

Review

Foraging Cognition: Reviving the Ecological Intelligence Hypothesis

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What are the origins of intelligent behavior? The demands associated with living in complex social groups have been the favored explanation for the evolution of primate cognition in general and human cognition in particular. However, recent comparative research indicates that ecological variation can also shape cognitive abilities. I synthesize the emerging evidence that ‘foraging cognition’ – skills used to exploit food resources, including spatial memory, decision-making, and inhibitory control – varies adaptively across primates. These findings provide a new framework for the evolution of human cognition, given our species’ dependence on costly, high-value food resources. Understanding the origins of the human mind will require an integrative theory accounting for how humans are unique in both our sociality and our ecology.

The Evolution of Cognition

Understanding why differences in cognitive capacities emerge is one of the most fundamental questions about the origins of intelligence, including for our own species. There are two broad explanations for the evolution of primate cognition. The social intelligence hypothesis argues that aspects of social life – such as living in large groups, the need for political or ‘Machiavellian’ maneuvering, cooperative breeding, or social learning – have been the primary force shaping intelligent behavior [1–7]. By contrast, the ecological intelligence hypothesis focuses on features of the diet, including the complex spatiotemporal distribution of foods, use of extractive foraging techniques, or responses to a fluctuating environment [8–13]. However, complex sociality has predominated in explanations for primate intelligence over the past 40 years.

The emphasis on social explanations for primate cognition has its roots in observations that wild primates are characterized by complex social interactions [5,14]. Subsequent experimental studies then demonstrated that many primates exhibit sophisticated social cognition [15,16]. Finally, neurobiological comparisons have shown that several brain measures correlate with some indices of social complexity, such as group size [2,6]. However, there are reasons to doubt that sociality comprises the whole story. For example, dietary niche is also an important predictor of many of the same neurobiological characteristics [17–19]. In addition, ecology predicts aspects of cognition, neurobiology, and behavior in other taxonomic groups, such as birds [12,13,20–22]. The ecological hypothesis for primate cognition therefore warrants a fresh look, grounded in direct comparisons of specific cognitive abilities across species.

Here I evaluate the empirical evidence from ‘foraging cognition’, the cognitive abilities used to acquire food resources. Many diverse cognitive skills could fall under this umbrella but I focus on a suite of cognitive skills comprising spatial memory, value-based decision-making, and executive control. I argue that: (i) these capacities vary adaptively with features of primate

Trends

Recent work comparing the cognitive abilities of multiple primate species has revealed adaptive ecological variation in several core processes essential for foraging: spatial memory, value-based decision-making, and executive control of responses.

While social and ecological explanations for the emergence of complex cognition are often treated as rival hypotheses, they are better construed as complementary.

Current evidence supports a mosaic view of primate cognitive evolution, such that social and ecological factors may have different effects across distinct cognitive domains.

The ecological intelligence hypothesis predicts that humans will exhibit specializations in foraging cognition due to unique aspects of the human hunter-gatherer ecological niche, such as high-quality diets, central-place foraging, and costly processing behaviors.

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ecology such as food distribution and diet quality; (ii) the social and ecological intelligence hypotheses can be integrated as complementary ideas with differing explanatory power across different domains of cognition; and (iii) this ecological framework for cognitive evolution in our primate relatives can provide a new view of cognitive uniqueness in the human lineage.

Foraging Cognition Varies Adaptively Across Primates

The first challenge in evaluating the ecological intelligence hypothesis is identifying and measuring relevant cognitive skills. Here I review experimental comparisons of cognition rather than anatomical proxies for cognition such as brain size (Box 1). The second challenge is detecting the signature of natural selection (Box 2). The most common approach used to study cognition is the **comparative method** (see Glossary), which relates different species' traits to evolutionarily relevant characteristics such as social structure or feeding ecology [23–25]. This approach is especially useful when comparing closely related species with divergent socio-ecological traits, thereby accounting for resemblance due to shared **phylogeny**. I therefore focus primarily on direct comparisons of closely related species. Such work mostly comprises pairs of species, as well as some potential instances of cognitive **convergence** across more distantly related taxa. Finally, I highlight several recent large-scale comparisons of multiple species that – while losing some resolution on the cognitive traits in question – can explicitly account for phylogenetic relatedness across more numerous species and contrast both social and ecological explanations.

Spatial Memory

The ability to recall the location of resources and navigate efficiently between them is a key component of complex foraging behaviors, and memory of a representational 'map' of space is a key cognitive system underpinning such behaviors [26]. However, not all foods impose the same demands on memory, as some are more spatially dispersed than others. A striking

Box 1. Defining and Measuring Intelligence

Cognition comprises mental processes for acquiring, storing, and manipulating information. One important problem is defining what kinds of mental processes constitute 'intelligence'. Some approaches treat cognition as a collection of domain-specific systems that operate in a relatively modular or independent fashion [108]. Other approaches focus on domain-general processes (e.g., [109]) such as executive functions, which enable inhibiting, shifting, and updating responses in new situations [64]. A related proposal concerns whether animals exhibit 'general intelligence' – a theoretical construct describing correlations in individual performance across diverse contexts [71,110,111]. Thus, some aspects of intelligent behavior – such as possessing robust mental maps of space – may involve more domain-specific cognition whereas others – such as many conceptualizations of behavioral flexibility – are more domain general.

Measuring cognitive traits poses a special problem: whereas morphological traits (such as body size) or behavioral traits (such as propensity to groom) can be directly observed, cognitive processes can be only inferred. As any given observable behavior could be implemented through many diverse cognitive mechanisms, controlled experiments are necessary to pinpoint the specific cognitive processes underlying that behavior. Given the difficulties of executing large-scale comparisons of cognition across many different species [24], much work in primate cognitive evolution has used neurobiological correlates, such as whole brain or neocortex size, as a proxy for intelligence [2,6,12,13,18,19]. Brain size indices are an appealing way to probe patterns of cognitive evolution because they can be directly measured, and are available for many diverse species.

However, total brain or neocortex size comprises multiple functional areas. Such broad neurobiological measures may correlate with some cognitive processes, typically ones falling under the rubric of executive function or general intelligence [71,73,112]. However, they are a rough index of more specific cognitive abilities. Closely related species may have similar overall brain size but nonetheless exhibit important differences in some cognitive abilities (as in chimpanzees and bonobos [29,33,46,113]). Thus, using broad neuroanatomical measures to infer specific cognitive abilities is a case of 'reverse inference' from brain to cognition – a form of inference that can be problematic in cognitive science [114]. Illuminating the evolutionary relationship between minds and brains in primates will therefore require linking cognitive functions to more specific neurobiological systems. A prime example of this approach is work on the relationship between spatial memory and hippocampal volume in birds [21,22,27].

Glossary

Central place foraging: a pattern of foraging in which a forager or foraging group brings resources back to a central location.

Comparative method: a technique in evolutionary biology that involves relating differences and similarities in a trait across species, or populations, to aspects of those species' environment or socioecological characteristics.

Convergence: the independent evolution of similar characteristics across different, unrelated species that experienced similar socioecological conditions.

Domain general: aspects of the mind that can be used to process many different kinds of information. Domain-general learning mechanisms are often proposed when similar abilities or learning phenomena are observed across distinct contexts.

Domain specific: aspects of the mind that are specialized for certain kinds of content: either innately specified knowledge or learning mechanisms that utilize only certain kinds of information. Many views propose that domain-specific cognitive mechanisms are mental adaptations tailored by evolution to specific environmental circumstances.

Folivore: a species that predominantly feeds on leaves.

Frugivore: a species that predominantly feeds on fruits.

Gummivore: a species that predominantly feeds on gum, sap, and other tree exudates.

Hunter-gatherers: humans living in a traditional society in which most food is obtained by collecting wild plants and hunting wild animals.

Last common ancestor: the most recent species from which living members of the genera *Homo* (humans) and *Pan* (chimpanzees and bonobos) are directly descended.

Phylogenetic signal: a measure of the statistical dependence among species' traits due to their patterns of relatedness, such that more closely related species tend to more strongly resemble one another.

Phylogeny: the pattern of relatedness between species and other taxonomic groups, representing the evolutionary branching pattern of speciation leading to living species.

Box 2. Detecting Cognitive Evolution

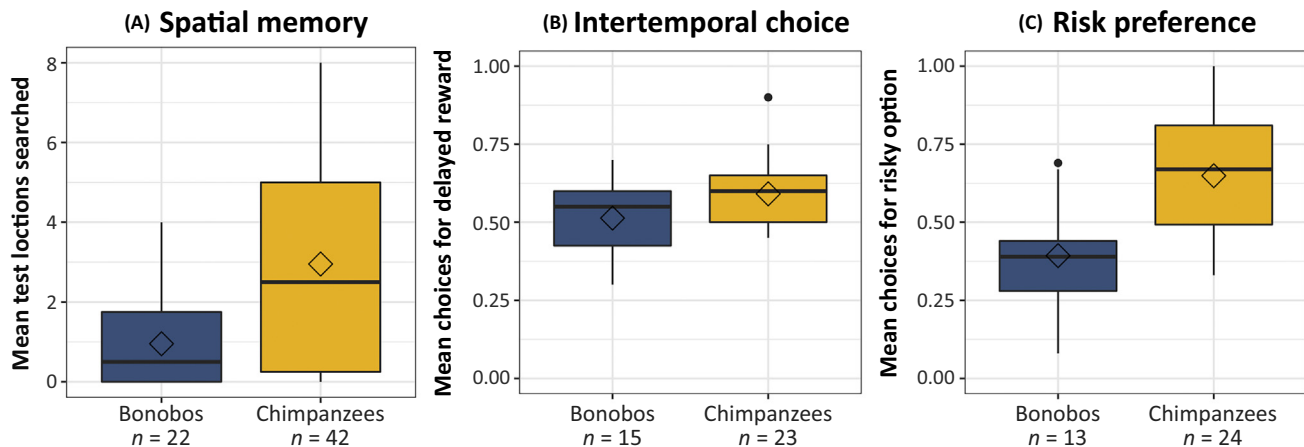
Evolutionary biologists have developed multiple tools to detect natural selection on different traits. Cognitive abilities have been most intensely studied using the comparative method to examine variation in population's or species' traits to infer the historical process of natural selection [23,24], a technique used extensively by Darwin [25]. Other approaches involve identifying signatures of selection in gene sequence data [115], but this method is currently less tractable for complex cognitive traits with unclear genetic substrates.

Adaptive explanations for traits must ultimately show that there is heritable variation in traits across individuals and that this variation affects reproductive success. This highlights the importance of understanding not just the average expression of a trait between species (the focus here) but also individual variation within a species, as such variation is the grist for the mill of natural selection. Accordingly, individual variation in primate cognition is a flourishing area of research [30,71,84,116,117]. For example, a recent study used a test battery to identify domains or latent 'factors' of cognition in children and chimpanzees [116]. Children exhibited three distinct factors for spatial cognition, physical cognition, and social cognition whereas chimpanzees exhibited only the spatial factor. Like children, dogs also showed a distinct social factor [62], which may reflect cognitive convergence in canids. Such work can therefore reveal how the structure of cognition changes across species.

There has also been progress on measuring the heritability of cognitive traits in primates and other animals [118]. For example, the cognitive test battery mentioned above was also used to show that different latent factors of cognition in different populations of chimpanzees, such as the 'spatial' factor, exhibited heritable variation [117]. However, the fitness consequences of such cognitive variation are currently less well understood. There is increasing evidence that variation in primate behavior, such as how sociable an individual is, can impact fitness in wild populations [119]. However, such fitness analyses require that animals live in natural contexts with free breeding (or mortality), and most studies of primate cognition are conducted in captive populations with veterinary interventions and controlled reproduction. Thus, experimental cognitive work in wild or more naturally living populations, although extremely challenging, will be necessary to address how primate cognitive abilities impact fitness [120].

example is variation in food caching across bird species. Whereas some species depend on an ability to store food across hundreds of thousands of locations, others cache in only a few locations or none at all. The adaptive relationships among natural history, spatial memory, and the hippocampus in birds is one of the most well documented in comparative psychology: species that are more dependent on caching exhibit more accurate spatial memory and enlarged hippocampal volume [21,22,27]. Primates do not engage in food-storing behaviors but they do vary in their dependence on patchy, widely dispersed foods. Surprisingly, relatively little work has directly compared multiple primate species' hippocampal size or memory capacities, but there is accumulating evidence for adaptive variation in primate spatial memory that maps onto ecology.

First, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) exhibit variation in their spatial memory skills. In comparisons of spatial memory in naturalistic foraging contexts where individuals must navigate to patches distributed in a large space (Figure 1A), as well as in more tightly controlled tasks involving multiple potential locations for food, chimpanzees exhibit more accurate memory than bonobos [28] (A.G. Rosati, unpublished). Importantly, the two species exhibit comparable performance in motivation controls as well as in simple object permanence tasks where they must track the location of a reward over short periods [29], so this difference appears to be specific to mental maps of the distribution of rewards in space. *Pan* also exhibits variation in hippocampal structure: chimpanzees' hippocampus is less asymmetrical and marginally larger than bonobos' [30] and has greater connectivity with other brain regions. Evolutionarily, what can account for these differences? While chimpanzees and bonobos share the same basic social structure and broad ecological niche, they exhibit important differences in the specifics of their diet: chimpanzees are more dependent on patchy fruit resources and less dependent on homogeneously distributed terrestrial herbs and exhibit larger day ranges and longer travel times between patches than bonobos [31–34]. As our closest living relatives, the differences between these species are also critical for reconstructing the mind of the **last common ancestor** to make inferences about human evolution (Box 3).



Trends in Cognitive Sciences

Figure 1. Foraging Cognition in Chimpanzees and Bonobos. Comparisons of cognition in chimpanzees and bonobos living under similar conditions in African sanctuaries; in box plots, lines indicate medians and diamonds indicate means. (A) In a spatial memory task [28], apes observed food being hidden at ten test locations in a large outdoor arena; another ten pieces had previously been hidden at ten matched control locations. After a delay the apes could search for food. (B) In an intertemporal choice task [43], apes chose between a smaller reward (one piece of food) that was always available immediately and a larger reward (three pieces of food) that was available after a delay of 1 or 2 min. (C) In a risky choice task [43], bonobos and chimpanzees made choices between a risky gamble that provided either a highly preferred or a non-preferred food type with equal probability and a safe alternative that always provided an intermediately preferred food type.

Other comparisons also provide support for the proposed relationship between dependence on patchy, distributed resources and robust spatial memory. For example, golden lion tamarins (*Leontopithecus rosalia*) show more accurate spatial memory over longer time intervals than Wied's marmosets (*Callithrix kuhli*) in both in a radial arm maze and a spatial delayed matching-to-sample task [35]. Although these two New World monkeys are closely related, with similar social organization and lifestyles, tamarins and marmosets exhibit key differences in their ecology. Marmosets from the genus *Callithrix* are obligate **gummivores** with specialized teeth, gut, and nails for gouging holes in trees and consuming the sap that exudes – a very spatially localized resource within small home ranges. By contrast, tamarins eat gum only opportunistically, instead ranging farther to feed on insects and patchily distributed fruit [36,37].

Additional evidence comes from comparisons of memory capacities in Malagasy lemurs exhibiting major differences in dietary niche. Ruffed lemurs (*Varecia* spp.) are extreme **frugivores** with diets exceeding 90% fruit, ring-tailed lemurs (*Lemur catta*) and mongoose lemurs (*Eulemur mongoz*) have mixed diets, and Coquerel's sifakas (*Propithecus coquerelli*) are **folivores** with a specialized gut to process leaves [38,39]. Across three tests of spatial memory

Box 3. Chimpanzees, Bonobos, and the Last Common Ancestor

Chimpanzees and bonobos are humans' closest living relatives, sharing approximately 98% of their DNA with humans [121]. These species are therefore our best model to reconstruct the cognitive profile of the last common ancestor of humans with nonhuman apes. Many evolutionary reconstructions use chimpanzees alone as a model for the last common ancestor, but there is increasing evidence that chimpanzees and bonobos differ in their cognition and behavior in some important ways. The two species exhibit similar fission–fusion social organizations where males remain in their birth group and females transfer to a new group at puberty. However, chimpanzees exhibit male–male bonds and more intense aggression, whereas bonobos exhibit increased tolerance and stronger bonds between females [33,34]. An influential hypothesis directly links these social differences to apes' feeding ecology: chimpanzees are thought to live in more 'difficult' environments where they depend more on fruit resources than terrestrial herbaceous herbs, feed on less-abundant food patches and face greater feeding competition, and depend more on costly foraging behaviors like tool use and hunting [31,32,34,50]. There are fewer long-term data on wild bonobos, but both observations and controlled behavioral experiments indicate that human behavior overlaps with both species in some respects [122]. Thus, the last ancestor may have exhibited a mosaic of chimpanzee-like and bonobo-like cognitive traits.

– recall of a single location after a 1-week period, use of allocentric spatial encoding rather than habit-based egocentric encoding to locate food, and recollection of multiple baited landmarks in a complex environment – ruffed lemurs consistently outperform the other species, and especially sifakas [40]. Thus, species with stark ecological differences exhibit variation in spatial memory skills.

Value-Based Decision-Making

All foraging behaviors necessarily involve decisions about value: given all the available alternatives, what is the best course of action? Two foundational components of decision-making are intertemporal choices concerning tradeoffs between time costs and the value of rewards and risky choices concerning tradeoffs between expected value and the probability of different outcomes. Such decisions are sometimes considered ‘self-control’ or impulsivity problems [41], but value-based preferences may also be tailored to particular environmental contexts [42]. There is emerging evidence that the ecological features that vary with primate memory – diet and home range size – also shape preferences about value.

First, chimpanzees are more patient than bonobos in direct comparisons of intertemporal choice [43,44]: they are more likely to choose a larger reward after a delay than a smaller reward available immediately (Figure 1B). Chimpanzees are also more risk-seeking than bonobos [43,45–47] when faced with choices between a ‘risky’ option that could provide either a high- or a low-value reward versus a ‘safe’ option that reliably provides an intermediate-value payoff (Figure 1C) – despite the fact that the two species show similar comprehension and are adept at tracking probabilities [48]. As with spatial memory, this cognitive variation maps onto features of their wild ecology. Chimpanzees face higher time costs stemming from travel times between patches and temporally costly extractive foraging behaviors. They also experience greater risk due to greater seasonably variation as well as hunting, an economically risky strategy that requires the investment of time and energy in pursuit of an uncertain outcome [49–51]. By contrast, wild bonobos hunt much more rarely and have not been observed to use tools for foraging in the wild [34]. Chimpanzees therefore face more difficult foraging problems characterized by economically variable foods and effortful, temporally costly processing.

Exacerbated patience is also seen in other species that feed on time-intensive resources. A recent phylogenetic comparison of intertemporal choice patterns across 13 primate species compared how both social and ecological factors predicted patience. One important predictor was home range size: species that traveled longer distances in the wild were more willing to wait in experimental tasks [52] (but note that home range size correlated with body size and other allometric measures in this sample, so their influence could not be dissociated). By contrast, indices of social complexity did not predict patience. The specialized feeding ecology of callitrichid monkeys provides another test of this claim, as temporal and effort costs are dissociated in their wild foraging behaviors [42]. Marmosets are gummivores who must wait long temporal delays to exploit sap, whereas tamarins pay greater effort costs to forage on fruit. In line with these differences, common marmosets (*Callithrix jacchus*) are more patient when choosing to wait passive delays but cotton-top tamarins (*Saguinus oedipus*) are more willing to pay effort costs by traveling farther distances for rewards [53–55].

Additional work provides support for the relationship between risk preferences and ecology. A direct comparison of risky preferences across all four great ape species [47] found that orangutans (*Pongo abelii*) and chimpanzees were relatively risk prone whereas gorillas (*Gorilla gorilla*) and bonobos were more risk averse. This aligns with their respective ecologies: like chimpanzees, orangutans feed on seasonably variable fruits and engage in extractive foraging [56], whereas gorillas depend on more continuously available leaves, piths, and roots and do not use tools [57]. Capuchin monkeys (*Sapajus* spp.) likewise provide evidence from

evolutionary convergence. In matched comparisons with chimpanzees and bonobos, capuchins exhibit more risk-seeking preferences as well as relatively higher levels of patience than other New World monkeys [58,59]. Their resemblance to chimpanzees in decision-making contexts is striking given that capuchins are thought to be convergent in their wild feeding ecology, exhibiting both costly tool use and risky hunting behaviors [60,61]. Finally, the relationship between hunting and risk-seeking strategies is further supported by work in canids [62], which are often used as a model of cognitive convergence with humans: wolves, which are dependent on hunting, exhibit more risk-seeking choices than do dogs in the same primate risk task [63].

Executive Control

Executive functions are a suite of cognitive processes that allow individuals to flexibly control their behavior, overriding reflexive responses that would otherwise be performed automatically. This includes several capacities for self-regulation, such as inhibiting inappropriate motor responses, reactivity in new situations, and updating behavioral strategies [64]. While some proposals have highlighted the potential role of social systems in shaping executive functions [65], recent work has revealed a strong connection with ecological niche.

One foundational component of executive function is the ability to inhibit undesirable but pre-potent actions [66]. A recent study compared 23 species of lemurs, monkeys, and apes on two related problems tapping into such motor inhibitory control. In the A-not-B task, individuals experienced a reward that was repeatedly hidden in one location (A) but was then visibly moved to a different location (B). In the 'cylinder' task, individuals first learned to reach through the side of an opaque cylinder to access food and then on test trials faced the same problem with a transparent cylinder. Both tasks therefore assessed whether animals could inhibit a pre-potent reach to a reward or rewarded location. After controlling for phylogenetic relationships between species, the primary socioecological predictor of primate performance was dietary breadth – the number of distinct food items in their diet [23]. By contrast, social indices such as group size did not predict inhibitory control (see [67] for a similar result from carnivores supporting this general conclusion). Thus, the most comprehensive studies to date of inhibitory control revealed adaptive variation with an ecological rather than a social characteristic.

Another component of executive control concerns reactivity to novel contexts [68,69]: do individuals seek out or avoid new aspects of the environment or new social partners? This aspect of self-regulation is a key component of flexibility in response to novel contexts and appears to cut across both social behavior (reactions to other agents) and foraging behavior (reactions to food or objects in the physical environment). A direct comparison revealed that chimpanzees and orangutans were more interested in food and novel objects, approaching more quickly than did bonobos, but there were no differences in these species' willingness to approach an unfamiliar human [70]. Thus, responses to environmental novelty mapped onto their ecology, similar to the comparisons of these species' risk preferences [43,45–47], whereas they showed similar reactions to social novelty despite variation in their social systems.

Finally, it is important to note that many components of executive control may exhibit a strong **phylogenetic signal**, such that variance in abilities maps onto species' relatedness [64] and thereby obscures any variation due to socioecology [24]. More concretely, a cognitive problem that is challenging for a lemur can result in ceiling-level performance from apes, so comparisons across distantly related species often unsurprisingly find that apes outperform other primates. For example, reversal learning is a simple form of behavioral updating where individuals initially learn one rule but then the correct response shifts. Although there are few direct comparisons, similar reversal learning tasks have been implemented in many species and apes generally are more successful at picking up the new contingencies [71,72]. Thus, one challenge for testing

hypotheses for the evolution of executive control is devising cognitive problems that can detect variation in abilities both between and within taxonomic levels.

Ecological and Social Explanations for Distinct Domains of Cognition

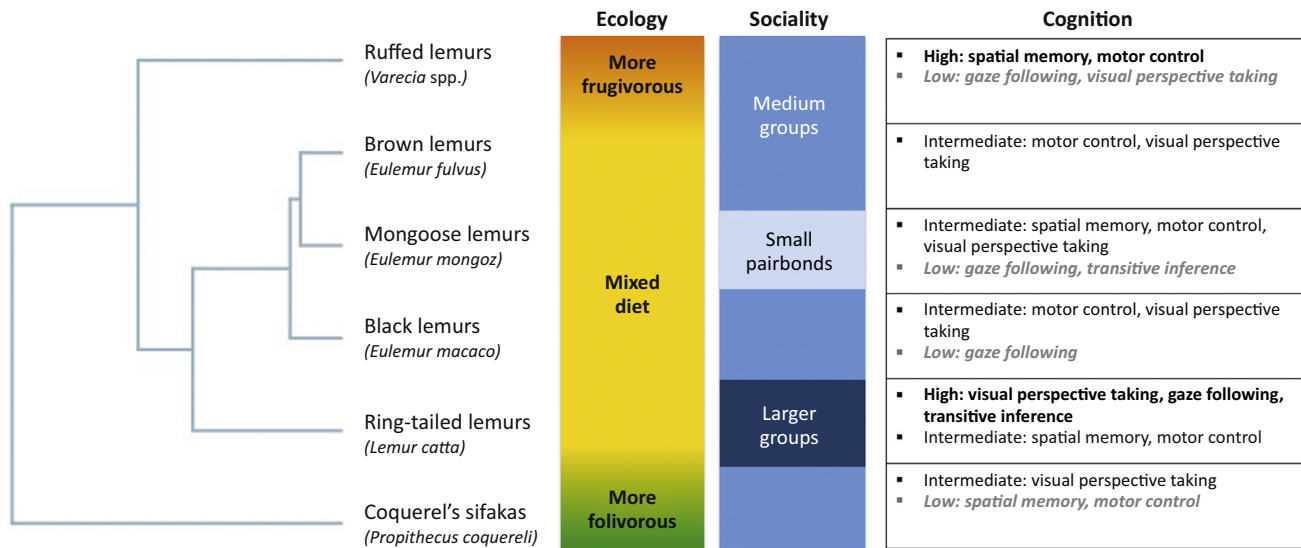
This comparative work provides initial support for the hypothesis that ecology leaves an adaptive signature on primate cognition. Two large phylogenetic comparisons described earlier [52,73] directly contrasted social and ecological predictors, and both found that measures of ecological complexity but not social complexity predicted patience and inhibitory control. These results contradict formulations of the social intelligence hypothesis proposing **domain-general** effects, such that social complexity shapes many diverse cognitive functions ranging from social cognition to memory and behavioral flexibility more generally [2,6,65]. However, the social and ecological hypotheses are not mutually exclusive. Other views propose more **domain-specific** effects: social complexity may have a targeted impact on social learning or theory of mind (e.g. [74]) whereas ecology may shape other cognitive systems. Current evidence aligns with this second view. That is, both the social and ecological hypotheses can explain variation in cognition but each is relevant in distinct cognitive domains.

Recent work on lemur cognitive variation provides an illustrative example (Box 4). Lemurs with more complex diets, such as frugivorous ruffed lemurs, show more sophisticated memory and inhibitory control capacities, especially compared with folivorous species like sifakas [40,75]. However, patterns of variation across species are very different for social cognitive capacities. For example, ring-tailed lemurs live in large groups with complex dominance hierarchies [76]. Although they exhibit intermediate performance on several foraging cognition tasks, in line with their intermediate diet, they exhibit exceptional sociocognitive skills. Ring-tailed lemurs can successfully exploit social cues such as gaze direction [74] and lemur group size predicts more robust visual perspective taking [75]. Ring-tailed lemurs are also more skillful at making transitive inferences, a skill thought to be useful for understanding dominance hierarchies [77]. Thus, while foraging cognition varies with ecology, social cognition varies with social complexity in lemurs. Overall, this work suggests that cognition can evolve in a mosaic pattern, with different evolutionary processes shaping different cognitive domains (Figure 2).

An important consideration in understanding when these different evolutionary processes come into play is the behavioral context in which a given cognitive skill is used. For example, foraging behaviors in gregarious primate species often involve cooperation or competition with others. Along these lines, chimpanzees exhibit more robust social inhibitory control than bonobos [78]: chimpanzees can better refrain from making ineffective reaches towards a social agent and are more adept at reversal learning in a social context. Yet these social

Box 4. Lemurs as a Model for Cognitive Evolution

Strepsirrhine primates (lemurs, lorises, and galagos) exhibit high levels of diversity in many evolutionarily relevant characteristics, including sociality, activity patterns, and diet [39]. Malagasy lemurs in particular are a closely related monophyletic group [123] that exhibit unusual levels of diversity in both social structure and diet [38,39]. For example, lemur species range from relatively solitary lifestyles (a rarity among monkeys and apes) to species living in large groups with complex dominance hierarchies. In terms of diet, lemur species feed on a wide variety of leaves, fruits, insects, and small prey. Some, such as aye-ayes (*Daubentonia madagascariensis*), even engage in complex, multistep extractive foraging techniques. This independent variation in both sociality and ecology means that lemurs are an important taxonomic group for testing the predictions of the social and ecological intelligence hypotheses. Moreover, lemurs are more distantly related to humans than are anthropoid primates (monkeys and apes), so they can be used to assess the generality of evolutionary theories explaining variation in cognition, as well as to help reconstruct primate cognitive origins [124]. Although strepsirrhine cognition has been incredibly understudied compared with anthropoid cognition, research in the past 10 years comparing different lemur species have revealed important variation in aspects of their social cognition, memory, decision-making, and executive control (see Figure 2 in the main text). Future work on the cognition of more diverse species could therefore provide critical insights into the processes of cognitive evolution in primates.



Trends in Cognitive Sciences

Figure 2. Lemur Cognition and Socioecology. Comparisons of cognition across closely related lemurs varying in dietary ecology and social complexity. In comparisons of spatial memory [40], frugivorous ruffed lemurs exhibit the highest performance, especially relative to folivorous sifakas. In comparisons of motor inhibitory control [73,75], ruffed lemurs again exhibit the highest performance in initial test trials, especially relative to sifakas. In comparisons of visual perspective taking [74,75], ring-tailed lemurs (who live in larger groups with complex dominance hierarchies) exhibit the most robust performance, especially relative to ruffed lemurs. In comparisons of gaze following [74], ring-tailed lemurs follow an experimenter's gaze whereas mongoose, black, and ruffed lemurs do not. Finally, in tests of transitive reasoning [77] ring-tailed lemurs outperform mongoose lemurs.

differences have been attributed to their ecology: wild bonobos face more relaxed feeding competition than chimpanzees due to greater food availability, and thus such inhibitory control in social feeding contexts is more important for chimpanzees [33]. Thus, some aspects of social decision-making capacities may, counterintuitively, be characterized as components of 'foraging cognition' because they have an ecological function.

An Ecological Framework for Human Cognitive Uniqueness

The idea that primate cognitive evolution can be shaped by ecology has important implications for understanding the origins of human cognition. Most theories about human uniqueness have focused on special features of human social cognition and behavior, such as theory of mind, cooperation, communication and language, and cultural transmission of knowledge and skills [1,79–83]. This focus on human sociality obscures the fact that humans also exhibit several specialized ecological characteristics. The human ecological niche is best illustrated by the lifestyle of **hunter-gatherers** and other foragers living in small-scale societies, whose lives reflect the ways that humans have lived for most of our species' history [84]. Although there is significant diversity in lifestyles across different forager groups, human behavioral ecology also differs from that of other primates in several critical respects [84–86].

First, humans tend to exploit high-value foods that are costly to obtain. Most obviously, humans eat more meat – a high-value resource that requires investment of time and effort in an endeavor with low rates of success – as well as more foods requiring costly extractive techniques, such as nuts or honey [86,87]. Other valuable foods that require time-intensive processing and cooking include starchy tubers [88]. Second, these resources tend to be widely dispersed in space and time, as reflected by human foragers exhibiting longer daily ranging patterns than other apes [84]. Furthermore, food is collected using a human-unique pattern of **central-place foraging**, where individuals bring food to a centralized camp, in contrast to apes, who consume food on the go. Finally, many of the social capacities that are thought to

uniquely characterize our species – cultural learning, tolerance, and cooperation – play a foundational role in these foraging behaviors. For example, humans often exploit foods using complex sequences of tools; such skills are often acquired through cultural learning but are then used to solve ecological problems. Humans also exhibit extremely high rates of food sharing among adults compared with other apes, who rarely transfer food between adults [89]. Such food sharing is a paradigmatic example of human cooperation, but again solves an ecological problem: the high risks associated with the human diet. For example, hunting is a high-risk strategy, as an individual might spend days in pursuit of game but bring home nothing. However, even if one hunter failed, another might have succeeded, and women in the group spent the day foraging for other foods. Redistribution of food mediates the inherent risk posed by human diets [86,89,90]. That is, human societies provide a safety net that reduces risk by better equalizing food intake across individuals.

Humans are therefore unique in both sociality and ecology, suggesting that these special ecological characteristics may shape several unique features of human cognition. First, humans should exhibit more accurate spatial memory given our species' dependence on patchy foods, large ranges, and use of central-place foraging strategies. Second, humans should exhibit exacerbated patience, given the long travel times and investment in costly extractive foraging. Third, humans should be more tolerant of risk in returns, given the great variation in foraging payoffs and presumption of a social safety net to buffer risk. Finally, humans should exhibit more robust executive functions, given that the same dietary features predict self-control.

This ecological framework therefore situates human cognitive abilities in terms of their behavioral function, providing a new view of the ultimate evolutionary reasons for humans having such skills. For example, humans are thought to solve spatial problems with a degree of flexibility and accuracy not seen in other species, in part because language reshape spatial representations [91–93]. Neurobiological theories similarly presume that humans have especially robust executive function, given our species' large frontal cortex [94–96]. Both of these are proximate accounts focused on cognitive or neural mechanisms, and this framework provides an integrative evolutionary explanation. Other ecological predictions are more surprising, such as the proposal that humans should be relatively risk seeking compared with other primates. There is overwhelming evidence that humans tend to be risk averse [97], but such work mainly involves decisions about money [98] and people can be risk seeking when making decisions from experience about biologically central rewards [99,100]. Similarly, humans are thought to be an outlier in our ability to delay gratification and plan for the future [101,102], but little work has examined human future-oriented cognition in foraging contexts (but see [44]). Thus, direct comparisons of memory, decision-making, and executive control strategies between humans and other primates – in evolutionarily relevant contexts – is needed to test this ecological hypothesis.

Concluding Remarks and the Future of Foraging Cognition

The ecological intelligence hypothesis is currently at a crossroads. There is accumulating evidence that some primate cognitive capacities – such as spatial memory, decision-making, and executive control – are shaped by ecology. However, there is also clearly much work to be done (see Outstanding Questions). First, large-scale comparisons of many species using phylogenetic comparative methods [52,73] are a powerful approach to understanding patterns of evolutionary variation in cognition. However, such studies are relatively rare due to pragmatic constraints [24]. Moreover, some species are greatly under-represented in comparative work to date, such as folivorous primates [103] – critical taxonomic groups for testing ecological hypotheses. Thus, understanding the origins of complex cognition in primates will require examining more diverse species as well as a focus on larger-scale comparisons of cognition.

Outstanding Questions

Large-scale comparisons of different cognitive skills, using phylogenetic comparative methods, can provide a strong test of whether different cognitive domains are shaped by different evolutionary processes. Do such evolutionary patterns support distinct domains of social and ecological cognition?

Primate cognition research has generally focused more heavily on frugivorous species, but leaf-eating species provide an important test of the ecological hypothesis. What are the cognitive abilities of folivorous primate species?

Does foraging cognition and its neural substrates coevolve across primates, similar to the observed relationship between spatial memory and hippocampus size in bird species?

Is individual variation in foraging cognition abilities related to fitness outcomes such as number of offspring or survival?

Recent work has highlighted that both social and ecological factors may shape patterns of primate tool use. Should skills, like tool use, that are learned socially but serve a foraging function be conceptualized as social adaptations, ecological adaptations, or both?

How do humans use spatial memory, value-based decision-making, and executive control in foraging contexts?

Is the human mind unique because both social and ecological evolutionary forces shaped complex behaviors that require the seamless integration of multiple capacities?

A second gap concerns the relationship between social and ecological intelligence. I have argued that the social and ecological intelligence hypotheses may have differential explanatory power across different domains of cognition. The challenge is in identifying those domains in the first place. I suggest that the first step is to pinpoint the behavioral contexts in which different cognitive skills are used – some seemingly ‘social’ skills, such as social inhibitory control [78], might serve an important foraging function, and vice versa. Other capacities may emerge through interplay of both social and ecological processes, an issue exemplified by patterns of tool use across primates [50,104,105]. On the one hand, much wild-primate tool use has an ecological function – obtaining food resources – and successful tool use depends on foraging skills such as intertemporal choice and action control. On the other hand, tool use may be socially learned, and the characteristics of social groups – such as population density – may shape how tool behaviors are learned from social models. However, because social and ecological hypotheses have so often been contrasted as mutually exclusive, little is known about how these processes can interact to build complex skills. As foraging-related tool behaviors have been observed in only a few wild primates – chimpanzees, orangutans, capuchins, long-tailed macaques (*Macaca fascicularis*), and, of course, humans – understanding why such behavioral patterns emerge will be critical for understanding human cognitive evolution.

The final gap concerns the unique aspects of human cognition. While many views on human uniqueness focus on the special nature of human sociality, I have emphasized that humans also stand out among primates in terms of our ecological niche. Moreover, many aspects of human social behavior – like food sharing and cooperation – serve an ecological function and many social capacities – like cultural transmission – are used to acquire ecologically relevant skills. In this sense human cognitive uniqueness may be best conceptualized as a suite of capacities cutting across psychological domains. This perspective aligns with theories from cognitive science proposing that unique components of human cognition stem from novel interconnections between different abilities [106–108]. However, the focus of this evolutionary approach is on how these different capacities jointly contribute to complex human-unique behaviors. Hunting, foraging, and food sharing all necessarily require the smooth integration of multiple cognitive capacities spanning both the social and the ecological domain. Comparisons of cognition across species, integrated with information about wild socioecology and behavior, will therefore be critical for understanding how such integrated suites of cognitive abilities emerge in tandem.

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