



Insights from matched species comparisons for understanding cognition in the wild[☆]

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Studies of cognition in the wild are crucial for understanding cognition in natural contexts, but studies of animal cognition in captive populations, living in conditions resembling those of their natural environment, complement this approach and provide new insights into the evolution of cognition. To show how these approaches can work in tandem, we use data from recent comparisons on cognition across different primate species in similar settings. We discuss how this work can disentangle stable species-specific differences in cognition from local environmental effects, distinguish specific cognitive mechanisms supporting behavior, and reveal hidden variables that shape cognition in captivity and the wild. Integration of research in both captive and wild settings will therefore provide a holistic understanding of the origins and function of different cognitive processes.

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Introduction

Why do some species use tools, have better memory, or engage in complex coalitions whereas others do not? Animals show variation in their behavior in part because of variation in the underlying cognitive mechanisms that produce these behaviors. As cognitive traits are shaped by natural selection, there is an increasing focus on

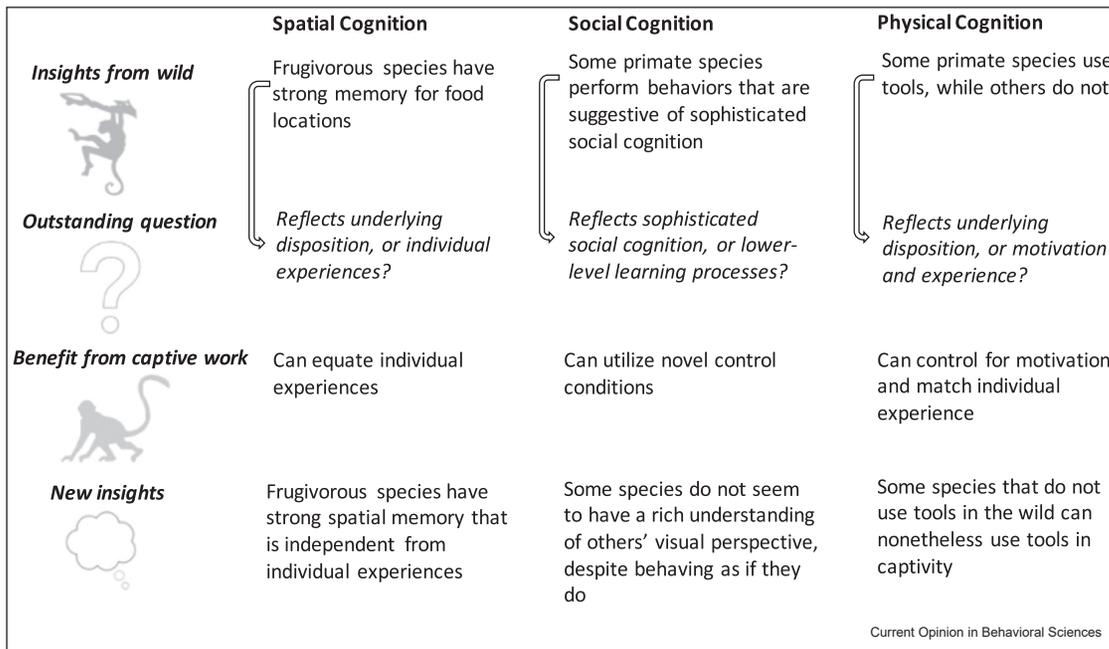
understanding real-world social and ecological problems shaping the structure of animal minds. Here, we argue that comparisons of animal populations living in captive contexts that are well matched but ecologically relevant, in that they share some core features of the natural social and ecological environments of each species, can provide crucial insights into core questions about the evolution of cognition that complement studies of natural populations in the wild.

Studies of cognition in the wild have recently emerged an important shift from approaches in comparative cognition that traditionally focused on animals in captivity. Field experiments are essential to understand how animals respond to and use information from their natural environment, to test the consequences of cognitive abilities on animals' survival and reproductive success, and to expand the study of cognition to more diverse species that are underrepresented or absent in captive settings [1,2]. This work has also spurred important discussions about how we should interpret and generalize experimental findings from captive populations [3]. However, it is also increasingly clear that hybrid approaches that bridge both captive and field studies are crucial [3–5]. Our goal here is to detail how captive studies can inform our knowledge of cognition in the wild by addressing key questions about the mechanisms supporting behavior that are difficult or impossible to assess in wild contexts.

Understanding the evolution of cognition requires two main components. First, this work necessitates *experimental* studies to infer underlying cognitive mechanisms. As cognitive abilities are mechanisms that underpin behavior, they cannot be directly observed: behavior and cognition do not have a 'one-to-one' mapping, as many possible cognitive mechanisms could produce a particular behavior at a particular point in time. Rather, cognitive mechanisms must be inferred by examining patterns of behavior across contexts, and carefully ruling out alternative explanations with systematic controls [5]. Thus, experiments are a primary way to establish causality and not mere correlation [5], including in-field contexts [1,3,6]. Second, a key to understanding the

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Figure 1



Integrating studies of captive and wild populations to understand the evolution of cognition. Studies of captive animals can complement research in the wild by answering questions that are difficult (or impossible) to address in the wild alone.

evolution of cognition in the wild is pinpointing the *distribution* of cognitive traits across different species. In particular, the comparative method examines the traits of different species in relation to the ecological or social context of that species, an important technique for evolutionary inferences [7]. In the case of cognition, studies testing multiple species can then link species differences in cognitive abilities to specific socio-ecological characteristics such as feeding ecology or social structure [7,8].

Given this, studies of animal cognition in captive populations such as in zoos or sanctuaries can also provide insights into the distribution of cognitive abilities across species that complement studies in the wild. In particular, matched experimental comparisons can (1) disentangle differences in cognition that are confounded by different environments in wild populations; (2) pinpoint specific cognitive mechanisms by presenting animals with novel situations they would not typically experience in the wild, and (3) directly account for motivational effects on cognition. By ensuring that different species are on an 'equal playing field' when assessing their cognitive abilities, studies of captive populations can help understand whether and how species differ in their cognition. This is not to say that patterns of cognition in captive environments are necessarily identical to those in the wild, as captive environments do not need to be *identical* to be *informative*. Rather,

comparisons of captive animals living in species-appropriate — but matched — environments can provide insights that studies in the wild alone cannot. Here, we use data from recent work on foraging and social cognition across primate species in captive or semi-free-ranging settings to highlight how such studies complement field studies and provide a holistic understanding of cognitive processes (see Figure 1).

Example 1: disentangling environmental effects from biological dispositions

Theories of cognitive evolution point to how social or ecological context may drive the evolution of more sophisticated cognitive abilities [9–11]. Species living in more complex social groups in their wild environments are hypothesized to have richer social cognitive abilities, whereas species facing more complex ecologies might have more complex spatial abilities [8–11]. While these proposals often focus on the evolution of cognition as a species-typical trait, an alternative hypothesis is that individuals who experience different habitats in the wild simply develop different skills. That is, wild animals likely acquire different cognitive skills in direct response to their individual experiences in different habitats, so apparent species differences may just reflect that these individuals live in different places rather than that they have different cognitive skills per se. Studies of cognition in well-equated captive contexts can explicitly test this experience-based alternative, and assess whether

species differences reflect more stable biological characters that arise more independently of local contexts.

A relevant example comes from comparative studies of primate spatial memory. Observational and experimental studies of spatial memory in wild primates have provided crucial information on how primates recall and navigate resources [12–16]. Yet different wild primate populations obviously eat different foods and experience different habitats, so any differences between populations may just reflect their individual experiences. Captive studies can address this possibility. For instance, in a study of four lemur species living at the Duke Lemur Center, the most frugivorous ruffed lemurs outperformed the others on several indices of spatial memory, especially compared to the folivorous sifakas [17]. While these species live in different habitats and are adapted to eat distinct foods in the wild, individuals in this study experienced similar physical environments and were all provisioned. Along the same lines, wild chimpanzees and bonobos show important differences in habitat and diet [18], so wild apes might show differences in spatial memory due to these local experiences. Yet semi-free-ranging, provisioned chimpanzees living in an African sanctuary exhibited more accurate memory than bonobos in a similar context [19,20••], indicating that memory differences arise even when individuals from these species develop in comparable environments. The degree of wild frugivory also predicts how captive-born populations of macaques and capuchins living in the same research center navigate in a naturalistic foraging task [21•], showing that systematic differences in memory can be detected in species who semi-free-range in equivalent environments.

Similar patterns emerge for species differences in decision-making, including choices between options that differ in reward variance (risky choices) and timing (intertemporal choices). In the wild, the same differences in ecology and habitat that may shape spatial memory also can impact other foraging patterns. For example, wild chimpanzees engage in more temporally costly extractive foraging, face longer search times, experience more seasonal variation, and engage in more frequent risky hunting behaviors than do bonobos [18]. These different experiences could plausibly shape individual decision preferences. Yet matched comparisons between chimpanzees and bonobos living in comparable zoo and sanctuary environments — where they do not hunt and have similar access to tools — reveal that chimpanzees are more patient and more risk-seeking than bonobos [22–26]. Other work reveals that species that feed on variable, risky, or costly food resources in the wild show this same pattern in captive studies: capuchin monkeys are also more patient and risk-seeking, similar to chimpanzees but distinct from more closely-related monkeys [27,28]. This shows how matched comparisons can also

shed new light on convergent evolution [29]. Together, this indicates that primate species experiencing similar environments can nonetheless exhibit significant variation in cognition that mirror their species-typical wild ecology.

Example 2: distinguishing specific cognitive mechanisms

A foundational idea within comparative cognition is that species have evolved different social cognitive abilities to respond to the social challenges that they experience in the wild [9,10]. Field experiments have provided key insights into the evolution of social cognition, including communication, social learning, and aspects of theory of mind [30–33]. Yet, by only observing individuals' behavior in the wild, it can be challenging to differentiate between different possible cognitive processes versus 'lower-level' processes. This is particularly the case in the social domain, as there are many examples of lower-level processes (such as simple learned behavioral rules) producing superficially similar social behaviors [34,35]. Captive studies are therefore a critical complement to wild studies, enabling researchers to make inferences about the cognitive underpinnings of social differences across species.

First, captive studies complement field experiments by examining how animals respond to novel situations [36–41•]. While an important strength of field studies is their grounding in ecologically relevant interactions, this can also limit inferences that require novel control conditions to rule out lower-level explanations. For example, studies in captivity have shown that both capuchins and chimpanzees follow others' gaze (chimpanzees; [36]; capuchins; [42]), so observations of their behavior in the wild may suggest similar social cognitive abilities. Yet matched comparisons in captivity reveal that while chimpanzees have a rich understanding of other's visual perspective, capuchins seem to use simpler behavioral rules to accomplish the same ends [37,38]. Similarly, work from captive and semi-free-ranging contexts shows that rhesus macaques [39] and chimpanzees [40], but not ring-tailed lemurs [43], are sensitive to what other individuals can hear. In these experiments, the key measure is whether animals preferentially steal food from a novel silent container versus a noisy one — situations that do not naturally occur in the wild but can provide important context for interpreting wild behaviors. For example, wild observations have suggested that females of some species will suppress copulation calls when they are 'secretly' mating with a subdominant male, such that a nearby dominant remains unaware [9]. Females might be sensitive to what the dominant male can hear, or they might simply learn through prior trial-and-error that producing copulation calls in this situation results in aggression. Captive

comparisons on auditory perspective-taking can differentiate between these possibilities.

Studies of social cognition in matched captive contexts can also match the identity and behavior of social partners across different species by using human actors [36,41•,44]. Wild studies necessarily involve conspecific social partners, and understanding how animals respond to conspecifics is clearly crucial for inferring how animals behave in real-world situations. However, the use of human partners can allow for new inferences by exactly equating the partner's behavior to see how different species respond. While responses to human actors do not necessarily generalize to conspecifics, in some species such as chimpanzees and macaques there is evidence that primates respond to humans and conspecific partners similarly [37,45–47]. More importantly, effective use of human demonstrators can eliminate important confounds due to the presence of an existing relationship between individuals or differences in the partner behaviors across species. For example, studies of conspecific gaze following in macaques show that interpersonal factors such as rank and friendship [48] can influence gaze following rates. The use of a human demonstrator can eliminate these confounds. In comparisons involving identical social stimuli in populations living in similar semi-free-ranging contexts, tolerant species may show different patterns than despotic species in gaze following [44] and comparisons of cooperative communication [49], but show similar knowledge attribution abilities [41•]. Along similar lines, sanctuary-living bonobos are more able to share food than are chimpanzees in a similar context when faced with a situation where they could compete with conspecifics [50,51], yet both species respond similarly when facing a human competitor with a matched behavioral repertoire [25]. Together these show that wild behavioral patterns may result from the interplay of both cognitive dispositions and responses to particular partner's social behaviors.

Example 3: assessing motivational effects on cognition

Finally, studies in captivity can examine the impact of internal factors like motivation on cognition. It is clear that motivational state can impact individual's engagement with novel problems, and consequently apparent variation in cognitive skills can sometimes reflect motivational differences. For example, sanctuary-living chimpanzees and orangutans that were bolder and approached novel situations more quickly also performed better in cognitive assessments of physical knowledge, suggesting that responses to novelty can impact cognitive performance [52]. While this is a well-recognized problem [3,53], it is extremely challenging to address in

wild contexts. For example, individuals in the wild could be less motivated to participate in cognitive studies for a variety of reasons, such as the presence of other conspecifics or the availability of competing activities at the moment of testing. Captive studies can therefore complement wild studies to address this challenge.

In particular, comparative studies in captivity can directly account for species' motivational differences by measuring how individuals respond to novel situations and how these responses vary across species. For example, when sanctuary-living great apes were presented with different novel foods, objects, and people, chimpanzees were bolder to approach than bonobos [54] — a difference that could be accounted for in subsequent cognitive comparisons [55]. In fact, in a field experiment measuring apes' response to novel camera traps, bonobos exhibited more neophobic behaviors than chimpanzees [56•], suggesting this temperamental difference may also influence their wild responses. Captive studies can further test exactly how ontogenetic experiences shape neophobia. For instance, orangutans that have contact with humans early in life show greater curiosity than wild-born individuals [57•]. Likewise, captive vervet monkeys approached novel stimuli more than wild conspecifics [58]. One possible explanation for these patterns is that in captive environments animals have more free time and energy to explore novel situations without risk [57•,59], so captive studies can reveal hidden aspects of species' psychological phenotypes that shape wild behavior.

Studies of tool use provide an illustrative example. On the one hand, studies of tool use in captivity have provided many results consistent with wild studies, such as showing that chimpanzees, orangutans, and capuchin monkeys are consummate tool users [59,60]. On the other hand, patterns of tool use can also differ between captive and wild populations. For example, bonobos — who do not engage in extractive foraging tool use in the wild — can be quite skillful tool users in captivity [59]. Other primate species that are considered essentially non-tool-users in the wild, such as baboons, tamarins, and vervet monkeys, also demonstrate understanding of tool properties in captive conditions [59,61], highlighting how experience and opportunity can spur the emergence of hidden cognitive abilities. That is, captive individuals can often outperform wild ones in tests of tool knowledge and skillfulness [59]. This may be because captive animals have more time to devote to tool use, or it may be because of differences in motivation, interest, and exposure to tools [59,62••]. This suggests that factors like motivation and experience, rather than cognition or knowledge alone, may shape differences in the tool use of wild animals, and provide new data on inferring the mechanisms underpinning these wild patterns.

Conclusion

Research in species-appropriate but matched captive settings can provide a complementary and powerful tool for understanding animals' cognition in the wild. First, matched comparisons of species living in captive contexts have revealed that species' differences in some cognitive abilities, like spatial memory and decision-making, persist even under similar environmental conditions — suggesting these reflect more stable biological dispositions. Second, comparative work presenting animals with situations never experienced in the wild, including matched human social partners, have revealed that some species exhibit a more sophisticated understanding of other individuals' mental states than others, despite showing similar behavioral patterns. Finally, captive environments where individuals have more free time and energy to explore can boost individuals' motivation to engage with novel situations and, therefore, reveal latent cognitive skills and behaviors that are not necessarily apparent in their wild behavior. Thus, integration of research in captive and wild settings is crucial to understand species' cognitive flexibility across contexts and how cognition has evolved more generally.

Conflict of interest statement

Nothing declared.

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