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Editorial: Links between cognition and fitness: Mechanisms and constraints in the wild

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Editorial on the Research Topic

Links between cognition and fitness: Mechanisms and constraints in the wild

In the wild, animals frequently face environmental variations that can be predictable, for example seasonal climate variation, or not, such as habitat destruction or climate change due to the accelerating rate of anthropogenic activity. To cope with these variations, animals must adjust their decisions to the changing conditions. Cognitive abilities, widely defined as all the sensory, neurological, memory and decision processes used by individuals to interact with their environment (Shettleworth, 2001), can allow animals to gather and/or process information more efficiently, better exploit their environment and flexibly adjust their behavior to facilitate optimal responses to environmental changes (Wyles et al., 1983; Sol, 2008). Cognitive abilities can thus be expected to be a key component of animal fitness in the wild, shaping the potential for animal populations to rapidly adjust to a changing world.

A growing number of studies have recently explored whether cognitive performances are positively linked with fitness components in the wild, but the results are not always in line with such a prediction. Cognitive performances and fitness components can show positive links (e.g., Cauchard et al., 2013; Ashton et al., 2018; Sonnenberg et al., 2019), negative links (e.g., Mery and Kawecki, 2003), no links (e.g., Isden et al., 2013; Huebner et al., 2018), or even links dependent on the context or on fitness components suggesting trade-offs between investment in offspring and adult survival (e.g., Cole et al., 2012). Such varying results have frequently been attributed to differences in the design of the cognitive tasks used (which have to be adapted to the morphological and ecological constraints of the study model and site) and/or to other factors that can affect behavioral performance in general (such as personality traits, motivation, age, sex, etc.). However, once properly controlled for these potential biases (Schubiger et al., 2020), these varying results must above all reflect the complex relationships between

cognitive abilities and selective pressures under various ecological and social contexts. Moreover, whether the links, when detected, are causal remains unknown in most cases. Yet, identifying the mechanisms underlying the links between cognitive performances and fitness components and the constraints acting on these mechanisms is crucial to understand and predict how selective pressures can shape the evolution of cognitive abilities in the wild. This is a major gap in our understanding about how and when cognition can help animals to adapt to their changing environments.

In this introduction to the themed issue “*Links between cognition and fitness: mechanisms and constraints in the wild*,” we present an overview of potential mechanisms that could link inter-individual variation in cognitive ability and fitness components, and place the 15 contributions of this theme (5 reviews, 7 original research articles, 2 opinion pieces and 1 perspective) in context. Both direct and indirect mechanisms can link inter-individual variation in cognitive ability to fitness components. Direct mechanisms involve a causal link between cognition and fitness while indirect mechanisms involve cognition and fitness to be both influenced simultaneously but independently by a third variable, creating a correlational link between them.

Current literature on direct mechanisms suggests that individuals with better cognitive abilities might make a better use of their environment for fitness-related decisions, but evidence for such a causal mechanism is still very scarce, impeding our ability to draw general conclusions. Szabo et al. highlighted in their review the cognitive abilities relevant for species in conquering new habitats, targeting both invertebrate and vertebrate species, and examined which cognitive traits could give species an advantage in a competitive, novel environment. Going further, Cauchard et al. experimentally manipulated brood size in wild breeding great tits to explore causal mechanisms between reproductive success and the performance in solving a non-food motivated task presented at the nest. They showed that a significant increase or decrease in brood size did not affect problem-solving performance, thus excluding a direct causal relation through higher motivation to solve the task in more successful pairs. Yet within treatments, task solver pairs still reached higher reproductive success compared to non-solver pairs, which could at least partly be explained by a higher provisioning rate. These results are in line with the hypothesis that problem-solvers may achieve higher reproductive success through a better exploitation of the habitat. Such better habitat exploitation may require individuals to process information about the habitat more efficiently. In order to explore this question, White examined nest selection and its timing in nest-parasite brown-headed cowbirds (*Molothrus ater*). By experimentally manipulating the number of eggs present in mock nests and the timing of egg laying, White showed that female cowbirds relied on social information, i.e., information obtained from the presence, behavior or performance of others

(Danchin et al., 2004), to plan where, when and how many eggs to lay in a given host nest. This ability to optimally use social information can be hypothesized to require different cognitive abilities to process such information. In line with this prediction, the study by Morinay et al. experimentally showed that the use of social information for small-scale nest site selection depended on learning performance in wild collared flycatchers (*Ficedula albicollis*). Collared flycatchers are known to rely on heterospecific social information from titmice for breeding decisions, which leads to fitness increase (Forsman et al., 2002). The study by Morinay et al. revealed here a relation between learning performance and the probability to copy nest preference by sympatric titmice. Overall, learning ability may be particularly important to process information, driving the capacity to optimally deal with environmental changes. To dig this idea deeper, a first comprehensive review by Barrett et al. presented a compilation of theory and empirical evidence on how social learning can help or hinder responses of organisms and thus species to human-induced rapid environmental changes and how these changes can interfere with the transmission of social information. More particularly, a second review by Greggor et al. focused on how learning in general may allow individuals to avoid ecological traps driven by human-induced environmental changes, depending on constraints, type of learning mechanism and individual factors such as personality.

The ability to better use habitat may affect not only reproductive success but also survival, especially in spatio-temporally varying environments. In their study, Mettke-Hofmann et al. explored the response to habitat novelty in the Gouldian finch (*Erythrura gouldiae*), a polymorphic species showing a link between head color and behavioral phenotypes. They showed that black-headed birds are more reluctant to enter a new dense habitat than red-headed birds, which may negatively affect long-term population persistence to habitat change since 70% of birds in the wild are black-headed. Yet, very little is currently known regarding the links between cognitive abilities and survival. One reason for this may be challenges when studying cognition in the wild (Morand-Ferron et al., 2015). In particular, most studies in nature rely on limited sample size, preventing reliable survival analyses. To address this issue in a laboratory setting, Matzel et al. took advantage of genetically heterogeneous mice that express individual differences in general cognitive ability to explore associated differences in behaviors known to be related to survival in this species. They found that mice with a higher general cognitive ability score also showed a higher survival-readiness score, and results suggested that heightened attention may drive this relationship. In their review, Rochais et al. explored the existing literature linking cognition to survival in the wild in order to highlight the cognitive traits that can be expected to be ecologically relevant for survival, as well as the individual characteristics that might influence these

relationships. They discussed the challenges associated with investigating the links between cognition and survival in natural populations, and proposed a methodological approach to ward off these challenges.

Regarding indirect mechanisms, environmental variables such as habitat quality might affect both cognitive abilities and fitness components simultaneously but separately, outside any direct link between them. Using the extensive literature available on fish, [Jacquin et al.](#) highlighted in their comprehensive perspective article how exposure to pollutants from human-related activities can affect both cognition and fitness through various physiological and behavioral (personality) mechanisms. This study thus emphasized the urgent need for future studies to examine the links between ecotoxicology, cognitive ecology and evolutionary ecology in a multi-stress framework to improve our ability to predict the effects of anthropogenic stressors on wildlife. Parasitism is another environmental factor that can drive an indirect link between cognition and fitness. In their review article, [Ducatez et al.](#) proposed three scenarios on how cognition could affect the reciprocal pressures that hosts and parasites can exert on each other, shaping host-parasite eco-evolutionary dynamics. This review revealed the need for experimental studies to distinguish between direct (causal) and indirect (non-causal) effects of parasitism in the evolution of cognition.

Direct and indirect mechanisms may also operate simultaneously. For instance, in new habitats, new constraints should favor individuals with cognitive abilities enhancing their behavioral repertoire to cope with novel challenges and thereby achieve higher fitness. At the same time, new habitats may also host new stressors such as pollutants and parasites, or affect individual condition in general, impacting both cognition and fitness independently. In their comparative study, [Sayol et al.](#) showed that brain size was positively associated with urban tolerance, even if small-brained species can use alternative life history strategies, such as a higher number of low value reproductive events, to succeed in urban environments. Cognition-related differences in life-history strategies were also suggested in the study by [Johnson-Ulrich et al.](#) in wild female spotted hyenas (*Crocuta crocuta*), where innovativeness was linked to reproduction in multiple ways: innovative hyenas showed lower cub survival but higher annual cub production compared to non-innovative hyenas, leading to no overall difference between innovative and non-innovative hyenas in reproductive success. Another example where both direct and indirect mechanisms may operate together is between-species hybridization, whose effects on fitness have been frequently described, but potential influence on cognition is yet largely ignored. Adding to a previous paper ([Rice and McQuillan, 2018](#)) presenting how hybridization can negatively impact both hybrids' cognitive abilities and fitness, thus creating an indirect link, [Rice's](#) perspective discussed further how hybridization impact on cognition could lead to positive fitness consequences

and indirectly affect the expression of cognitive traits. By discussing how trade-offs between investment in cognition and other important functions, coupled with individual variation, can complicate patterns of selection on hybrid cognition, [Rice](#) questioned the role of cognitive performance in the maintenance of species boundaries, and the links between hybridization and the expression of, and selection on, cognitive traits in the wild.

Finally, when facing environmental variation, selection may favor flexible adjustment ability, and this may also apply to cognitive performance. In a mini-review, [Cauchoix et al.](#) compiled current evidence for such plasticity in cognitive performance, called “cognitive performance plasticity,” in response to environmental conditions and proposed methodological approaches to measure it, highlighting its role when exploring the repeatability of cognitive performance.

Overall, this body of research provides the first comprehensive overview of constraints influencing the evolution of cognition in the wild, highlights the multiple ways by which cognition can be linked to fitness and the needs for further research on this question. In addition to presenting novel results and methods, several authors presented a number of compelling ideas and perspectives that will help us to improve our understanding of this field.

Author contributions

LC wrote the first draft. Both authors contributed to the article and approved the submitted version.

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Conflict of interest

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