influence of Hybridization on Cognition. Front. Ecol. Evol. 8:39. doi: 10.3389/fevo.2020.00039

WHAT WE KNOW ABOUT HYBRID COGNITION

The effects of hybridization on cognition have been poorly studied, particularly in cases of natural hybridization. A recent study tested the relative spatial memory and problem-solving abilities of black-capped and Carolina chickadees and their naturally-occurring hybrids (McQuillan et al., 2018). Chickadees are scatter hoarders, caching food throughout the environment during the fall. They rely on spatial memory to retrieve this food in the winter, and individuals with better spatial memory are more likely to survive (Sonnenberg et al., 2019). Although black-capped and Carolina chickadees performed equally well on an associative learning spatial task and a novel problem-solving task, hybrids were less able to remember the location of a food item or to solve the problem (McQuillan et al., 2018). Further testing is needed to determine whether other aspects of cognition are similarly affected. In contrast to the results in hybrid chickadees, mules—hybrids produced by crossing domestic horses and donkeys—exhibit enhanced visual discrimination and problem solving compared to their parental species (Proops et al., 2009; Osthaus et al., 2013). Although mules are not subject to natural selection, being domesticated, these findings demonstrate that hybridization can also lead to enhanced cognitive abilities compared to parental species.

Together, these examples illustrate the potential for hybridization to both positively and negatively affect cognition; however, much remains unknown. How frequently does hybridization influence cognition in other taxa? By what mechanism(s)? For a given hybrid cross, does hybridization have similar or variable effects on the diverse aspects of cognition? What are the net fitness consequences in wild populations across a range of environments? And how does selection on hybrid cognition contribute to the evolutionary outcomes of hybridization?

DIRECT EFFECTS OF HYBRIDIZATION ON COGNITION

Cognition can be shaped by natural (e.g., Roth et al., 2012) and artificial selection (e.g., Mery and Kawecki, 2002), and individual variation in cognitive performance is repeatable (Cauchoix et al., 2018), leading to the conclusion that it has a heritable genetic basis (Croston et al., 2015). Therefore, hybridization should be expected to directly affect cognitive traits by the same mechanisms as it affects other traits.

Hybridization frequently leads to negative fitness consequences. Cognitive traits may be subject to genetic incompatibilities in hybrids (Dobzhansky, 1936; Muller, 1942; **Figure 1**), leading either to negative fitness consequences, or to asymmetric fitness consequences depending on the cross direction (Orr, 1995; Turelli and Moyle, 2007) or the sex of hybrid individuals ("Haldane's Rule," Schilthuizen et al., 2011). Likewise, when two parental species with cognitive abilities under divergent selection produce hybrids of intermediate ability, ecological selection may act against the hybrids (Hatfield and Schluter, 1999; McBride and Singer, 2010; **Figure 1**) following a classical "ecological speciation" scenario (Rundle and Nosil, 2005). Rice and McQuillan (2018) further elaborate on the direct mechanisms by which hybridization could affect cognitive traits, leading to negative fitness consequences and postzygotic reproductive isolation between parental species.

Hybridization could also directly affect cognition in ways that lead to positive fitness consequences, and facilitate adaptation to novel environments. The mule example above shows that in some cases, cognitive abilities may be enhanced in hybrids relative to parental taxa (Proops et al., 2009; Osthaus et al., 2013). Enhanced cognitive abilities could result from positive genetic interactions between loci in the parental species ("heterosis"; Dagilis et al., 2019), or from the recombination of additive alleles in F_1 and advanced generation hybrids ("transgressive segregation"; Rieseberg et al., 1999). Hybrids with enhanced abilities could experience high fitness (**Figure 1**), provided the fitness benefits of enhanced cognition in their specific environment outweigh any costs (Cole et al., 2012; Kotrschal et al., 2013). Such enhanced abilities, if caused by heterosis, may be transient, as it is less likely in advanced generation hybrids or back-crossed individuals (Barton, 2001). However, high fitness phenotypes in hybrids caused by transgressive segregation can persist across generations, as illustrated by the existence of stable hybrid species that are succeeding in novel or extreme environments, or are utilizing novel resources (e.g., Nolte et al., 2005; Gompert et al., 2006; Lamichhaney et al., 2018).

INDIRECT EFFECTS OF HYBRIDIZATION ON COGNITION

Hybrids often have lower success than parental species individuals in obtaining resources, or have less efficient metabolism, which could have indirect negative effects on cognition (**Figure 1**). Hybrids produced by parental species that have diverged in resource use may be intermediate in their

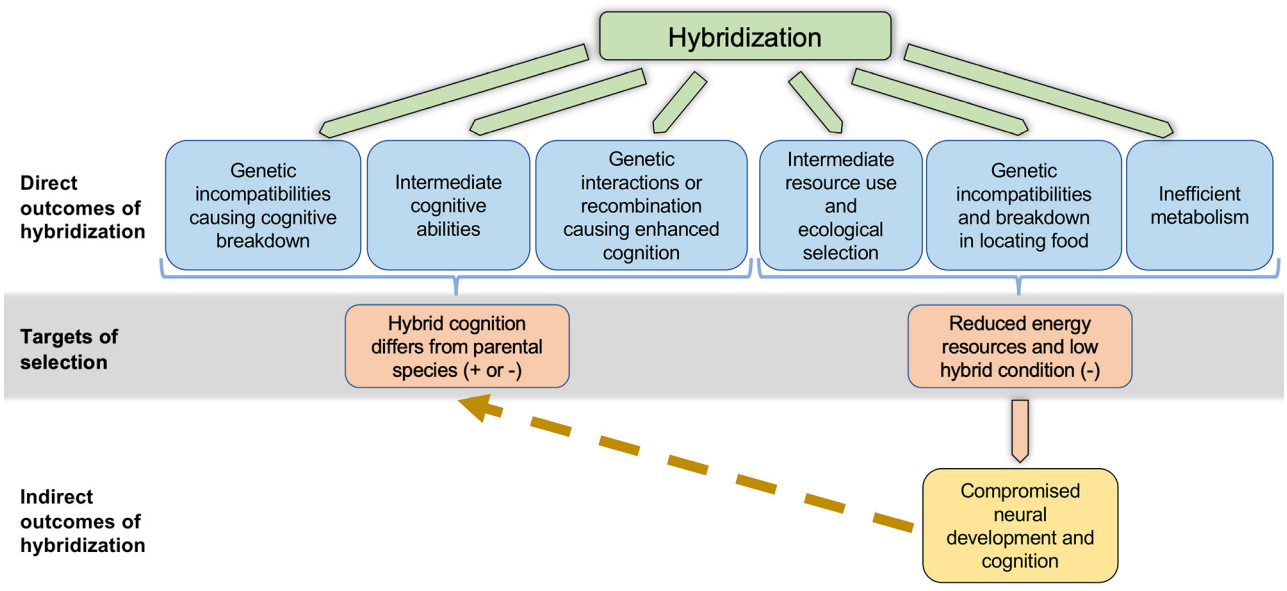

FIGURE 1 | Non-mutually exclusive pathways by which hybridization can affect cognition. Hybridization can have direct effects on cognition through positive or negative genetic interactions, or through combinations of additive alleles. Reduced, intermediate, or enhanced cognition may result in hybrids, and the fitness consequences could be either positive or negative, depending on a variety of factors (see text). Alternatively, or even simultaneously, hybridization can indirectly affect cognition through its direct effects on resource use phenotypes, metabolic efficiency, or abilities to locate food. All of these direct outcomes are likely to lead to reduced energy and low condition in hybrids, likely causing selection against hybrids. Reduced energy and low condition can subsequently lead to compromised neural development and cognition in hybrids, which can in turn cause hybrid cognitive abilities to differ from those in the parental species.

resource use phenotypes, and poor competitors in either parental environment (Hatfield and Schluter, 1999; Pfennig and Rice, 2007). Hybridization may also interfere with an individual's ability to locate food (Linn et al., 2004; Turissini et al., 2017). Such hybrids are likely to obtain fewer resources, and thereby experience reduced energy availability during development. Further, laboratory studies have demonstrated that mismatches between mitochondrial and nuclear genomes can affect metabolic function (Tieleman et al., 2009; Arnqvist et al., 2010; Hoekstra et al., 2013). Consistent with these findings, naturally-occurring hybrids from two different avian hybrid zones were found to be less efficient at energy metabolism (Olson et al., 2010; McFarlane et al., 2016). The fitness consequences of inefficient metabolism are likely to be environment dependent (Hoekstra et al., 2013), and could be further exacerbated if hybrids also have difficulties obtaining resources. Cognitive abilities and neural development are frequently condition dependent (reviewed in Buchanan et al., 2013). For example, birds experiencing restricted diets during development exhibited poorer spatial learning (Pravosudov et al., 2005) and auditory memory (Bell et al., 2018) as adults. However, poor nutrition does not necessarily affect all aspects of cognition similarly (Pravosudov et al., 2005). Given that hybridization can affect condition and energy availability through multiple mechanisms, indirect effects on some aspects of hybrid cognition are likely to be widespread (**Figure 1**).

TRADE-OFFS, THE ENVIRONMENT, AND SELECTION ON COGNITION

If hybrids differ from their parental species in cognitive performance, whether due to direct or indirect effects of hybridization or both (**Figure 1**), it will be important to estimate the magnitude and direction of selection on these traits. This will determine the impact of cognitive performance on the evolutionary outcomes of hybridization, which can include weakening or strengthening of species barriers, adaptive introgression, and even the creation of new hybrid species (Abbott et al., 2013).

Decreased cognitive abilities in hybrids could actually provide a fitness benefit in some environments, while enhanced cognitive abilities could result in lower fitness. This is because the energy demands of maintaining the brain tissue underlying cognitive abilities are expected to be high (Mink et al., 1981; Bordone et al., 2019), leading to a trade-off between investment in cognition and in other energetically costly functions and traits. For example, lines of *Drosophila* selected for enhanced learning ability experienced a decline in average lifespan compared to control lines (Burger et al., 2008). A consistent result was found in lines of guppies selected for large brains; the large-brained lines exhibited enhanced cognition (Kotrschal et al., 2013) but also shorter lifespan (Kotrschal et al., 2019). A trade-off between learning ability and competitive ability was uncovered in *Drosophila* as well (Mery and Kawecki, 2003), and families of cabbage white butterflies showing enhanced learning produced fewer eggs (Snell-Rood et al., 2011). Thus, the net strength and direction of selection on cognitive abilities will incorporate the costs to other functions important to fitness, and may differ among resource-poor and resource-rich environments. If hybridization occurs across a range of such environments and affects cognition, hybrids in certain environments may be strongly selected against, leading to a strengthening of species boundaries and potentially narrow hybrid zones, while the opposite could be true in other environments.

It is worth noting for at least three reasons, however, that hybrids may be particularly likely to find themselves in environments favoring enhanced cognitive abilities, even in the face of trade-offs. First, species range overlap is often associated with environmental gradients and can shift with the climate (Chunco, 2014; Taylor et al., 2015), such that the opportunity for hybridization may be especially high in variable or novel environments. Second, hybridization may facilitate the colonization of novel environments, either through the adaptive introgression of genes underlying functionally important traits, or as a result of transgressive segregation (Pfennig et al., 2016). Third, areas of sympatry, such as hybrid zones, are likely to be complex social environments, as animals must navigate and process both intra- and interspecific interactions and signals (Pfennig and Pfennig, 2012). Variable, novel, and socially complex environments are expected to favor enhanced learning, memory, and problem-solving (Sol et al., 2002; Dukas, 2013; Mery, 2013; Ashton et al., 2018), so that hybrids with such abilities could experience high fitness.

Selection on hybrid cognition is likely to be complex, and much additional research is required to assess how cognition contributes to the net fitness consequences of hybridization. Because hybrids may have reduced energy reserves compared to parental species individuals (see above), one interesting implication of the trade-off between investment in cognition and other functions is that the direction and magnitude of selection on cognition could vary between hybrids and parental species, even in similar environments. The optimal level of cognitive ability for a parental individual in a given environment might be higher than the optimal level for a hybrid—with reduced energy reserves—in the same environment. Expected patterns of selection are further complicated by the fact that individuals can vary in their performance across different aspects of cognition (DuBois et al., 2018; van Horik et al., 2018), and therefore hybridization may have variable effects on different aspects of cognition depending on which individuals are hybridizing.

CONCLUSION

Hybridization is likely to have important direct and indirect impacts on cognitive ability. Resulting cognitive performance in hybrids may lead to positive or negative fitness consequences. Further, the trade-off between investment in cognition and other important functions coupled with the potential for individual variation in performance across multiple aspects of cognition will complicate patterns of selection on hybrid cognition. The net strength and direction of this selection will determine how cognitive performance contributes to the ultimate evolutionary

outcomes of hybridization. Currently, very little is known about hybridization's impact on cognition, and there is large scope for additional research. Important questions include: How frequently does hybrid cognition differ from parental species, and in what systems? Is it more common for hybridization to affect cognition through direct or indirect mechanisms, or both? What is the direction and magnitude of selection on hybrid cognition, and how does it vary across environments? Many study systems, across a broad range of taxonomic diversity, are well-suited for addressing these questions, particularly those with existing knowledge of traits affected by hybridization. Such research is needed if we are to evaluate the role of cognitive performance in the maintenance of species boundaries, or the links between hybridization and the expression of and selection on cognitive traits in the wild.

AUTHOR CONTRIBUTIONS

AR wrote the manuscript.

FUNDING

AR was supported by National Science Foundation IOS-1754909, and Lehigh University.

ACKNOWLEDGMENTS

Thank you to the organizers of the Research Topic on Links Between Cognition and Fitness: Mechanisms and Constraints in the Wild, and to three reviewers for helpful suggestions on the first version of this manuscript.

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Conflict of Interest: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.