

Ecological variation in cognition: Insights from bonobos and chimpanzees

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Bonobos and chimpanzees are closely related, yet they exhibit important differences in their wild socio-ecology. Whereas bonobos live in environments with less seasonal variation and more access to fallback foods, chimpanzees face more competition over spatially distributed, variable resources. This chapter argues that bonobo and chimpanzee cognition show psychological signatures of their divergent wild ecology. Current evidence shows that despite strong commonalities in many cognitive domains, apes express targeted differences in specific cognitive skills critical for wild foraging behaviors. In particular, bonobos exhibit less accurate spatial memory, reduced levels of patience and greater risk aversion than do chimpanzees. These results have implications for understanding the evolution of human cognition, as studies of apes are a critical tool for modelling the last common ancestor of humans with nonhuman apes. Linking comparative cognition to species' natural foraging behavior can begin to address the ultimate reason for why differences in cognition emerge across species.

Les bonobos et les chimpanzés sont prochement liés, pourtant ils montrent d'importantes différences dans leur sociologie naturelle. Alors que les bonobos vivent dans des environnements avec peu de diversité de climat entre saisons et plus d'accès à des ressources de nourriture alternatives, les chimpanzés ménagent une compétition étalée spatialement et des ressources plus variées. Je soutiens que la cognition des chimpanzés et bonobos montre les signatures psychologiques de leur écologie naturelle divergente. Les témoignages courants montrent que, malgré les forts points communs dans en cognition, les grands singes expriment des différences au niveau de compétences cognitives importantes au butinage. En particulier, les bonobos démontrent une mémoire spatial moins précise, moins de patience, et plus d'aversion de risques que les chimpanzés. Ces résultats fournissent des signes dans l'étude de l'évolution de la cognition humaine. Les études des grands singe sont un outil d'importance majeure dans la modélisation du dernier ancêtre commun des humains et grands singes non-humains. Faire des liens cognitives comparatives entre le butinage des différentes espèces peut commencer à dévoiler les raisons pour les différences de cognition entre espèces.

Introduction

One of the most pressing problems for the comparative study of cognition is explaining the emergence of variation in psychological abilities across species. How and why do such differences in cognition arise? This is an especially important question with respect to understanding the evolutionary history of our own species: although humans show important cognitive continuities with animals, we also exhibit a suite of abilities that markedly differ from other species. These differences span domains

of behavior ranging from complex reasoning and planning to thinking about other's minds and to learning cultural norms of behavior. Consequently, illuminating the evolutionary mechanisms that shape cognitive capacities across species in general can shed light into the evolution of human-unique cognition specifically.

Many theoretical accounts argue that cognitive traits are shaped by natural selection, much like morphological traits. In primates, social organization in particular has long been thought to be critical in shaping the evolution of intelligent behavior

(Byrne and Whiten, 1988; de Waal, 1982; Dunbar, 1998; Humphrey, 1976; Jolly, 1966); that is, primates are thought to evolve especially complex cognitive skills in order to navigate their especially complex social world. However, there are also compelling arguments for the importance of ecological environments in shaping cognition across taxa (Byrne, 1997; Gibson, 1986; Milton, 1981). These proposals suggest that species facing especially difficult foraging problems may evolve psychological capacities in response to these environmental factors.

This chapter will focus on this second, less well-explored hypothesis by examining recent empirical research comparing cognition in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*). Comparative studies of the traits of different species are one of the most powerful tools in evolutionary biology for illuminating the historical process of natural selection (Clutton-Brock and Harvey, 1979; Harvey and Purvis, 1991; MacLean et al., 2012; Mayr, 1982). This chapter will examine whether there is a psychological ‘signature’ of these species’ natural history in the cognitive capacities that apes utilize in foraging contexts; that is, I will examine evidence that apes show differences in their cognition that parallel the sorts of differences in dentition or other morphological characters that map onto dietary ecology across many primate species (see also Rosati, in press).

Bonobos and chimpanzees are a particular useful model for examining the role of ecology in shaping cognition, as these species are closely related but they exhibit systematic differences in their wild feeding ecology. *Pan* can therefore serve as a model to test hypotheses about when and why different species differ in their cognition. Chimpanzees and bonobos are also our two closest living relatives, so they are the best model for the cognition and behavior of the last common ancestor of humans with other apes. In other words, these apes can provide special insights into the evolution of cognitive capacities in our own lineage.

The ecological hypothesis

Foraging problems are ubiquitous as all animals must identify appropriate food resources, locate them in their environment and make trade-offs between the benefits of pursuing a particular resource

and the costs necessary to acquire that resource. However, not all dietary niches necessarily require the same cognitive abilities to be efficiently exploited. Resources whose distribution varies in time (seasonal variability) or space (patchiness), as well as resources that require extensive behavioral processing (such as through extractive foraging) may require specific cognitive and behavioral skills relevant to these problems. In contrast, diets focused on foods that involve more homogenous spatial or temporal distributions, or whose consumption depends more on morphological adaptations in dentition and the digestive tract, may require a different set of abilities.

Along these lines, several proposals have been put forward arguing that cognitive evolution may be shaped by the different cognitive demands posed by various features of the diet. Some flavours of the ecological intelligence hypothesis have focused on the idea that animals consuming patchy foods, like fruit, may need to keep track of more information than animals that eat less variably distributed resources, such as folivores who consume more leaves (Milton, 1981). Other theories focus on the cognitive demands of extractive foraging or other aspects of ‘technical’ intelligence—the idea that processing food in several steps may require especially complex cognition (Byrne, 1997; Gibson, 1986; Parker and Gibson, 1997). Finally, some authors have linked variability in ecological conditions to the need for behavioral flexibility and innovation in cognitive skills (Deaner et al., 2003; Sol et al., 2002). Studies of brain evolution have provided some support for this ecological hypothesis. For example, frugivorous species tend to have larger brains than folivorous species (Barton, 1996; 2006; Clutton-Brock and Harvey, 1980; DeCasien et al., 2017; MacLean et al., 2009).

However, many of these proposals focus on the idea that ecology may spur the emergence of complex cognition in a general sense rather than specifying the particular cognitive skills that may play critical roles in foraging. Along the same lines, much of the evidence from variation in overall brain size (or the size of very large, functionally diverse areas such as neocortex or even frontal cortex) is at best a rough index of more specific cognitive functions. Yet many modern views from psychology suggest that there are, in fact, different domains of cognition

that may operate—and evolve—relatively independently (Barrett and Kurzban, 2006; Herrmann et al., 2007; Hirschfeld and Gelman, 1994; Shettleworth, 2012; Spelke and Kinzler, 2007; Tomasello and Call, 1997). Comparative studies of brain anatomy further show that neurobiological systems may evolve in a mosaic fashion, with certain functional areas changing in size or structure independent of others (Barton, 2006; Striedter, 2005). Thus, testing the ecological hypothesis requires more specific proposals about what cognitive abilities may be especially relevant for foraging.

Defining ‘foraging cognition’

What psychological capacities are actually utilized in foraging contexts? Many mental functions could fall under this rubric, ranging from perceptual abilities to detect certain classes of food (Dominy and Lucas, 2001), to collaborative interactions that allow individuals to exploit resources they could not acquire alone (Tomasello et al., 2012). Here, I will focus on three sets of skills: spatial memory capacities allowing individuals to remember the location of resources; patience, or decisions about deferring immediate gratification to seek out more valuable but delayed resources; and risk preferences, or willingness to accept variability in rewards. This is obviously not an exhaustive list of foraging-relevant skills in chimpanzees and bonobos; for example, there are clear differences in chimpanzee and bonobo propensities to engage in tool use and extractive foraging behaviors (Furuichi et al., 2015; Herrmann et al., 2010). However, both decision-making and spatial memory are intimately related to core problems presented by foraging, are relatively well-understood sets of psychological capacities and there is evidence that these skills vary across species with known differences in socio-ecology. These abilities are therefore good targets for considering the role of ecology in chimpanzee and bonobo cognition.

First, spatial memory is a foundational cognitive skill for foraging behaviors. It is essential for solving foraging problems that involve locating widely distributed resources and navigating between patchy food sources efficiently, two problems that all primates face to a greater or lesser degree (Janson and Byrne, 2007). Memory systems

allow organisms to use information acquired from past experiences to alter their currently behavior. It is clear from wild observations that animals can move through familiar spaces and successfully locate food (Normand et al., 2009; Normand and Boesch, 2009), but many potential underlying cognitive mechanisms could support such behaviors. Indeed, modern views from cognitive science and neurobiology highlight the fact that there are parallel but distinct memory systems in the brain that could support foraging behavior, not all of which actually involve thinking about spatial locations (Burgess, 2008; Sherry and Schacter, 1987). For example, animals could recall their own physical movements without tracking any relevant environmental features (Burgess, 2006; Packard, 2009). This review will focus specifically on spatial memory: how animals form cognitive maps of the locations of resources in space based on their previous experiences (Bird and Burgess, 2008; Menzel, 1973), in the absence of direct perceptual cues.

Studies of spatial memory comprise the strongest evidence that ecology can shape cognition across species. For example, variation in the spatial memory skills of different bird species (as well as the size of their hippocampus, a key brain region involved in encoding spatial locations) is related to the degree to which they depend on caching or storing food in the wild (Balda and Kamil, 1989; Basil et al., 1996; Bednekoff et al., 1997; Clayton, 1998; Clayton and Krebs, 1994; Healy et al., 2005; Kamil et al., 1994; Krebs et al., 1990; Pravosudov and Clayton, 2002; Shettleworth, 1990; Shettleworth et al., 1990). Although there has been less research in other taxa, there are some hints that similar relationships between ecology and spatial memory capacities hold in other species as well. For example, spatial memory varies by sex in vole species with sexually dimorphic spatial ranging patterns, but not in species that do not exhibit sex differences in ranging behaviors (Gaulin and FitzGerald, 1986; Gaulin and Fitzgerald, 1989; Jacobs et al., 1990). There is also accumulating evidence that ecology shapes spatial memory in some primates. Marmoset species are obligate gummivores that gouge holes in trees that are located in smaller home ranges, whereas closely related tamarin species exhibit much larger ranging patterns as they feed more on patchily distributed

fruit and insects. Accordingly, tamarins show more accurate spatial memory over longer time intervals than do marmosets in several spatial and visual memory tasks (Platt et al., 1996). Similarly, more frugivorous lemur species, who must recall the locations of patchily distributed fruits in their territories, show more accurate and flexible performance on a variety of spatial memory problems compared to folivorous species that eat homogeneously distributed leaves (Rosati et al., 2014).

Decision-making is another critical and universal cognitive component of foraging behaviors. At the heart of foraging is a series of decisions about value: given all the available alternatives, what is the best thing to eat? This sort of choice involves the integration of many disparate types of information, including the quality of the food, the likelihood that the food is actually available at any given time and the temporal and energetic costs of pursuing foods found in more distant locations. Here I focus on two foundational components of value-based decision-making: decisions about time, which involve trade-offs between the value of the reward and the temporal costs necessary to acquire it; and decisions about risk, which involve trade-offs between options that provide more constant rewards and options that provide more variable or risky outcomes.

Although decision-making has not been studied as extensively from a comparative perspective as spatial memory, existing evidence suggests that feeding ecology may also have a profound influence on different species' economic preferences. For example, cotton-top tamarins (*Saguinus oedipus*) and common marmosets (*Callithrix jacchus*) show different patterns of choice in both temporal discounting (Rosati et al., 2006; Stevens et al., 2005a) and spatial discounting (Stevens et al., 2005b) contexts. Specifically, marmosets are more willing to wait in temporal tasks to acquire more food, whereas tamarins are more willing to travel longer distances to acquire more food. This maps onto the aforementioned differences in their feeding ecology: marmosets may be more temporally patient because they are obligate gummivores who must wait for sap to exude from trees, whereas tamarins may be more willing to pay effort costs because they typically travel longer distances to forage on

insects and fruit. Moreover, work from behavioral ecology highlights the critical role of environmental contexts on decision-making more generally (Rosati and Stevens, 2009; Santos and Rosati, 2015). For example, risk-sensitivity theory proposes that decisions about variability in pay-offs should depend on energetic state, such that individuals in a poor condition are more risk-prone than individuals in a better condition (Caraco, 1981). That is, the impact of a pay-off on fitness depends on context: if an animal's current nutritional requirements exceed the pay-off offered by the safe option, then they should be more risk-prone, as the alternative is potentially death (Stephens, 1981; Stephens and Krebs, 1986). Overall, this theoretical work highlights the fact that decision-making can be tailored to the environmental context that individuals face, suggesting that species with consistent differences in ecology might exhibit consistent differences in their psychological preferences.

Predictions from bonobo and chimpanzee natural history

Chimpanzees and bonobos are human's closest extant relatives, sharing approximately 98 per cent of their DNA with humans (Prüfer et al., 2012). These species are therefore our best model for cognitive profile of the last common ancestor of humans with non-human apes. Importantly, chimpanzees and bonobos also exhibit a suite of morphological and behavioral difference even though they diverged from one other less than 1 mya (Won and Hey, 2005). In particular, studies from both captivity and the wild show that chimpanzees exhibit more pronounced sexual dimorphism and increased rates of escalated aggression, whereas bonobos exhibit increased socio-sexual behaviors and a social organization with stronger bonds between females (Hare et al., 2012; Parish, 1996; Surbeck et al., 2011; Wrangham and Pilbeam, 2001).

An influential hypothesis specifically links these behavioral differences to apes' feeding ecology: chimpanzees and bonobos are thought to live in environments with important ecological differences that alter the character of the foraging problems faced by these species (Kano, 1992; Wrangham and Peterson, 1996). In particular, compared to

bonobos chimpanzees are thought to utilize more patchy, seasonably variable fruit resources, feed on less-abundant food patches, and have less access to homogeneously distributed terrestrial herbaceous vegetation (THV) as fallback food (Malenky and Wrangham, 1993; White, 1989, 1998; White and Wrangham, 1988; Wrangham, 2000). Furthermore, wild chimpanzees at multiple sites regularly use tools to engage in temporally costly extractive foraging techniques, including insect fishing and nut cracking, whereas wild bonobos have not been observed using tools for feeding (Furuichi et al., 2015). Finally, wild chimpanzees exhibit high rates of hunting monkeys whereas bonobos only occasionally do so (Stanford, 1999; Surbeck and Hohmann, 2008), and hunting requires the investment of time and energy in pursuing an uncertain outcome (Gilby and Wrangham, 2007).

These ecological differences mean that bonobos spend less time and effort to find food and face less feeding competition while doing so than chimpanzees. This may have resulted in relaxed selection on aggressive behaviors and contribute to differences in their social structure (Hare et al., 2012; Wrangham and Pilbeam, 2001). Although apes may show important diversity in behavior (and ecology) across populations (Boesch et al., 2002; Hohmann et al., 2010), overall these observations suggest that chimpanzees may face more 'difficult' foraging problems in the sense that their diets are broadly characterized by high levels of effortful, temporally costly food processing, variation in pay-offs, and more intense feeding competition.

What does this ecological hypothesis predict concerning foraging cognition in bonobos and chimpanzees? First, chimpanzees should exhibit more accurate spatial memory abilities to locate their patchy food resources, given that bonobos depend more on resources that are homogeneously distributed in the environment like terrestrial herbs. Second, chimpanzees should exhibit higher levels of patience than bonobos, given that they must tolerate longer delays to access food both in terms of search times when locating patches, as well as increased temporal and work effort when engaging in extractive foraging. Third, chimpanzees should be more risk-seeking than bonobos, as chimpanzees feed on food that is more temporally, spatially and

seasonably variable than that of bonobos, and also regularly engage in risky hunting behaviors. Overall, these ecological differences predict that several memory and decision-making capacities should systematically differ between chimpanzees and bonobos, specifically those cognitive skills that map onto these aspects of their natural environments.

Empirical evidence for divergence in *Pan* foraging cognition

Is there evidence from ape cognition supporting these predictions derived from wild ape ecology? Studies in captivity allow for controlled experiments that can rule out alternative psychological explanations for observed patterns of results (Tomasello and Call, 2008), which can be very challenging in wild populations (Zuberbühler, 2014). Moreover, studies of ape populations in zoos or sanctuaries are better at equating the environments that individuals of both species experience over their individual lifetime. This minimizes the possibility that individual chimpanzees and bonobos acquire different skills over ontogeny in response to foraging actively in different types of habitats, as in wild populations. For example, African sanctuaries care for apes following relatively standardized procedures across sites (Farmer, 2002; Wobber and Hare, 2011). While apes semi-free-range in large, naturalistic rainforest enclosures within complex social groups, they receive the majority of their food through provisioning. These environmental similarities allow species comparisons to hone in on the psychological 'signature' of their cognitive adaptations to typical wild environments. Unfortunately, many direct comparisons of bonobo and chimpanzee cognition involve small sample sizes of at least one species (typically bonobos, who are relatively rare in captivity), making it difficult to detect species differences. However, there is accumulating evidence from studies with larger samples that they differ in some specific capacities.

First, these species show divergent responses to some spatial memory problems. For example, when confronted with a problem where they must recall the location of food hidden under one of four containers over a period of one minute (while their view is occluded), chimpanzees are more accurate

than are bonobos (Rosati and Hare, 2012a). Critically, this species difference in performance seems to emerge specifically when apes are faced with more complex problems where the location of food must be retained in memory for some time. In the same set-up, chimpanzees and bonobos had equivalent performance when they could make a response immediately; that is, when they did not have to remember the hiding location for as long. Along the same lines, chimpanzees and bonobos show similar performance when solving simple object permanence tasks where they must track the location of a hidden reward over short durations or across few possible locations (see Herrmann et al., 2010 for an example).

These differences in chimpanzee and bonobo spatial memory are further highlighted when apes must utilize their spatial memory skills in complex environments that emulate species-typical foraging problems. In one such test, apes saw a human hide ten pieces of food in a large, naturalistic outdoor enclosure; an additional ten pieces had also been hidden while the ape was out of view to control for the apes' ability to detect the food using other skills such as olfaction, rather

than using spatial memory specifically (Rosati and Hare, 2012a). Apes were allowed to search for food after a 20-minute delay, requiring that they use long-term spatial memory abilities rather than short-term memory skills. Infant apes of both species exhibited similar (poor) performance when faced with the sort of problem. However, species differences emerged with age: older chimpanzees exhibited much more targeted searches—recalling the hiding locations of multiple pieces—while older bonobos showed search patterns similar to infants (see Figure 11.1). Importantly, when faced with a second version of the task where apes only had to recall four locations, and were allowed to search immediately after the experimenter hid the food, chimpanzees and bonobos were both quite successful. This shows that the bonobos' poor performance in the first version of the task was not due to a general lack of motivation or a basic unwillingness to search for food in the enclosure but rather due to the difficult memory-specific demands of the task. Overall, these results support the ecological hypothesis: although bonobos also clearly can utilize spatial memory to recall the location for resources in space, chimpanzees exhibit

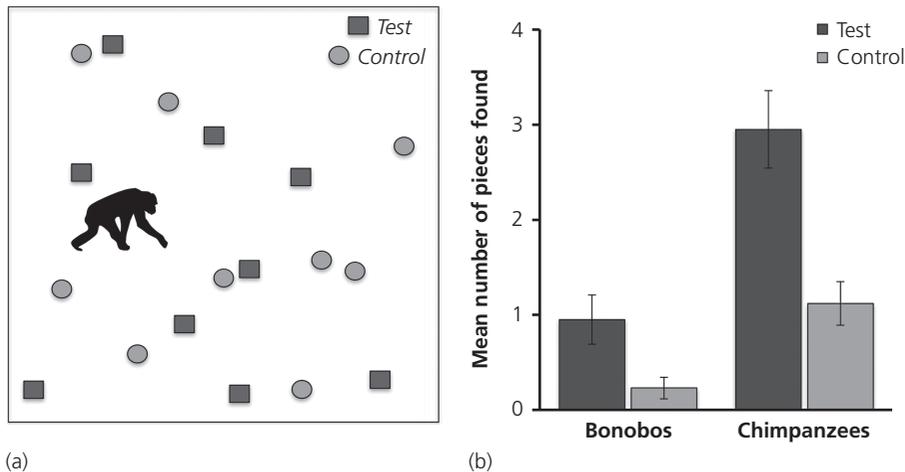


Figure 11.1 Divergence in *Pan* spatial memory. (a) Bonobos and chimpanzees observed food being hidden at ten test locations in a large outdoor arena; another ten pieces had previously been hidden at matched control locations. After a 20-minute delay, apes could search for food. (b) Chimpanzees were more successful than bonobos at retrieving the test pieces they had seen hidden. Adapted from Rosati and Hare (2012). (Divergence en mémoire spatiale. (a) Les bonobos et les chimpanzés ont observé la dissimulation de nourriture dans 10 emplacements dans une grande arène au plein air; 10 autres pièces ont été dissimulées à priori comme contrôle. Après une attente de 20 minutes, les singes pouvaient chercher la nourriture. (b) Les chimpanzés avaient plus de réussite que les bonobos à retrouver les pièces de contrôle. Adapté de Rosati and Hare (2012))

more accurate recall of such locations, especially in complex, naturalistic environments.

Second, patterns of decision-making in bonobos and chimpanzees also diverge in accordance with these ecological predictions. First, studies of intertemporal choice in *Pan* show that chimpanzees are more willing to pay temporal costs to acquire more valuable food rewards (see Rosati, 2017a). For example, in one study, apes were presented with a series of decisions between a smaller reward and a larger reward (Rosati et al., 2007). In this temporal discounting task, bonobos and chimpanzees made choices between a smaller reward that was always available immediately and a larger reward that was available after a delay. The time that apes had to wait to receive the larger reward was systematically adjusted across sessions to determine the delay at which each individual treated the larger and smaller rewards as equivalent. In fact, whereas chimpanzees were willing to wait 2 minutes on average before they switched to preferring the smaller, immediate option, bonobos were willing to wait only around 70 seconds (see Figure 11.2). This basic result—that bonobos are less willing to pay

temporal costs than chimpanzees—has been replicated in different populations of apes using different experimental methods (Rosati and Hare, 2013), suggesting that it is robust to some extent across populations and paradigms.

Third, there is even stronger evidence that bonobos are more risk-averse than chimpanzees when faced with decisions about variability in pay-offs (see Rosati, 2017b). For example, in one comparison, apes chose between two options that differed in the amounts of rewards they provided: a ‘safe’ option reliably provided four pieces of food, whereas a ‘risky’ option offered one or seven pieces with equal probability (Heilbronner et al., 2008). Here, both options provided the same average pay-off (four pieces). They differed only in whether they provided a constant average pay-off or whether the particular outcome of any given decision was associated with variance: apes might receive a high pay-off from the risky option on some trials but a relatively low one on other trials. In fact, bonobos preferred the safe option, whereas chimpanzees preferred the risky option, a difference in preferences that widened as the apes gained more experience with the problem.

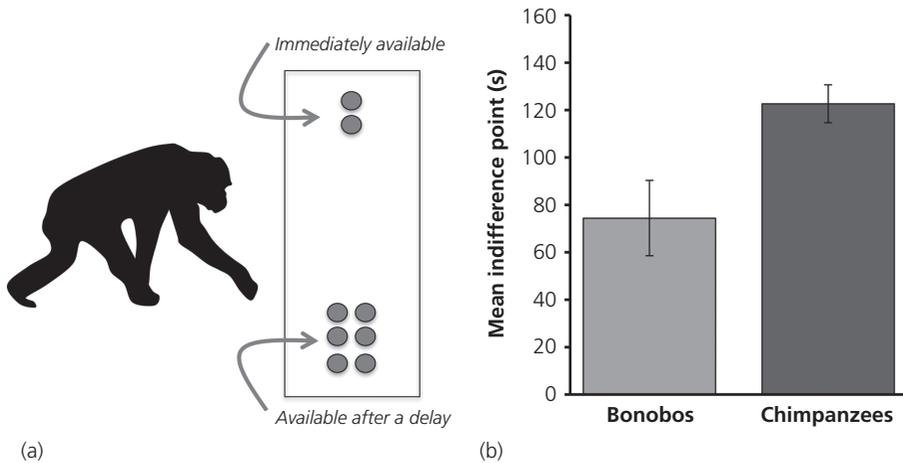


Figure 11.2 Divergence in *Pan* patience. (a) In a temporal discounting task, bonobos and chimpanzees made choices between a smaller reward that was always available immediately, and a larger reward that was available after a delay, in order to determine the how apes made tradeoffs between reward amount and reward delay. (b) Chimpanzees were willing to wait longer for larger reward than bonobos. Adapted from Rosati et al. (2007)

(Divergence en patience. (a) Durant une tâche d’actualisation temporelle, les bonobos et les chimpanzés ont pris des décisions entre une récompense plus petite qui est immédiatement disponible, et une récompense plus grande qui est faite disponible après une attente. L’objectif est comprendre comment les singes décident entre la somme de récompense et l’attente. (b) Les chimpanzés avaient plus de volonté à attendre plus de temps pour les grandes récompenses que les bonobos. Adapté de Rosati et al. (2007))

Other studies have examined apes' more spontaneous reactions to uncertainty using paradigms where animals can infer their chance of winning on a trial-by-trial basis. One example of such a risk paradigm tested how chimpanzees and bonobos make decisions about reward quality, where the risk involved concerned the *type* of food they received rather than the quantity (Rosati and Hare, 2012b; Rosati and Hare, 2013). Here, apes saw an intermediately preferred food type (such as peanuts) placed under one container (the safe option). A second container was baited with either a highly desirable (banana) or less-desirable (cucumber) food: apes initially saw both types but knew that only one had been placed in the container, so this option represented a risky choice (see Figure 11.3). In another inferential paradigm, apes could infer the hiding locations of rewards that were distributed under different containers (Haun et al., 2011). Whereas a smaller reward would be placed under one known container, a larger reward would be placed under one of a whole set of containers. Since the apes did not know which container in that set had the bigger piece of food, a selection of one of these containers similarly represented a risky choice as they might

select an empty container. As in the choice situation involving risk in the amount of food received (e.g., Heilbronner et al., 2008), results from both of these inferential tasks showed that chimpanzees were more willing to gamble on the possibility of receiving the more valuable reward than were bonobos.

Evidence for targeted cognitive divergence in *Pan*

Importantly, this new formulation of the ecological intelligence hypothesis—which focuses on the relationship between ecology and specific domains of cognition rather than on general cognitive abilities—does not predict that chimpanzees and bonobos should differ across all possible cognitive skills. Rather, they should exhibit specific *targeted* differences in cognition related to specific differences in their typical foraging problems. Indeed, chimpanzees and bonobos share many commonalities in their social structure and diets, given that both are frugivores that live in male philopatric societies (Boesch et al., 2002; Kano, 1992; Stanford, 1998). Along these lines, there is increasing evidence that chimpanzees and bonobos show broad

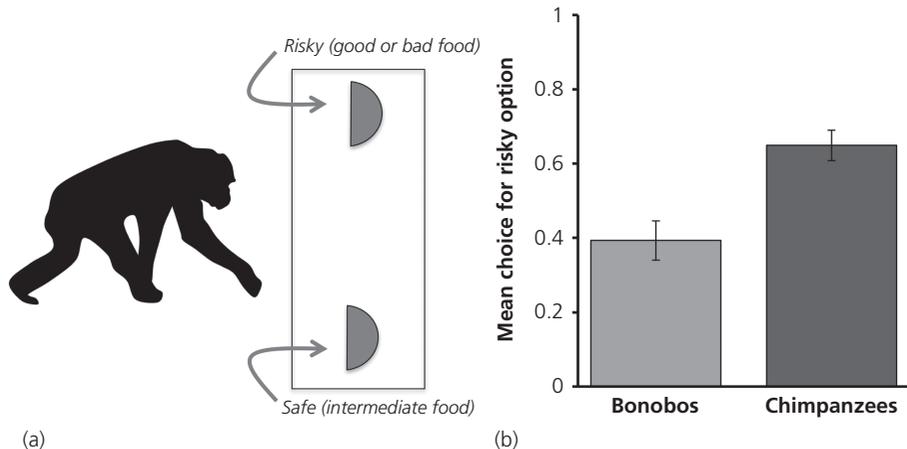


Figure 11.3 Divergence in *Pan* risk preferences. (a) In a risky choice task, bonobos and chimpanzees made choices between a safe bowl that they had seen baited with an intermediately preferred food option, and a risky bowl that they knew contained either a highly preferred food (good outcome) or a non-preferred food type (bad outcome). (b) Chimpanzees preferred to gamble on the possibility of receiving the good food outcome from the risky bowl, whereas bonobos preferred the safe bowl. Adapted from Rosati and Hare (2013).

(Divergence en préférences de risque. (a) Dans une tâche de choix risqués, les bonobos et les chimpanzés ont fait des choix entre un bol sûr qui contient de la nourriture à préférence intermédiaire et un bol risqué avec la nourriture plus préférée (bon résultat) ou la nourriture moins préférée (mauvais résultat). (b) Les chimpanzés ont préféré les bols risqués alors que les bonobos ont préféré le bol sûr. Adapté de Rosati and Hare (2013))

similarities across many cognitive domains unrelated to their socio-ecological differences. For example, when compared in a cognitive test battery probing a variety of cognitive skills—ranging from basic skills like numerical discrimination and simple spatial inferences to social learning and producing communicative gestures—both species show similar performance across many of these contexts (Herrmann et al., 2010; Wobber et al., 2014). This shows that bonobos and chimpanzees share many commonalities in the fundamental cognitive tools they use to think about the world.

Indeed, while chimpanzees and bonobos show robust variation in their decision preferences for risk and time, they do not necessarily show such differences in other decision-making contexts for which there are not strong predictions based on feeding ecology. One such example is preferences for ambiguity, or situations where decision-makers have incomplete or absent knowledge about reward contingencies. Although economists and psychologists tend to link ambiguity preferences with risky choice (Camerer and Weber, 1992), decisions about risk involve known variation, whereas decisions about ambiguity involve unknown variation where the set of potential outcomes is itself unclear. In contrast to the evidence that chimpanzees face greater seasonal variation and engage in risky hunting at higher rates than bonobos, there is no strong ecological prediction for ambiguity biases in these species. That is, there is no reason to suspect that one species has access to more or less knowledge about the resources available in their natural foraging environment, and therefore might be more tolerant of choices that involve ambiguity. In line with this analysis, chimpanzees and bonobos show similar responses to ambiguity in experimental paradigms when their basic risk preferences are first equated (Rosati and Hare, 2011). Similarly, chimpanzees and bonobos show similar responses to framing, where either the positive or negative attributes of potential options are highlighted (Krupenye et al., 2015)—another type of decision bias without a clear ecological prediction.

Other differences in chimpanzee and bonobo cognition further highlight the central importance of foraging behaviors in understanding these species' divergences. As mentioned previously,

foraging almost always involves social interactions in gregarious species, including most primates. Consequently, social behavior and foraging behavior are almost always intertwined in species that must compete (or cooperate) with group mates to acquire food. In fact, chimpanzees and bonobos also differ in cognitive capacities that are relevant to these sorts of social foraging interactions. For example, wild bonobos face relaxed feeding competition compared to chimpanzees, a fact that is intimately related with the differences in patch size and resource distributions in their environments (White, 1989; White and Wrangham, 1988; Wrangham and Peterson, 1996). Accordingly, bonobos are more tolerant of conspecific partners when faced with experimental tests of social feeding (Hare et al., 2007; Wobber et al., 2010). Moreover, given these differences in feeding competition, chimpanzees are likely to require greater levels of inhibitory control in social contexts to control responses that are likely to be undesirable such as snatching a desirable food item out of a conspecific's grasp. In fact, chimpanzees seem to develop more robust social inhibition than bonobos (Wobber et al., 2010). Together, these results further support the hypothesis that these two species exhibit targeted differences for specific set of skills that relate to differences in their wild socio-ecology.

Implications for human evolution

As previously mentioned, the best current model for our last common ancestor's psychology is the living great apes. Although theoretical claims about behavioral and cognitive evolution in humans tend to use chimpanzees alone as a model for the last common ancestor (Wrangham and Pilbeam, 2001), recent research suggests that the last common ancestor may have had a mosaic of chimpanzee-like and bonobo-like traits (Hare and Yamamoto, 2015). This indicates that a true understanding of the origins of human cognition generally, as well as foraging cognition specifically, requires the integration of data on cognitive skills in both bonobos and chimpanzees. Comparative studies of these species can thus provide critical insights into the potential functions of uniquely human cognition (Rosati, in press).

In fact, human feeding ecology differs from that of other great apes in several important ways

that parallel the socioecological differences seen in chimpanzees and bonobos. For example, human hunter-gatherers have larger home ranges than other apes and exhibit a unique pattern of central place foraging where individuals return to a centralized location with food (Hill et al., 2009; Marlowe, 2005). Consequently, humans are more reliant on distant food sources that are more temporally expensive to exploit. This shift in feeding ecology probably poses new problems for humans concerning locating food, navigating between resources, as well as anticipating and planning for future food consumption. These observations suggest that humans may also exhibit targeted differences in evolutionarily relevant skills supporting this human-specific pattern of foraging, such as the memory skills and patience needed to locate widely distributed resources and plan for their exploitation. In fact, humans are thought to develop an increasingly flexible representation of space integrating multiple cues (Hermer-Vazquez et al., 2001, 1999; Newcombe and Huttenlocher, 2006). Moreover, several theorists have argued that humans are uniquely well endowed in our ability to think about and plan for the future (Stevens and Stephens, 2008; Suddendorf and Corballis, 2007).

Similar inferences may be possible for other human decision-making traits as well. I have argued that the differences in risk preferences seen in chimpanzees and bonobos may be accounted for by the relative variability these species experience in the natural environments, with chimpanzees experiencing more variability in pay-offs when foraging than bonobos (both in terms of seasonal variability and hunting). This account is also applicable to humans, as several aspects of human hunter-gatherer foraging behavior have been hypothesized as mechanisms for risk reduction. In particular, strategies such as hunting have variable pay-offs: the majority of hunter-gatherer groups are successful at most only half the time, or at even lower rates (Hawkes et al., 2001; Hill and Hawkes, 1983). In other words, foragers face a food supply that is superabundant on some days but absent on others. Thus, one way for humans to reduce the variability in their resources is to share food with group-mates (Hill and Kaplan, 1993; Kaplan et al., 2012). This suggests that our species' willingness to accept risk

may also be shaped by ecology, much like in apes. Moreover, the function of human risk preferences may actually be closely linked with human social decision-making strategies like reciprocity; sharing or other cooperative behaviors that are thought to depend on some type of reciprocal exchange can be construed as 'risky' in the sense that social partners may not repay those favours. Along these lines, although people are generally risk-averse for monetary rewards, humans show a fairly risk-prone pattern of decision-making when faced with choices about food emulating foraging decisions (Hayden and Platt, 2009), quite similar to chimpanzees when tested on a matched problem (Rosati and Hare, 2016).

Conclusions

I have argued that linking comparative cognitive studies with information on species' natural behavior can begin to address why differences in cognitive traits may evolve. Using bonobos and chimpanzees as models, I showed that even closely related species can exhibit variation in cognitive skills depending on their respective socio-ecological characteristics. *Pan* shows important differences in their wild feeding ecology: whereas chimpanzees depend more on seasonally and temporally variable food resources that are patchily distributed in space, bonobos can exploit more constant, homogeneously distributed foods. Moreover, chimpanzees regularly pay temporal and risk costs to engage in extractive foraging or hunting, whereas bonobos much more rarely (if ever) exhibit these behaviors in the wild. In line with these ecological differences, bonobos and chimpanzees show a suite of targeted divergences in their foraging cognition: bonobos exhibit less accurate spatial memory, reduced patience and increased risk aversion compared to chimpanzees. These differences in cognitive capacities seem to be targeted, as *Pan* does not exhibit general divergences in cognition across the board but rather shows changes in skills specifically related to their respective socioecological niche. Overall, these findings suggest that studying bonobo cognition in tandem with that of chimpanzees can provide important insights both into the mechanisms of

cognitive evolution as well as our understanding of human evolutionary history.

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