

Review



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# Balancing costs and benefits in primates: ecological and palaeoanthropological views

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Maintaining the balance between costs and benefits is challenging for species living in complex and dynamic socio-ecological environments, such as primates, but also crucial for shaping life history, reproductive and feeding strategies. Indeed, individuals must decide to invest time and energy to obtain food, services and partners, with little direct feedback on the success of their investments. Whereas decision-making relies heavily upon cognition in humans, the extent to which it also involves cognition in other species, based on their environmental constraints, has remained a challenging question. Building mental representations relating behaviours and their long-term outcome could be critical for other primates, but there are actually very little data relating cognition to real socio-ecological challenges in extant and extinct primates. Here, we review available data illustrating how specific cognitive processes enable(d) modern primates and extinct hominins to manage multiple resources (e.g. food, partners) and to organize their behaviour in space and time, both at the individual and at the group level. We particularly focus on how they overcome fluctuating and competing demands, and select courses of action corresponding to the best possible packages of potential costs and benefits in reproductive and foraging contexts.

This article is part of the theme issue ‘Existence and prevalence of economic behaviours among non-human primates’.

## 1. Introduction

Understanding the balance between costs and benefits is a central research goal of economists, behavioural ecologists and palaeoanthropologists. By analogy with economic markets, ‘biological markets’ refers to the exchange of commodities (e.g. food resources and services such as, for example, grooming) between individuals belonging (or not) to the same species [1]. In that frame, individuals choose among a number of potential partners or between resources of differing values based on their expected net benefits (e.g. feeding or reproductive benefits in terms of energy input or fitness advantage), given their expected costs (e.g. distance travelled and energy expenditure to reach the partner or the resource, and the associated risks and dangers). The exchange of commodities is determined by the law of supply and demand, and depends upon intrinsic (e.g. physiology) and extrinsic (e.g. environmental, social) factors [2,3]. But beyond the analogy with financial markets, one can wonder what are the behavioural strategies and the actual mechanisms involved in decisions in animals.

For all animal species, decision-making implies identifying the best course of action given all the available alternatives, to optimize the costs and the benefits linked to a particular behaviour in a particular context. But the

underlying mechanisms regulating decision-making could take a variety of forms, ranging from a set of simple behaviours such as reflexes to critical environmental events (stimuli) to high-level cognitive representations of potential actions and their consequences. All species display reflexes that enable them to avoid predators or potentially costly actions, and to approach potential sources of food or sexual partners [4]. These reflexes are thought to have evolved in order to provide optimal behavioural responses in relatively stable socio-environments, in which they could be sufficient to enable approaching an optimal trade-off between costs and benefits. But, such stereotyped behavioural responses would probably not be sufficient for species living in complex and rapidly changing socio-environments. For such species, actions are most probably also controlled by executive processes, which enable individuals to organize their behaviour in space and time. By contrast with reflexes, these behaviours [5] are modulated by a cognitive representation of the goal, which includes the outcome value.

In humans, it is generally accepted that decision-making involves computing the value of distinct options using cognitive processes, and the resulting choice consists in maximizing the benefits/costs ratio [6,7]. These processes include computing the options' value, episodic representation and memory (i.e. the ability to recall specific events in the past), long-term planning (i.e. the capacity to mentally envisage its own needs in the future, and to act now to maximize the chance that they can be met), executive control (i.e. a flexible and goal-dependent control of behaviour, overriding reflexive responses) and transitive inferences (i.e. a form of deductive reasoning allowing derivation of a relation between items that have not been explicitly compared before) [6–10]. But the extent to which other species use such cognitive processes remains unclear (e.g. [11–14]). Moreover, understanding the variability of the cognitive processes that are mobilized across species showing distinct socio-ecological features still remains a challenging issue.

Several elements suggest that primates (both modern and extinct species) are good models for understanding the variability in the cognitive processes associated with decision-making over a long time frame. Indeed, since most primate species live in complex socio-environments, behaviours related to foraging, socializing and reproduction all involve complex decisions contingent on the environmental context [15], where potential costs and benefits include numerous parameters. Moreover, as long-lived animals, primates (especially gregarious species) have to deal with long-lasting social interactions that can incur delayed benefits and require evaluating other individuals over a long time. Indeed, when competing or cooperating with one other, social animals must make rapid, adaptive decisions based not only on the current behaviour of their social partner or competitor, but also on the history of their past interactions with those individuals and those individuals' allies and kin [16]. Thus, at least at this general level, the socio-ecological system appears complex enough to require cognitive processes, which provide the behavioural flexibility that enables primates to respond optimally to rapidly changing constraints. Thereby, natural selection should be favouring species/individuals that possess the cognitive skills allowing them to flexibly adapt to changing environments and to make rapid decisions about when/whether to forage/mate/socialize and with whom.

Our aim here is to provide concrete elements of behavioural ecology and palaeoanthropology supporting the idea that several primate species could use cognitive skills to make complex decisions, needed to overcome specific socio-ecological challenges. In our conceptual frame, the relative development of these cognitive processes across species should be directly related to the nature and the extent of socio-ecological challenges. Thus, rather than trying to examine directly the expression of cognitive processes across hominins and other primates, we will consider some of the socio-ecological conditions that might require these processes, and will use a comparative approach to discuss the extent to which different primate species (both modern and extinct) could rely upon cognitive processes, rather than reflexes, to make decisions about the ratio between costs (e.g. energy expenditure, dangers, risks) and benefits (in terms of food, services and sexual partners).

We will consider the cost–benefit perspective of a range of behaviours relevant to hominins and other primates living in different socio-ecological contexts that could promote or constrain the occurrence of these economic behaviours. We will tackle this complex regulation of costs and benefits at two levels, at the individual level (i.e. individual decisions based on the sensory environment and individual characteristics) and the collective level (i.e. decisions made by a group of individuals that increase their beneficial outcome relative to acting alone (cooperation) or could result in unbalanced costs/benefits (competition)). For this, we will present the possible cognitive and physiological mechanisms (neural and endocrine) involved in two detailed examples of economic strategies, from actual and extinct populations, used to balance costs and benefits at the individual level in the context of reproduction (e.g. mating decisions) and at the collective level in the context of foraging (e.g. hunting). With this review paper, we aim at illustrating the complexity and diversity that can be found in the primate order when making adaptive decisions related to the optimization of benefits and costs.

## 2. Balancing costs and benefits at the individual level—reproductive strategies and mating decisions

Differential costs/benefits trade-offs should lead individuals to allocate their time, energy and effort to activities in ways that increase their fitness, so that they evolved conditional strategies guided by environmental cues. In the case of sexual activities, mating strategies involve multiple behavioural tactics, i.e. specific actions in which individuals will engage when pursuing a given strategy. These strategies will influence how and when individuals select mates, the proportion of time and energy they invest in those activities (versus others like foraging) and how much mating effort and parental effort they expend. In those particular cases (mating versus foraging; parenting versus mating effort), the two 'commodities' can be considered as two options, for which both availability and value fluctuate in time. These two options are particularly in competition in species where conception peaks occur during periods of high fruit availability (e.g. sifakas (*Propithecus* spp.); orangutans (*Pongo* spp.) [17]) or where mating is strictly seasonal (e.g. Japanese macaques (*Macaca fuscata*) [18]; Assamese macaques

(*Macaca assamensis*) [19]), which means that if an individual fails to mate during one mating season, its reproduction is delayed by an entire year (i.e. a greater impact on fitness than in non-seasonal species). By analogy with food, for which value depends (negatively) upon availability [20], we expect an influence of females' availability and monopolization on males' mating decisions and an influence of the operational sex ratio (i.e. the ratio of the number of fertile adult males to the number of potentially fertile females in a group at a given time) on the choosiness of females on the mating market. Moreover, rewards are devalued by the costs of waiting or physical energy necessary to obtain them [21], such that the amount of time and/or energy spent in the search of a(nother) partner, together with the increased predation risks during searches and investment in the assessment of the potential partners, imply a significant amount of effort that individuals must make in order to mate.

This has two critical implications: individuals should choose mates not only based on their potential benefits, such as high reproductive quality and dominance status, but also based on potential costs (delay, effort, etc.). Individuals should thus be able to dynamically and flexibly integrate information about these potential benefits and costs and generate an appropriate decision rule. Given the complexity of social interactions in primates, a significant part of this information implies high-level cognitive representations because it is not directly explicit [6,7,22]. For example, choices should be based on the recognition of other individuals' relative dominance ranks and social relationships, but also on the nature and quality of recent interactions, the value of particular partners and perhaps even other individuals' intentions [23]. Thus, it seems that mating decisions are unlikely limited to reflexes to simple stimuli and presumably involve cognitive processes. In laboratory settings, the exertion of cognitive control (to overcome reflexes and obtain a more costly but more favourable reward) implies a specific set of prefrontal cortical structures including the dorso-lateral prefrontal cortex and the anterior cingulate cortex [8–10]. Thus, it is likely that the relative development of these brain structures across species scales with the amount of cognitive control associated with mating. Testing this hypothesis would require comparing the relative size of these brain regions across species characterized by distinct levels of mating-associated costs. For example, these structures should be more developed in species for which breeding is seasonal, since seasonality implies more temporal constraints on the general organization of behaviour. Along the same lines, these structures should be more developed in species displaying costly behaviours, i.e. paying short-term costs to allow a long-term benefit for reproduction (e.g. mate guarding, see below). Indeed, paying immediate costs for later benefits (delay discounting, typically) is known to require cognitive control and prefrontal cortex activation in laboratory settings [8–10]. But beyond these general principles that apply to both sexes, each sex must make rapid and adaptive mating decisions depending on the specific constraints that it faces.

### (a) The perspective of males

Primate males constantly need to make mating decisions, which implies mitigating the costs associated with mating activities (e.g. physiological and physical costs: intra-sexual competition and associated aggressions, increased vigilance,

altered travel and grouping patterns, chronic stress and reduced feeding time or efficiency, mate guarding [24–27]) and increasing the benefits (i.e. achieving a higher reproductive success). Male mating tactics in general, and mate guarding decisions in particular, vary in both costs and benefits and are influenced by individual features, such as competitive ability or energetic status, and by contextual factors, such as reproductive seasonality, the number and quality of sexually available females, the number of competitors and food availability [28]. Thereby, males of seasonal breeding species can most likely afford to engage fully in stressful intra-sexual competition and female guarding over a short period of time without facing the high risk of exposure to chronic stress. By contrast, males of species with unpredictable timing of reproduction are more likely to face long-term exposure to physiological stress and may thus have evolved an 'incomplete female monopolization strategy' in order to limit this cost [29]. In cases where ecological pressures are very high (territory defence, predation [19]), i.e. making the male unable to guard females effectively, mate guarding behaviours can even be totally absent. Moreover, a high female cycle synchrony will limit the possibility of mate guarding and mating all females during a short period of time, just as the male's sensory abilities to discriminate the timing of ovulation within a cycle (e.g. [18,30]) or the reproductive potential of a female will affect mate guarding activity and mating success. Food availability is also expected to influence the decisions to engage or not in costly mate guarding behaviours. In a context where males trade-off feeding time against vigilance time (which is energetically demanding and stressful, since mental effort is costly [8–10]) to monitor females, it is also expected that males would make the decision to favour energetic needs over mate guarding investment in periods of food shortage (e.g. [31]), in order to prevent an exposure to chronic energetic stress. Finally, rank is also known to influence mate guarding behaviours, and in a context where the alpha male monopolizes females, a balanced decision-making for subordinate males would consist of either using sneaky copulations (which presumably involves metacognitive processes) or giving up copulations during the ovulation window until opportunities of mating increase again (which are probably associated with a decrease in fertilization success).

The underlying physiological mechanisms regulating male socio-sexual behaviours, and particularly mate guarding behaviours, seem to involve temporal fluctuations in androgen levels, with the 'challenge hypothesis' being broadly used to conceptualize those relationships [32,33]. For instance, it has been shown that, in a breeding context, androgen levels increased during consortships (e.g. savannah baboons (*Papio cynocephalus*) [34]; chacma baboons (*Papio ursinus*) [35]), in the presence of fertile females (white-faced capuchins (*Cebus capucinus*) [36]; chimpanzees (*Pan troglodytes*) [37]), and correlated positively with the occurrence of mate guarding behaviour (e.g. savannah baboons [34]; long-tailed macaques (*Macaca fascicularis*) [38]). Moreover, a revision of the 'challenge hypothesis' predicts a stronger androgen response to challenges associated with high fitness benefits [39], which is the case for mate guarding, which has been shown to significantly increase male reproductive success in a number of primate species, especially for high-ranking individuals (rhesus macaques (*Macaca mulatta*) [40]; long-tailed macaques [41]; Japanese macaques

[42]; mandrills (*Mandrillus sphinx*) [43]). This is particularly true in species where there is a high level of monopolization of females (e.g. chimpanzees, savannah baboons, mandrills, long-tailed macaques, white-faced capuchins [36,41,43]), i.e. species in which being a high-ranking male provides a substantial reproductive advantage and in which, as a consequence, males challenge other males to achieve high ranks. In this case, individual males may further optimize their competitive abilities by raising their androgen levels (which facilitates the expression of aggressive behaviours [44] and enhances muscle performance) above those of their conspecifics only when the reproductive benefits of doing so are high enough and outweigh the potential costs of elevated androgen concentrations (e.g. physiological costs such as the downregulation of immune function, increase in metabolic rates, energetic costs and increased predation risk [33]). Elevated androgen levels during mate guarding might also be beneficial as they enhance males' abilities to monitor females, increase the efficiency of vigilance [29] and help in sustaining directed attention [44]. Finally, an increase in androgens promotes sperm production [25], which in turn enhances the chance for the mate-guarding male to fertilize the guarded female. Collectively, it seems that elevated androgen levels during mate guarding increase the fitness benefits derived from this behaviour, but these benefits will also depend on the quality of mating opportunities available, i.e. on female reproductive and social value (strength of female-male bonding) and on females' mating preferences (see below).

Males are predicted to allocate their mating effort towards the most valuable females, with males preferentially mating with high-ranking and/or parous females (that have a better access to food resources and often produce more offspring and offspring of better quality [45,46]) (e.g. long-tailed macaques [31]; chimpanzees [47]; mandrills [48]; savannah baboons [49]; Japanese macaques [18]). In some species, males also exhibit mating preferences towards females with whom they have strong social bonds (see below, 'friendships'), independent of female rank, parity or fertility status (e.g. savannah baboons [49]; rhesus macaques [50]; Japanese macaques [51]). Besides biasing their mate choice towards certain females, males of several species also seem to modulate their investment according to the likelihood of ovulation/conception (long-tailed macaques [52]; chacma baboons [53]; Japanese macaques [18]; mandrills [43]; white-faced capuchins [36]). The concentration of mating effort to the time when fertilization is most probable might be a way of conserving energy and limiting energy expenditure, especially in species where there are frequent ejaculations, which are costly to produce [54]. However, the question of whether males do act in a manner indicating that they have the ability to make mating choices based on ovulatory/conceptive probabilities still remains to be investigated. Similarly, whether male primates have the cognitive abilities to track the fertility status of several females simultaneously while mate guarding remains to be explored. This also leads to questions about what explicit cues males might be using to track female reproductive status, and to what extent they rely upon mental representations (rather than explicit cues) to infer the female reproductive value. Moreover, even if physiological changes (e.g. hormonal levels) are likely influencing mating decisions, the relative influence of these physiological processes on reflexes versus cognitive processes also remains an open question.

In conclusion, males continuously adjust their mating decisions to maximize the benefits versus the costs. The more these decisions rely upon integrating a multitude of socio-ecological factors, the more they should rely upon cognitive functions, which enable flexible planning and overcome reflexes to simple stimuli.

### (b) The perspective of females

As discussed above, evolution should favour male mating decisions such that those decisions bring benefits at both proximate (reduced costs of mating activity) and ultimate (higher reproductive value) levels. This also, and even more, applies to females, because they are usually the sex that bears higher reproductive costs [55], and hence they should be more selective in their mating decisions. Moreover, because female primates have slow life histories, have long investment periods and produce relatively few offspring, mate selectivity is expected to be relatively high in this order [56], but with higher sexual dimorphism and higher reproductive skew leading to a decreased role for female mate choice (e.g. greater scope for direct female choice in rhesus macaques versus mandrills). Female mating decisions are indeed constrained by male aggression and sexual coercion ([57]: forced copulation, harassment (repeated attempts to copulate inducing eventual female submission), intimidation (physical punishment of female refusals to mate increasing the likelihood of matings in the future) and mate guarding), especially in male-dominant species such as baboons or chimpanzees. Sexual coercion is often a long-term strategy that achieves its goal by manipulating the future, rather than simply the immediate behaviour of the victim [58]. Such coercion imposes costs on females, in terms of energy spent to escape from males and in terms of increased physiological stress [59]. Trading these costs implies that females will compete for mate quality (and/or number) or for other benefits, such as protection or increased access to resources [60]. Such a scenario may be particularly relevant if sexual (e.g. 'good quality' mates) and non-sexual (e.g. food, social benefits) resources are limited.

Females can mate promiscuously, allowing sperm competition and/or cryptic female choice to operate (review in [54]). Alternatively, females may exert choice for mate directly by mating selectively. Females can also follow a mixed strategy of promiscuity and selective mating (i.e. mating with multiple males throughout their mating period but with different mating rates between males during the fertile period). The proportion of promiscuous and selective mating undertaken by a female within a mating period is most likely shaped by trade-offs between costs and benefits (see [61] for discussion). Thereby, if females can discriminate males based on heritable traits conferring benefits to offspring, then females will be expected to mate exclusively with the best males. However, if these advantageous and heritable traits are associated with the males' sperm, it is unlikely that females will identify individual males' quality and, in this context, females are predicted to mate promiscuously so that sperm from various males will compete for fertilization, with possible benefits such as a reduced risk of infertility, increased protection of offspring against predators, increased investment to offspring by multiple males and genetic diversity.

When females exert direct (i.e. precopulatory) choice, male traits that females might select for in a mate are

dominance rank, unfamiliarity (for avoidance of infanticide or inbreeding), and sexual ornaments and weapons (badges of status [25]). Female choice of high-ranking males is predicted, for example, in species when there is a risk of male infanticide (e.g. chimpanzees), with the high-ranking male being able to provide the best defence of the offspring. However, in species vulnerable to infanticide, unbiased promiscuity (and longer receptive period) could also act as a counterstrategy to confuse paternity [62] and protect the offspring.

Besides social rank, females can also base their mating decisions on sexually dimorphic male ornaments, such as the red face and genital sex skin in mandrills and Japanese macaques, the cheek flanges of orangutans (*Pongo* spp.), enlarged noses of proboscis monkeys (*Nasalis larvatus*), etc. (see [25]). Some of these testosterone-dependent traits (e.g. nose size in proboscis monkeys [63], face redness in mandrills [64], darkness of chest stain in sifakas [65]) have been suggested to serve as advertisements to females in their mate selection and to influence female preferences, with females preferring for instance redder/darker males (rhesus macaques [66]; mandrills [67]). Using such traits could enable mating decisions to be achieved by reflexes, but since these decisions also involve several social components, cognitive processes are likely to play to enable efficient decisions.

Females might also select a male based on the bonds they have created with him, also called 'friendships' (i.e. close spatial proximity, frequent affiliative behaviour and low rates of aggression between males and non-fertile or lactating females [49,68]). These strong ties have been reported in a number of cercopithecine primates (e.g. olive baboons (*Papio anubis*) [69]; Barbary macaques (*Macaca sylvanus*) [70]; Assamese macaques [71]). These male–female bonds may represent a form of male parenting effort enhancing the survival of females' progeny. Indeed, females will get direct benefits such as protection of their offspring against harassment by other females (yellow baboons [72]), offspring care and access to food resources. These female benefits can be of particularly high value in species in which feticide and/or infanticide are important sources of mortality (e.g. chacma baboons [73]; yellow baboons [74]), but also in species in which infanticide is rare, as males may protect both mothers and infants from predation or non-lethal harassment by conspecifics [68,72]. A recent study in olive baboons also showed that females' ties to the sires of their current infants often persisted after they resumed cycling, which suggested that males may continue to provide benefits after infants' weaning [75]. For the male friend, the benefits that can be obtained could consist of (i) using his friend's offspring as a buffer against attacks from other males, (ii) receiving grooming, which confers both health and social benefits and could be traded (as a commodity in biological markets [76]) in exchange for itself or for other services, (iii) increasing his attractiveness as a mate and gaining additional matings (presently or in the future) with other females that observe his behaviour [77], and (iv) in some cases, having higher chances of copulating with his friend and siring the friend's next offspring when she will resume cycling ('care-then-mate' hypothesis proposing that close ties between males and females represent a form of male mating effort [70,75]; but see also [71,72]: ties to lactating females did not predict male consort success or the probability of siring the female's next infant). This last case (iv) assumes that females prefer to mate with males that

behave benevolently towards them and their current offspring; it also assumes that females can express active mate choice, i.e. that it is limited to species in which the extent of male reproductive skew is low (e.g. olive baboons). This means that individuals may choose whom to mate with based on benefits they got in the recent past or expect to get from this behaviour. This also means that males can identify their own offspring with some degree of accuracy (i.e. paternal kin recognition). Thereby, a male's decisions to form a friendship with a particular mother–infant dyad could be based on phenotype-matching or behavioural proxies that are reliably associated with paternity [78], such as the mating history or more generally the strength of the relationship with the female around the time of conception to gauge the probability of his paternity ([79, p. 1007]: 'males may benefit by investing preferentially in those infants that they are most likely to have fathered'). However, friendships also incur some opportunity costs for males, in that it may reduce the current likelihood of mating with other females. Moreover, favours are not immediately traded but are rather based on long-term equitability that may, in fact, be violated in favour of one partner over short periods, but which is tolerated by the other partner by virtue of the long-term benefits. Therefore, males should make decisions about pursuing or giving up friendships, taking into account the costs associated with those aborted mating opportunities while representing putative long-term benefits associated with potential future copulations with his female friend.

At the physiological level, the underlying mechanisms regulating female socio-sexual behaviours involve glucocorticoid hormones (since having a male friend could buffer lactating females from the stress associated with heightened infanticide) and temporal fluctuations in oestradiol and progesterone levels, with oestradiol enhancing sexual behaviour and progesterone having inhibitory effects [25]. In strepsirhines, there is a behavioural oestrus period around ovulation to which mating is restricted, with a strict hormonal control. In haplorhines, sexual receptivity (female's willingness to accept the male's mounts and to facilitate intromission and ejaculation during copulation) is no longer under strict hormonal control and mating may occur throughout the cycle. The extent to which variation in sexual hormone levels will be associated with female proceptivity (i.e. active male solicitations), receptivity and attractivity (i.e. female's value as a sexual stimulus) will vary across species and across social contexts [18]. In nearly all species, sexual behaviours increase in the periovulatory period relative to the non-fertile periods of the cycle, though the magnitude of this change may be subtle or dramatic. Nevertheless, even if the female ability to mate is no longer under hormonal control, her desire and then her decision to mate can be an important regulator of sexual behaviour, with females being able to exhibit more flexible responses to social and environmental contexts. For instance, copulations outside of the fertile period (and even during pregnancy, i.e. when there is no chance of conceiving) can be viewed as part of female sexual strategies to confuse paternity [80]. These post-conceptive sexual behaviours are expected to occur more often in species vulnerable to infanticide (e.g. Hanuman langurs, chimpanzees) than in species with low infanticide risks and/or living in harsh environments (e.g. Japanese macaques). In this latter species, females could indeed benefit from stopping copulations during pregnancy in order to avoid wasting energy on non-reproductive

mating, decrease male harassment and free resources to allocate to fetal growth (and not to mating costs). For males, giving up copulation during pregnancy could also provide some benefits, as they do not waste energy in sperm production or in active mate guarding of pregnant females.

The cognitive mechanisms underlying partner choice and socio-sexual behaviours might often be complex. First, even if females could use reflexes based on sexually dimorphic male ornaments, the critical influence of social interactions on female reproductive success strongly suggests that they would not be sufficient to provide a reliable estimate of the costs and benefits associated with their potential choices. Second, even if hormonal changes are associated with mating behaviour, female primates probably need to mobilize complex and context-dependent mental representation of the social and reproductive value of their potential partners to selectively interact and plan their mating/association decisions, as we saw above for males. These processes involve a myriad of brain regions, and their implication in complex social interactions has raised a strong interest in recent years [22,81]. However, there remain gaps in our understanding of the cerebral bases underlying social/sexual partner choice and the questions of (i) the level of cognitive complexity required to track previous exchanges with partners and compare simultaneously the relative value of the different benefits provided by each potential partner, and (ii) whether all primates possess these enhanced cognitive skills, for instance, in terms of memory and ability to quantify, remain to be clarified and represent a critical but challenging avenue for future research in natural settings (as tested in the laboratory with ad hoc cognitive tasks).

### (c) What about human and extinct hominin mating markets?

When it comes to humans and extinct hominins, the question of how cultural variation will affect 'biological' and 'economic' partner choice necessarily emerges. As in most non-human primates, mating markets in humans are influenced by environmental factors and are characterized by both sexes exerting preferences and having several partners to choose from simultaneously. Women make trade-offs between male genetic quality and parental investment and men adjust their mating tactics to the behaviour of women [82]. Thereby, in an environment requiring biparental care where male parenting qualities are needed and valued, women would place more weight on the investment potential of prospective mates and less weight on indicators of their genetic fitness, with a larger proportion of women adopting long-term mating tactics almost exclusively. In response to this, males should devote greater effort to parental investment and variance in men's reproductive success should be reduced. On the other hand, in an environment where men's genetic fitness is more needed and valued (e.g. pathogen-prevalent environment), women should be more willing to engage in short-term matings, and consequently, men should devote greater effort to short-term and extra-pair mating. Indeed, women could benefit from polyandry under certain circumstances [83] and there is some evidence showing that the range of variation in extra-pair paternity across human populations is substantially greater than previously thought [84]. In some contexts, men may be choosing to provide care for non-biological children as part

of the duties of social fatherhood in return for greater security for their own children or the benefits of strong male alliances [85]. Other examples in which women adjust their mating tactics come from studies focusing on women's control of resources (see review in [82]). Thereby, women's ability to accumulate wealth in modern cash economies could be less important than their access to power in the adjustment of their mating strategies [86,87], which can mirror the influence that social hierarchy can have on mating tactics in non-human primate societies. Nevertheless, as adding wealth is likely to have direct reproductive benefits, i.e. increased fertility and reduced mortality of mother and child [88], economic considerations still play an important role in human partner choice for both sexes.

Regarding extinct hominins, it is difficult to have a comprehensive picture of their mating systems and to infer mating behaviours and mate choices because they do not leave direct evidence in the fossil record. However, anatomical (e.g. sexual dimorphism) and cultural (e.g. stone artefacts) markers of life history and behavioural patterns can help to infer the social structure and/or mate choice of some extinct hominin species.

Sexual dimorphism, and especially canine height dimorphism, is often used to infer extinct hominin mating system (e.g. [89]). Among mammals, a low level of sexual dimorphism is often associated with monogamy, which increases the coalitionary power of females in relation to unrelated males (e.g. [90]). Moreover, polygyny is suggested to have emerged with the Australopithecines and may have been due to enhanced male mate guarding of a small number of partners within multi-male/multi-female social groups [91]. However, a study on *Ardipithecus ramidus* (4.4 Ma) [92] and statistical models of *Australopithecus afarensis* (3.8–3.1 Ma) sexual dimorphism [93] showed that these species had reduced sexual dimorphism and canine height. These findings suggest a strong decrease in the intensity of male–male competition and that these species already had a monogamous mating system. This transition to strong pair-bonding could have opened a path to higher male parental investment [94]. For *Homo erectus sensu lato*, two models have been proposed to explain their social organization, which could be then used to infer their mating system. The first one [95] proposes that the emergence of multi-level societies with male and female bonding [90] (observed in extant hamadryas baboons for example) could have characterized this taxon. According to this model, multi-level societies in extinct hominins would have increased benefits for both sexes in terms of reproduction, feeding and protection of the offspring. Indeed, bonds between females would have been highly beneficial, as they would have allowed some cooperative foraging and breeding, which can decrease the individual costs [96,97]. Regarding males, the variable spatial distribution of female *H. erectus* at least seasonally may have placed selective pressures on them to become the resident or the alpha male of small groups [94] and to keep track of a limited number of females to facilitate mating access. The benefit to males is an exclusive access to mates and a better chance to obtain female sexual fidelity and paternity certainty. Moreover, the fact that the male stays in the group carries benefits for both sexes via protection from infanticide. An alternative model, the large fission–fusion society [80], has been proposed for *H. erectus*, assuming that this species was living in chimpanzee-like fission–fusion groups, with immigrant females

and a large number of bonded males. Fissions represent an opportunity to flexibly adjust behaviours and to recalibrate the trade-offs that individuals experience by living in groups. For instance, females are suggested to spread out when resources become scarce in order to reduce feeding competition, but when food is abundant they can forage together and aggregate, which could bring some benefits in terms of food access and ultimately reproductive advantages. Willems & van Schaik [98] also suggested that *H. erectus* lived in very large groups with many males, which gives the opportunity to cooperatively defend the group against carnivore predators, and could be beneficial for both sexes.

If sexual dimorphism has been often used to infer hominin mating system, it was also shown that facial dimorphism can be an indicator of mate choice. Indeed, according to several studies [99–101], the facial features and facial symmetry are major targets of selective mate choice. Thereby, females with child-like faces would be more attractive to males, whereas males with high cheekbones or strong jaws, which are testosterone-dependent features, would be preferred for copulation [100]. Like in other primates (see the above section (§2b) on female perspectives), it seems that female hominin mating decisions could have been linked to sexual dimorphic ornaments. As enlarged cheekbones are linked to attractiveness in humans (e.g. [102]), Weston *et al.* [103] proposed that the evolution of a broad face (e.g. zygomatic region) and the loss of large canines in hominin males result from sexual selection operating mainly through mate choice. Besides morphological targets of selective mate choice, Kohn & Mithen [104] have proposed that Acheulean handaxes, i.e. stone manufactured artefacts, which were found during the Pleistocene (first occurrence at 1.76 Ma) and often associated with *H. erectus sensu lato*, could be considered as sexual ornaments and reliable indicators of a potential mate's quality that females could have used to make their mating decisions.

In conclusion, like in extant primates, different social and mating systems have been proposed depending on the hominin taxa. As for extant primates, male and female hominins presumably relied upon cognitive operations to make appropriate mating decisions, rather than upon reflexes. Indeed, these decisions probably involved complex and context-dependent mental representations of the reproductive and social value of their partners. This implies abilities in terms of decision-making and planning, which were likely highly developed in extinct hominins, presumably at an intermediate level between modern monkeys and humans, and sharing some similarities with modern apes. Indeed, such processes involve some regions of the prefrontal cortex (e.g. frontal pole, dorsal prefrontal cortex) that are characterized by an exceptional expansion in both human and great apes, with the origin of this enlargement being estimated at the root of great apes (19–15 Ma) [105].

### 3. Balancing costs and benefits at the collective level—meat resources and hunting

#### (a) Meat resources and hunting in extant non-human primates

According to the 'optimal foraging theory' [106], animals should optimize their energetic balance while foraging, i.e. maximize benefits (energy intakes) and minimize costs

(time costs and energy expenditure for accessing or manipulating food). It is generally accepted that virtually all primates engage cognitive operations to approach maximum foraging efficiency [107,108]. Indeed, given the distribution of their food in space and time, they could not rely on simple rules (e.g. random search) or reflexes (e.g. approach food). Primate foraging strategies depend upon species (e.g. energy maximizers or time minimizers) and individuals (based on their needs, age, reproductive state, etc. [109]), but also upon social factors such as intra-group, inter-group or inter-species competition and predation [110,111]. To optimize their energetic balance (see review in [112]) while dealing with the inherent competition with co-feeders, primates must flexibly and rapidly adjust their foraging strategies, which is thought to involve cognitive processes [112]. Following Garber *et al.* [111], primates would integrate both social and ecological information with a set of 'decision rules', i.e. information being organized hierarchically with the most important information for that decision being given the largest weight. For example, species living in large social groups should be particularly sensitive to information about quantity, whereas species with a specialist diet would be particularly sensitive to information about food type. Comparatively, spatial and temporal information might have less weight on decisions. These decision rules should thus be characteristic of a given species, but will also depend on individual variables (e.g. social rank, sex, age) and their changes over time. The complexity of the set of rules, together with the level of metacognitive control with which these rules are supervised and potentially adjusted online, should be closely associated with the level of cognitive sophistication, and potentially with the level of brain development of each animal.

In specific foraging contexts such as social predation (hunting in group), specific cognitive skills such as metacognition, traditionally associated with complex social interactions (e.g. theory of mind), presumably play a crucial role [14]. Indeed, social hunting, which is developed only in a few primate lineages such as chimpanzees, capuchins and hominins, requires that multiple individuals synchronize their moves or coordinate in space (see [113] to distinguish between various kinds of social hunting: synchrony, coordination and collaboration), with the prey generally being shared after successful capture. Hunting is mainly pursued by males, but even if the likelihood and success rate of social hunts generally increase with the number of male participants in most chimpanzee and capuchin populations, there is no clear tendency regarding the meat obtained *per capita* when the number of hunters increases [80], i.e. the individual benefits. One can, therefore, wonder what drives the individual decisions to engage in social hunting, what are the trade-offs involved in such decision-making processes, and why social hunting (with food transfer) evolved in so few of the meat-eating primate species.

There has been much debate over the putative social benefits of hunting [114–116], with social hunting being more frequent in male-bonded species, which creates the tolerance and trust allowing social capture and selective transfer with allies. In this context, social hunts could be a major way to cement social bonds, and then to positively affect individuals' fitness [22]. However, the social value of hunting could also rely upon the nutritional value of the meat [117], i.e. energy-rich diet, with meat being used as an exchange commodity or reward. Most research indeed suggests that meat

is a concentrated source of vitamins, minerals and other essential micronutrients that are beneficial for an individual, even in small quantities [118,119]. In chimpanzees, for example, the valuable micronutrients contained in meat [117,120] could complement a predominantly plant-based diet, with a small amount of meat representing a favourable payoff. Moreover, the proteins from vertebrates tend to be of higher quality, owing to favourable ratios of essential amino acids relative to plant foods [121]. For all these reasons, if the likelihood of obtaining meat increases with the number of hunters, then social predation would be nutritionally profitable.

Nevertheless, hunting is also costly and dangerous. Indeed, the chase of a fast and arboreal prey is arguably energetically expensive [118], and entails considerable risk, in terms of failure, falling and injury [113,122]. Moreover, consuming and processing raw meat can be time costly [123], as the gut of non-human primates, which is adapted to a primarily frugivorous and folivorous diet, may not be very efficient in this context. Thus, feeding on meat can be considered as 'high-risk, high-yield', with primates facing the packaging problem, which is, as described by Altmann [124, p. 615], the fact that 'Costs and benefits—good and bad—always come packaged together ... No perfect food exists'. According to the 'optimal foraging theory', hunting primates should, therefore, feed on prey that offer the highest ratio of benefits/costs, which depends upon various intrinsic, demographic and environmental conditions. These conditions include: (i) seasonality: hunting may not be optimal when other valuable and less costly items are present, e.g. fruit availability affects overall meat distribution and more individuals receive a share of the meat with decreasing levels of general fruit availability [125]; (ii) opportunity: a hunt is more likely to succeed if many adult males are present; (iii) individuals' energetic condition: individuals having a positive energy balance are more willing to target resources associated with high risk and high cost, which is typically the case for meat [122]. These several constraints, among others, could explain differences in hunting behaviours, frequencies, success rates and prey preferences (i.e. species, size), not only across primate species, but also across communities from the same species, and across individuals within a group. Regarding the differences between species, it seems that baboons [126] and bonobos (see references in [127]) hunt only occasionally, mainly because of the absence of strong male–male bonds in these species, even though some bonobo populations have been reported to consume meat at much higher rates than previously thought [127]. There are also differences across communities from the same species [128], with some possible socially transmitted differences in prey preferences (chimpanzees: [129]).

At the group level, some sex differences have been reported in hunting behaviours and in the costs and benefits of hunting. Indeed, females are expected to be more risk-averse than males for two reasons. First, they should be more sensitive to food shortage because variation in female reproductive success is determined more by food access than by access to mates [55]. Second, females are often carrying young offspring, which incurs higher movement costs [130] and may reduce their ability to catch prey. It seems, therefore, that the hunting strategy followed by female non-human primates is similar to the ones used by women in hunter–gatherer populations, who typically target small and sedentary prey. Even if this strategy implies less

energetic benefits, it also entails a reduction in risk (less exposure to predators and potential falls) and in the probability of failure [131].

Besides sex differences, the overall size of the group can also explain some differences, i.e. there is more hunting in larger groups, with the hunting costs per hunter being expected to decrease as the number of hunters increases because it becomes more difficult for the prey to either escape or defend themselves [132]. Some individual behavioural tendencies have also been proposed to explain variation in hunting patterns within (and between) populations (and species), but also temporal variation in hunting frequency within groups [120]. Therefore, the fact that more hunting occurs in larger groups in chimpanzees can be partly explained by the presence of 'impact hunters' [133], i.e. individuals with high hunting rates, the presence of which in a group makes hunting more likely both by their own efforts and by increasing the likelihood that others hunt. As shown by Gavrilets [134], those that contribute the most towards production of collective goods (i.e. hunt initiators) are those (i) that are particularly skilled, or (ii) for whom the benefits are especially high, or (iii) for whom the costs are relatively low. They also create low-cost opportunities for others to benefit by joining a hunt in progress [120].

The mechanisms underlying these joint acts might be relatively complex. Gaze-following (i.e. orienting attention in the same direction as another individual) and joint attention could be critical for coordinating actions among hunters, and as discussed above, cognitive processes including metacognition and theory of mind are probably involved to support complex and dynamic interactions among individuals [81,14,135]. Besides coordination, group hunting presumably also implies planning, which is thought to be critical not only for hunting *per se* but also for hunt patrols, i.e. pre-hunt searches for prey (highly coordinated activities, during which individuals travel cohesively, with frequent pauses, and rarely forage or vocalize [125]). Indeed, these patrols, which usually indicate an upcoming hunt, are initiated hours prior to hunt attempts, which implies not only planning but also coordination among future hunters [113,136].

At the neurophysiological level, hunting behaviours could imply the oxytocinergic system. Indeed, joint actions activate areas of the brain associated with the processing of reward, and these behaviours are facilitated by oxytocin [22]. Several studies also showed that oxytocin could enhance cooperation and coordination in joint group activities, such as hunting parties [125,137,138]. However, it remains unclear whether oxytocin acts directly on coordination (i.e. relatively high-level processes) or indirectly, on lower-level processes such as tolerance or vigilance, which are also critical for participation in joint group activities. The neural circuits mediating the behavioural and cognitive actions of oxytocin also remain unclear. At the cortical level, hunting presumably involves a myriad of structures since it implies numerous levels of behavioural and cognitive control. As discussed above, these cognitive processes include: (i) planning and working memory (known to rely upon the dorso-lateral prefrontal cortex and the parietal cortex [9]); (ii) context-dependent representation of the goal value (known to rely upon the ventromedial prefrontal cortex [6,7]); (iii) cognitive control and the computation of the costs/benefits trade-off (known to involve the anterior part of the cingulate cortex



[10,139]); and (iv) a form of metacognition to allow coordination and planning at the group level [135,140]. Further work is necessary to accurately identify the neurocognitive processes underlying group hunting in primates. Besides classical laboratory approaches with captive animals performing specific cooperative tasks mimicking social hunting that would allow dissection of these processes very precisely, neuroanatomical comparisons across species in which the behavioural and ecological components of hunting have been well identified (as in [141] for foraging behaviours in general) could also shed light upon the neurocognitive bases of group hunting.

## (b) Meat resources and hunting in humans and extinct hominins

Understanding the relative benefits and costs of acquiring and consuming different forms of animal matter by extant non-human primates is also critical for identifying the selective pressures responsible for increased meat consumption in the hominin lineage.

Meat has been exploited by hominins for at least 2 Myr using at the beginning confrontational scavenging by driving large carnivores from their prey. Hominins, especially after 2 Ma (e.g. *H. erectus sensu lato*), had a small gut, which is required to efficiently process food of low digestibility, such as meat [142]. The energetic content of meat is suggested to have critically influenced the evolution and the maintenance of birth rate, body size and brain size (e.g. [142–144]) and costly activities such as endurance running.

One step further may have involved the use of processing methods, such as pounding (e.g. [145]), which has occurred since the lower Pleistocene (around 2 Ma) and even earlier at 3.3 Ma. This could have provided an important increase in energy gain over unprocessed raw diets. Lithic tool-kits may have been highly beneficial in allowing extinct hominins to have access to fleshed carcasses, with cutting edges for processing soft tissue, which was not possible with their masticatory apparatus (reduced prognathism and relatively small incisors and canines), as well as percussion tools to extract the marrow. If the first archaeological evidence of stone-tool-making [146] and stone-tool-using [147] is dated to 3.4–3.3 Ma, the tool-kits grew in terms of complexity after 2.3 Ma. Plio-Pleistocene hominins used stone cutting tools for pre-oral food processing, which require collecting raw material and extracting flakes bearing sharp cutting edges from raw material, and then probable remarkable cognitive and motor abilities. Through time, there was an increase in raw material transportation distance in order to find the most efficient material, and an intensification of processing of animal tissues including meat and marrow extraction. These processes probably involved an increase in the level of decision-making and planning. But eating scavenged meat could also be highly dangerous, as the carrion could have been contaminated by bacteria. However, this cost could have been reduced by selecting only the marrow (where fewer bacteria grow), by eating the freshly killed carcass or by cooking it [148].

Cooking, initially very occasional, using, for example, hot springs, could have occurred with *H. erectus* in Africa (ca 1.9 Ma) [149]. However, the oldest evidence of intensive and habitual cooking, based on archaeological evidence and reinforced by genetic analyses, is from the Middle

Pleistocene (400 000–300 000 years ago), suggesting that this behaviour is relatively recent (e.g. [150]), i.e. human adaptation to a cooked diet had begun before the split between modern humans, Neanderthals and Denisovians (at least 275 000 years ago) [151]. Cooking facilitates the mastication, kills food pathogens, and induces a rise in the energetic gain of the meat, including an increased energy extraction per unit mass compared with raw food and increased digestibility value of proteins, a reduction in the costs of digestion and a modification in the speed of meat protein digestion (e.g. [152–154]). It also raises glutamate and sugar availability, appreciated by primates (e.g. humans, and also chimpanzees and gorillas), which seem to prefer cooked food to raw food in captivity) [155,156]. Cooking also induces amino acid residue level modifications which contribute to advantageous traits in a food product (e.g. formation of peptides which are resistant to further breakdown into free amino acids by digestive enzymes; [157]). However, the adoption of cooking also comes with some costs in terms of loss of vitamins (e.g. vitamin C) and of delay before the consumption of the food, which has to be brought to the processing area or stored.

The control of fire for cooking, but also for boiling and smoking the foods to preserve them, was firstly evidenced 790 000 years ago in the Near East and 450 000 years in Europe [158]. This control is beneficial as it provides light, heat, and protection against predators, and comes with technical progress (e.g. preparation of resins or improvement of knapping capacities of certain raw materials or hardening of wooden spears). But, the control of fire is also cognitively demanding because it requires a considerable amount of knowledge about the environment, ranging from the collection of fuel (choice of wood, bones, plants, minerals, stones, etc.), to the implementation of the fireplace (stone structure, dug pit, location, orientation, etc.), to its lighting and maintenance.

Cooperative (i.e. social) hunting using exhaustion pursuit occurred quite early in hominin evolution (lower Pleistocene, around 1.8 Ma). According to van Schaik [80], the model of fusion–fission proposed for *H. erectus sensu lato* could explain the origin of cooperative hunting followed by the sexual division of labour. Moreover, the morphological features associated with endurance running in early *Homo* have been suggested to enable them to practise persistence (long-distance pursuit) hunting, i.e. chasing an animal until it reaches exhaustion, potentially during the hottest time of the day, thus driving prey into hyperthermia [159–161]. However, chasing prey for extended periods of time in hot temperatures is also obviously energetically demanding, and could have represented a substantial energetic cost in early *Homo*, even for chasing medium-sized prey [162]. Therefore, persistence hunting is obviously critical for the cost/benefit balance, and cooperative strategies associated with persistence hunting might have greatly reduced the costs encountered at an individual level.

The costs and benefits of cooperative hunting could have differed depending on the size of the game. Hunting small and fast game (birds, leporids) had low risk of injury and could have provided some fur (which can be used for clothing by hominins in high latitudes during cold seasons) and some raw material for ornaments (e.g. eagle bones). However, it provided a small amount of meat per prey. Hunting big game could have been energetically more expensive with high risk of injury and risk of failure, but the amount of meat to share

could have been considerable. Cooperative big game hunting may necessitate an organization of the work force to plan how to acquire large animals and bring them back to the camp, with this cooperation reducing the risk of failure. Complex forms of cooperative hunting using weapons (e.g. wooden spears, throwing sticks), which require advanced planning in terms of manufacture and use, emerged around 300 ka [163]. When weapons systems allowed prey to be hunted from a long distance, the risk of injury was reduced and the role of women as hunters increased [164]. According to Kuhn & Stiner [164], Neanderthal females and juveniles participated in the hunting of large terrestrial game. Neanderthals were faced with the dilemma of improving the extractable benefits (with the participation of women or old juveniles in hunting) and minimizing the survival risk to their offspring due to the danger.

In modern hunter–gatherer populations, hunting is also conducted in groups, which implies a regulation of costs and benefits at the population level. In most cases, the meat of large animals is widely shared with a meat-to-meat repayment. The cost of sharing is quite low, since the amount of meat is greater than what each hunter and his family can eat at one time. Sharing also reduces the cost of storing such a large amount of meat, which could quickly get spoiled. At the population level, the benefits of repayment are quite high as it reduces the probability of meat shortfalls for individuals. However, this type of meat-to-meat transfer is not found in all hunter–gatherer populations, with hunters in Hadza populations (organized in bands with no governing hierarchy [165]) being instead repaid in currency other than foods (i.e. other goods or services). In these populations, the carcass is more like a public good and the hunters do not control its distribution. Therefore, the hunter has no family provisioning insurance and this does not reduce his daily risk of failing to supply food to his household. Nevertheless, it has been shown that even if hunters do not get more meat repayment for their own families, they acquire a better hunting reputation, enhance their status as desirable neighbours [165], and have some reproductive benefits, i.e. higher fertility and reproductive success (e.g. [166]).

Meat consumption and hunting, therefore, lead to major evolutionary changes in the hominin diet and subsistence behaviour. They serve a social as well as a nutritional purpose, with hunting being an indicator of leadership qualities for early human groups but also for extant primates. There is a great diversity in hunting behaviours across primate and extinct hominin species, but also across communities of the same non-human primate species, or across hunter–gatherer populations (e.g. division of labour in some of them but not in all). Though extant primates and extinct hominins present some similarities for meat acquisition, there are still some differences, notably in terms of the size of the prey and in terms of the processes used to acquire meat. Through time, meat has been exploited by hominins first by confrontational scavenging, followed by cooperative hunting using exhaustion pursuit, and ultimately by a more complex form of cooperative hunting using weapons, with a division of labour in the most recent populations. Regarding extant primates, confrontational scavenging has been rarely reported [167] and social hunting seems to be less frequent than in the hominin lineage. The complex form of cooperative hunting with weapons and the division of labour, as well as processing techniques (e.g. pounding and cooking), appear

to be unique to hominins, and could have allowed them to maximize the ratio of benefits/costs of this foraging strategy.

As we saw above for extant primates, social/cooperative hunting most probably implies well-developed metacognitive skills, and early hominins, like modern humans and chimpanzees, were very likely to possess such skills. Like social hunting, stone-tool-making and cooking (only in hominins) imply a very high level of planning and metacognition because they require complex causal inferences and very distant and indirect benefits. Indeed, cooking implies multiple steps that need to be coordinated and such complex goals are thought to involve high-level recursive planning. Likewise, manufacturing stone tools (unique to hominins) implies building a representation of the tool (the direct goal) as well as a higher representation of how the tool would be used, i.e. in a very distinct context and time frame compared with its manufacture.

#### 4. Conclusion

Extant primates (including humans) and extinct hominins are suggested to show some behavioural plasticity that enables them to respond optimally to rapidly changing environments. Natural selection has favoured individuals that are equipped with the cognitive canvas to make efficient decisions about the management of multiple resources (e.g. food, services, partners), both at the individual and at the group level, in order to regulate the balance between the costs and benefits for accessing the goal (e.g. mating with a chosen partner, hunting a prey). In most situations, costs and benefits come together as ‘packages’ such that, rather than trying to maximize the cost/benefit ratio in the absolute sense, most primates presumably use cognitive skills to identify the best of the potential packages, given the context. Nevertheless, these packages do not come as discrete independent options. Rather, in their natural environment, primates must coordinate multiple needs and potential plans of actions, and manage a constant flux of information from the environment. Moreover, like other long-lived species, they need to navigate a social world in which they must base their decisions not only on the current behaviours of the other group-members, but also on the history of their previous interactions with those individuals. This implies recognition of not only other individuals’ relative rank and social relationships, but also the nature and quality of recent interactions and the value of particular partners. Thereby, they have probably developed a set of cognitive skills (e.g. episodic memory, value-based decision-making, planning) to make adaptive decisions, such as choosing partners based on the expected benefits (based on past and ongoing interactions) they could provide, and selecting options that fulfil not only individual needs but also collective needs (e.g. hunting and meat transfer) that should allow supplying of future individual needs. Evidence from the archaeological and fossil record suggests that, early in the evolutionary history of primates, selection should have favoured the development of cognitive mechanisms that shaped these economic behaviours. These evolutionary developments were further refined across hominins and enabled them to handle packages of increasing costs and benefits. Distinct extinct hominins and extant primate species developed specific sets of solutions based on their needs and environmental constraints as well as opportunities, and more studies are still needed to shed light on the complexity and

diversity that can be found in primates making adaptive decisions related to the optimization of benefits and costs.

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