Journal of Archaeological Science 185 (2026) 106441

Contents lists available at ScienceDirect

Journal of Archaeological Science

journal homepage: www.elsevier.com/locate/jas

Social and emotional cognition in Pleistocene hominin evolution: The role of biocultural processes

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ARTICLE INFO

Keywords:
Cognitive evolution
Social cognition
Emotional cognition
Biocultural
Hominin niche
Human mind

ABSTRACT

Patterns and processes of social cognition underlie much of the behavioral and ecological flexibility and adaptive capacity that characterizes the primate order. The hominin lineage emerged from a branch of primates, hominoids, particularly reliant on the navigation of complex intra and inter-group social relations as a central dynamic of their niche. Over the past few decades much research on hominin evolution has resituated focus from explaining the uniqueness of the big-brain, hyper-social, cognitively distinct *Homo sapiens*, to a broader inquiry into the potential process, pathways, and dynamics of the evolution of a hominin niche, or niches, rooted in increasingly complex social cognition. In this essay we review key aspects of this current paradigm and argue for the expanded inclusion of the possibilities of socio-emotional cognition in a biocultural approach as advantageous in developing a more robust descriptive framework for theory and method in the study of human evolution. We combine several sources and examples to highlight specific theoretical approaches to assist in developing a common and more integrative framework for investigating social and emotional cognition as a key component of the biocultural niche in Pleistocene hominins.

1. Introduction

For primates, the patterns and processes of social cognition underlie much of the behavioral and ecological flexibility and adaptive capacity that characterizes the order (Cheney and Seyfarth, 2008; Tomasello and Call, 1997; Van Schaik, 2015). The hominin lineage emerged from a branch of primates, the hominoids, particularly reliant on the navigation of complex intra and inter-group social relations as a central dynamic of their niche (Malone et al., 2012; Van Schaik, 2015). *Homo sapiens*, often heralded as the pinnacle of social cognition and its concomitant neurobiological complexity, is recently understood to be less distinct in our cognitive capacities relative to other hominins (at least in their material correlates), especially in the later Pleistocene. Over the past few decades new discoveries, advances in analyses, and restructuring of perspectives on human evolution have resituated inquiry away from trying to explain the uniqueness of the big-brain, hyper-social, cognitively distinct *Homo sapiens*, to a broader inquiry into the potential process, pathways, and dynamics of the evolution of a hominin niche (or niches), rooted in increasingly complex and multifarious social cognition. In this essay, we review key aspects of this current paradigm and argue for the inclusion of socio-emotional cognition (see Table 1) and an explicitly biocultural approach as beneficial in developing a more robust descriptive framework for the study of human evolution—in terms of both theory and methodology— in the 21st century.

2. Pleistocene hominin niches: a central role for social and emotional cognition

A niche is the structural, ecological, temporal, and social context in which a species exists (Wake et al., 2009). Paleoanthropologists and archaeologists endeavor to reconstruct and analyze Pleistocene hominin niches, as best as possible, via the examination of spatial, structural,

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This article is part of a special issue entitled: The Mind in Deep Time published in Journal of Archaeological Science.

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https://doi.org/10.1016/j.jas.2025.106441
Received 8 March 2025; Received in revised form 4 November 2025; Accepted 22 November 2025

Table 1
Core Definitions: social and emotional cognition.

Social cognition	Conscious and subconscious perception, interpretation, and response to social information, signals, actions, and contexts.
Emotional cognition	Emotional self-awareness as a cognitive process. Feeling and regulating emotions such as empathy, being able to recognize these emotions in others (emotional discernment), integrating emotions into short and long term decision-making, and thinking through the emotional effects of behaviours on oneself and others in the long term.
Emotional regulation	Capacity to regulate emotion in behavioral and cognitive contexts
Emotional self-awareness	Ability to recognize emotions as they occur and be able to reflect on them as an initial requirement to be able to assess their effects on one's body and relationships

climatological, nutritional, and other physical factors. These factors were experienced by hominins, and were restructured by hominin actions, as well as by competitors, collaborators, and other agents in a shared environment (e.g. Fuentes 2015, Lala(nd) and O'Brien, 2011, O'Brien and Lala(nd), 2012). Behavior and concomitant cognitive dynamics may leave little fossil or material trace. Still, researchers increasingly recognize the centrality of social relations, social behavior, and social cognition in hominin lives and in the processes of hominin evolution (e.g. papers in Gamble and Porr, 2005; Gamble et al., 2011).

Due to the widespread recognition of the core role of social relations/behavior in the hominin niche, proposals for human evolution often center on hypotheses and models for increased and/or more complex modes of social collaboration (e.g. Burkart et al., 2009, Gamble et al., 2011; Hrdy, 2009, 2024; O'Brien and Lala(nd), 2012). In many of these cases, 'social collaboration' often implies strategic/analytical collaboration between social partners or group mates. However, emotionally based collaboration with a major role for empathic relations between individuals (and groups) is also a possibility (Hrdy and Burkart, 2020; Burkart and Southgate, 2025). While the details of the presence, roles and impacts of empathic relations and skillsets are debated across many other animal lineages, primates are often reported to rely heavily on emotional relations and humans are explicitly recognized as organisms wherein empathic skills are central to successful sociality and group cohesion (Adriaense et al., 2020; Decety, 2015, De Waal and Preston, 2017). It may be that for humans empathic relations via a form of emotional cognition are a key mechanism or process equally, if not more, effective than collaboration based on reason/logic. Emotional cognition, in humans, involves emotional self-awareness– the feeling and regulating (bringing into rational thought) of emotions such as empathy, being able to recognize these emotions in others with whom alliances are formed (emotional discernment), and thinking through the effects of behaviors on oneself and others in the long term. We suggest that such emotionally based social collaboration becomes more significant, particularly after two million years ago, in some hominin lineages.

The genus *Homo* includes diverse species and lineages that underwent different patterns of morphological change during the Pleistocene. Other hominin genera also existed during the Early Pleistocene, including *Australopithecus* and *Paranthropus,* and likewise diversified prior to their subsequent extinctions. Such morphological diversification strongly implicates various behavioral correlates, from diet and locomotion to habitat preferences, range sizes, group sizes, and life history strategies. The dynamics of social lives matter immensely in understanding the behavioral and cognitive shifts that may be less easily measurable yet are of central interest in developing coherent theoretical framings of human evolution. The last 500,000 years of the Pleistocene are particularly notable for the emergence of what one can term "core patterns" of contemporary human niche dynamics (Galway-Witham et al., 2019; French, 2021; Kissel and Fuentes, 2021; Scerri and Will, 2023). These patterns emerge across a range of times and places during this span and are evidenced by greater complexity of the material record and greater connectivity as shown by geographic distributions of artifact types, raw material transport, and shared behavioral patterns. The behavioral and social dynamics of the genus *Homo* came to include hyper-cooperation and complexity in parenting, lengthy childhood development, intricate and diverse foraging and hunting patterns, novel and dynamic material and symbolic cultures, increased intensity and diversity of care for conspecifics, and complex communication and information sharing within and between groups (Bogin et al., 2014; Hrdy, 2024; Galway-Witham et al., 2019; Kissel and Fuentes, 2021; Malafouris, 2013; Ocobock and Lacy, 2024; Rosenberg, 2021; Scerri and Will, 2023; Spikins et al., 2019).

The centrality of distinctive social, semiotic, and cognitive processes in human evolutionary histories suggests that increased attention to social and emotional relations and processes, including their cognitive dynamics, can enhance understanding of the hominin and human story. Over the past 30 years, paradigms and analytic approaches in the disciplines engaging most directly with human evolution have changed substantially, expanding the toolkit for assessing behavioral processes. The evolutionary sciences are amid a substantive expansion in theoretical diversity and foci including the Extended Evolutionary Synthesis, feminist science, De-colonial and Indigenous approaches, etc., (e.g. Ackermann et al., 2025; Lala et al., 2024; Levis et al., 2024; Schroeder and Ackermann, 2023). Simultaneously, theoretical framing in human evolutionary studies has explicitly acknowledged the complex and central roles of social learning via cultural processes (Boyd et al., 2011; Boyd and Richerson, 2024). This diversity of frameworks is reframing some inquiry into the processes and patterns of hominin and human evolution, enabling perspectives that can enhance those approaches to human evolution that are grounded in the material facets of paleoanthropology and archaeology.

Previously central views such as a human cognitive revolution (Mithen, 1996; Klein, 1999), the assumption of the gradual evolution of a fixed package of "modern human behavior" (McBrearty and Brooks, 2000), or even something that can be effectively defined as "modern human" in the archaeological record are being discarded (Athreya and Hopkins, 2021; Kissel and Fuentes, 2021). Such framings are being replaced by a growing recognition that social and emotional relations are key elements in the hominin and human niches and that modelling/reconstructing the cognitive processes involved are of substantive interest. For example, Hrdy and Burkart (2022) argue that by 2 million years ago, slowed developmental processes combined with social selection was facilitating the emergence of cognitive and emotional phenotypes in hominins that were different from those of the Last Common Ancestors with chimpanzees and other apes. They argue for an "emotional modernity" paving the way for anatomical modernity. While we reject the term (and concept) "modernity" as a marker of cognitive (or anatomical) processes, we do recognize what the term "emotional modernity" delineates: that the capacities to gauge other's thoughts and feelings develops into a more sophisticated understanding/perception facilitating a shared intentionality (Burkart et al., 2009; Tomasello, 1999) and greater capacities for intersubjective sharing (Tomasello and Carpenter, 2007) and that this appears to have played a central role in the human lineage. A key challenge to this approach is that much of it is based on comparative work with living primates and contemporary humans, and its subsequent extrapolation to hominin behavior/processes. However, it is also the case that the archaeological record itself, those materials created, altered and left by earlier humans and other hominins, can also offer insight into these evolutionary dynamics and facilitate analysis of the social, the cognitive, and the emotional. Given the current archaeological evidence of, for example, complex childcare and other caretaking, mortuary behavior, ochre use and other forms of meaning-making, long-distance transport and/or exchange of materials, and dynamic social relations between groups and between taxa, it appears that complex social cognitive dynamics are present earlier in the Pleistocene than previously thought (Shea, 2011; Scerri et al., 2018; Sterelny and Hiscock, 2014; Kissel and Fuentes, 2021; Spikins et al., 2021; French, 2021; Zollikofer et al., 2024). This offers a rich context for examining the role of social relations/behavior, and as we'll demonstrate here, a pattern of socio-emotional cognition, in the hominin niche.

Many Pleistocene hominins, not considered to be the same taxa as *Homo sapiens*, such as Neanderthals, Denisovans, *Homo naledi,* and even *Homo erectus* exhibited more cognitively complex behavior than previously assumed. That this variation is not necessarily tied directly to the often-assumed hallmark of cognition, brain size, also suggests the need for an enhanced focus on social and emotional cognitive capacities and processes in the hominin niche. Considering the current state of knowledge in the study of Pleistocene hominin evolution, we argue that framing inquiry into, and models of, human evolution more profoundly around the understanding and manifestations of social and emotional cognition in a biocultural context offers a particularly powerful toolkit.

We offer three key facets as central to this proposal.

a) Pleistocene hominin evolution should be understood as a biocultural process,
b) A focus on "rational" cognition and technical problem solving may impede recognition of the underlying social and emotional basis of hominin cognition,
c) Social relations and emotional cognition—and their material correlates— are likely salient targets for evolutionary inquiry into Pleistocene hominins.

In support of these assertions, we discuss elements of the archaeological and fossil records that offer insight into evolutionary dynamics and their connections to social relations and emotional cognition, including overlaps and commonalities between *Homo sapiens*, Neanderthals, *H. naledi*, and others as evidence of socio-emotional cognitive dynamics in the later Pleistocene hominin niche.

3. Pleistocene hominin evolution is best understood as a process

While there is little debate that much of the Pleistocene hominin record can be described as biocultural (Colagè and d'Errico, 2020, 2025, Galway-Witham et al., 2019; Slimak et al., 2024; Scerri and Will, 2023), there remains the need to clarify and augment methodological and theoretical details of such approaches when engaging the deep past. A biocultural research paradigm views the biological and cultural as dialectically and inextricably intertwined in the hominin niche, explicitly emphasizing the dynamic interaction between individuals, groups, and their larger social, cultural, and physical contexts (Fuentes, 2015, 2016; O'Brien and Bentley, 2021; Prince-Buitenhuys and Bartelink, 2020; Zuckerman and Martin, 2016). To be human is a process and, as Ingold (2004) reminds us, it is a process involving a constant state of becoming; the human interface with the world is always relational, biological, and social, simultaneously. Most agree that this intertwining of the biological and cultural did not appear de-novo in contemporary humans and thus one can expect that such dynamics reside deep in our evolutionary history. Pleistocene hominin bodies and physiologies were not only shaped by direct selection created by specific ecological challenges but also by the things that those hominins created, the affordances they constructed in their habitats, and the relationships they maintained with other individuals and groups. It is thus misguided to see cultural perceptions and social and emotional experience as disentangled from biological form and function, even when we have limited access to the lives, and bodies, of the past humans, and hominins, that constitute the targets of our inquiry (Speth, 2022a, 2022b).

The underpinnings of the framework we highlight here include two understandings of the scope and distribution of "culture". First, culture is not unique to humans and many animals have culture (Whiten, 2021). However, the phylogenetic continuity of culture in humans and our relatives does not negate the recognition that human culture in its contemporary instantiation is hyper-complex and multimodal relative to most other animal cultures. Contemporary human culture is perceptual, material and behavioral and shared across space and time. It is symbolic, linguistic, dynamic, experienced both communally and individually, perceptually and materially. Human culture has rules and organizations, interlaced with patterns of social constraint and facilitation and multifarious structures and processes that have specific histories, inherited ecologies, and institutions. This differentiates it, in complexity and structure, from the cultures of other animals.

Second, there are ongoing debates in the anthropological literature about what culture is and how one should or should not use the term. For the purposes of thinking with biocultural processes in the Pleistocene, a shorthand definition of "culture" can focus upon its practical aspects as follows: "the quantifiable, inferable, or otherwise assessable ways in which hominins/humans engaged with, perceived, constructed, shared, and generally participated in the world" (Fuentes, 2016, S18). Culture is not a social, material, historical, and perceptual veneer laid over a basal set of physiological capabilities and biological structures. It is, rather, an integrative dynamic entwining bodies, behaviors, ecologies, and histories (see Fuentes et al., in press). There is little doubt that hominin experiences and actions were developed, constrained and afforded by behavior, material technologies, social and demographic behavioral contexts, ecologies, physiologies, evolutionary histories, and more.

Because in human evolution the biological and cultural are not distinct (Boyd et al., 2011, Colagè and d'Errico, 2025; Marks, 2015), an integrative approach offers a suite of theoretical and methodological approaches that enable understanding of the interactions of biological and sociocultural modes across individual, group, and community levels. For a system examined with a biocultural approach, these various elements are co-constitutive, with no necessary hierarchy of value or relevance of either biological or sociocultural dynamics. This approach opens more effective consideration of the ways that behaviors interface with what we can know about the biology, ecological contexts and niche dynamics of the sites, populations, individuals that comprise the available material evidence (Fuentes, 2015, 2016; Kim and Kissel, 2018; Lacy and Ocobock, 2023; Wragg-Sykes, 2020). Such an approach offers an operational frame within which to examine the entangled patterns and processes at play in hominins/humans who evolved in, shaped, and are shaped by complex, dynamic, and very social niches.

Key to a biocultural approach to the understanding of increased social cognition (and related to the frame of emotional cognition we offer below) is the central proposal for a focus on relationships between cooperative reproduction and increased socio-emotional cognition (Hrdy and Burkart, 2022). However, it is worth noting that there is some contention about whether the terms "cooperative reproduction" (e.g. Burkart, Hrdy and van Schalk 2009) or "biocultural reproduction" (e.g. Bogin et al., 2014; Fuentes, 2025) are the better frames for thinking with the human lineage. The two are a bit different, with the biocultural reproduction framework not wholly derived from systems modeled as continuous with other primates (such as cooperative breeding tamarins and closer phylogenetic but non-cooperative breeding chimpanzees) and potentially having a slightly different dynamic regarding the development of the physiological and behavioral processes involved (e. g. Burkart et al., 2025). For example, current human family systems are clearly complex and not necessarily solely emergent from adaptations for child-rearing/care-talking (Kramer, 2021; Sear, 2015; Fuentes, 2025). In fact, there is evidence that complex cooperation and the ground work for the kind of emotional cognition we lay out preceded solid evidence of massive encephalization and slowed developmental dynamics in *Homo* and may have in fact been a necessary precursor to facilitate the extensive multi-individual/multi-role caretaking that evolves in the human lineage (Burkart et al., 2025; Fuentes, 2017a; Kuzawa et al., 2014; Rosenberg, 2021). It is argued that the general social and physiological context of cooperative caretaking (Burkart et al., 2009; Hrdy and Burkart, 2022; Cerrito and Burkart, 2023) and/or allocare dynamics (Cerrito and DeCasien, 2021) may have facilitated the augmenting of social and emotional cognition in the human lineage. But it might also be worth considering that the dynamics of increasingly complex social and emotional cooperation across many facets of hominin life may be relevant as a core evolutionary stimulus and/or response to aspects of social and emotional cognition that emerged before or simultaneously with cooperative/biocultural caretaking. We do not deny in any way the important role of the caretaking of young in the hominin lineages, and in human evolution, but we do offer the possibility that it might not be the explanatory lynchpin or primary prerequisite for the emergence of increasingly complex cognition related to empathic skillsets and social relations.

4. More than rational cognition in hominin evolution

Cognition is a key aspect of biocultural dynamics, and social and emotional cognition played a central role in the lives and adaptive dynamics of Pleistocene hominins (for definitions see Table 1). The hominin niche is always socially mediated and social cognition is key in navigating it. Humans do not live as individuals outside of social groups, at least not for long or typically. Earlier hominins were not different in this respect. Interaction with other individuals in temporally and spatially dynamic social relationships is the primary mode by which Pleistocene hominins interfaced with their ecologies.

Despite this, modeling of past hominin behavior has commonly assumed an optimality framework. Within this framework, individuals rationally seek to minimize costs or risks while maximizing fitness or return rates. This perspective has been applied in contexts as varied as foraging decisions, raw material acquisition, locomotor energetics, mating, and life history. But actual hominins rarely, if ever, engaged with evolutionarily relevant challenges outside of a cultural network of social and emotional relations. Foraging, transport, mating, child-rearing, and other behaviors are learned socially and require flexible coordination and signaling, for which emotional cognition is essential. Pleistocene hominin behavior was contingent on a variety of social/emotional relationships, preexisting and newly developed, that gave rise to a set of shared knowledge and behavioral practices (culture) that facilitated the niche interfaces of individuals, groups, and larger communities. Approaches to studying and modeling Pleistocene hominin evolution can take these features as their starting point and central theme (e.g. Colagè and d'Errico, 2020; Fuentes 2017b; Henrich, 2015; Spikins, 2022).

Social and ecological relations are ongoing processes that can be coopted for problem solving but in and of themselves have not been "developed for" or need be constantly attuned to such ends. Social relations are a core part of the hominin niche since before the hominins diverged from other hominoids in the Miocene (Burkart et al., 2009; Malone et al., 2012) and should be seen as a core niche process as opposed to an adaptive solution to specific challenges. While social cognition may help individuals and groups arrive at more optimal or functional solutions to many problems, social cognition is not necessarily algorithmic in the optimal or functional sense. Trying to model agency or cognition with algorithms has severe limitations and is often futile (e.g. Jaeger et al., 2024). This means that reconstructions and analyses of social cognition, and the relations and behavior it manifests, need not primarily focus on optimality striving or direct functional explanations. Because of the social landscapes and the social relations that constitute the hominin niche, inquiry into cognitive dynamics across the Pleistocene should onboard the reality that social relations are mediated, facilitated, and impacted by emotional signaling, and these are not always tied to direct functional or fitness enhancing outcomes. We recognize at first glance this frame might seem to fly in the face of the classic approaches to studying the evolutionary contexts/impacts of behavior (e.g. Tinbergen, 1963 and also Mayr, 1961) but it is not actually so outside of contemporary engagement with hominin and human evolutionary studies (e.g. Gamble and Porr, 2005; Grove and Coward, 2008; Fuentes, 2017b; Kissel and Fuentes, 2021; Schroeder and Ackermann, 2023) and the broader debate about the proximate-ultimate distinction in evolutionary biology (Lala et al., 2011; Dickins and Barton, 2013, Ramsey and Aaby, 2022). Thus, we suggest that engaging emotional cognition and its processes may be central to understanding the dynamics and patterns of social relations and their associated behavior.

Take for example the classic human evolutionary example of tool making and cognition. The bulk of traditional approaches examine the structural efficiency and technical difficulty in construction of stone tools and attempt to connect these to specific challenges, constraints, or affordances in cognitive processes (Stout, 2011). If they do include social dynamics and related social cognition it is usually presented in a functional framing such as sexual and/or competitive signaling within or between groups. Even recent work on the social contexts of stone tool making teaching and learning (Paixão et al., 2025) still focuses on energetic costs and the differences in quality and efficiency between expert and novice tool makers. These approaches help to understand some of the physical constraints on tool making, but they omit many socially and emotionally mediated aspects of this activity. Tool making by hominins required communicative and relational aspects, including the establishment of relations of care, trust, and tradition/skillsets associated with tool construction and use (e.g. Hutchence and Scott, 2021). The development of communication, relations, and coordination around the gathering and transport of raw materials, and their modification into tools and subsequent use, involve a suite of cognitive dynamics that may be distinctive relative to many other organisms and may reflect critical facets of socio-emotional relations in the hominin social niche.

Social collaboration facilitated by social cognition can sometimes imply strategic/analytical processes driving the collaboration. However, emotional cognition is also present in much social collaboration and related behavior. Such collaborations and behaviors can be more effective than collaborations primarily based on reason/logic/rules (strategic/analytical) as they involve high levels of give and take (such as in altruistic care or defensive risk taking), long term commitments to others' interests, and substantive shared intentionality and empathy. It is possible that emotionally based (and/or mediated) collaboration becomes more significant for hominins, particularly after two million years ago, with increasingly vulnerable young, more complex social relations and communication, changes in predatory niche and risks from predation. As this happens, more pressures came to bear on emotional cognition and its roles in cognitive behavioral dynamics expands.

5. Emotional cognition within a biocultural framework in human evolution

Social collaboration and social solidarity in contemporary humans draw heavily on emotional cognition and emotional regulation. Social understanding of emotions is widely accepted as adaptive for social primates (Nieuwburg et al., 2021), and thus was likely important to the cognitive toolkit of Pleistocene hominins. The importance of emotions within the evolution of mammalian social systems has been part of evolutionary biology since its beginnings (Darwin, 1872). Comparative research on human emotions from an evolutionary perspective tends to focus on specific emotions which are shared with other apes, or other nonhuman animals, and which have direct influences on behavior. Decety et al. (2012) for example focus on empathy, Gilbert on compassion (Gilbert, 2020) and Burkart et al. (2018) on shame and guilt. For the contemporary human context, however, our emotions are moderated by emotional self-awareness and cognitive appraisal in order to function in a social context. Empathy may be the glue that holds social relationships together, and anger a means of self-protection, but neither are typically simply acted on without a level of awareness. Indeed, to act on anger is considered pathological or, particularly in acts of violence, even criminal. Abilities to integrate emotions within rational thought are thus key to social functioning and group collaboration. Emotions which lie within the 'window of tolerance' (Siegel, 2010) (i.e. emotional functioning in which emotions are felt and brought into rational thought) are also part of essential emotional co-regulation between people which is the basis for emotional wellbeing.

An example of this emotional self-awareness and appraisal might be the level of consideration which Hrdy argues is taken in cases of maternal abandonment (Hrdy, 2000). Conversely, dysregulated anger, for example, can lead to aggression (whilst over regulated anger can lead to passive aggression). As Briggs (1970) notes, human foragers typically have low tolerance for overt displays of dysregulated anger and expect that adults will be able to fully regulate their emotions, as we might expect within all highly collaborative contexts. There is of course no entirely clear dividing line between humans and other animals, with nonhuman animals sometimes engaging in emotional regulation. Dogs for example regulate feelings of frustration in order to fit into human social lives and can use techniques such as distraction to do so (Range and Virányi, 2016).

Emotional regulation and self-awareness are likely prerequisites for much human social behavior involving solidarity and cooperation, including cultural learning, language, and provision of extended care (Spikins et al., 2018). Visceromotor and sensorimotor foundations for emotions are shared across mammals and these building blocks of emotional cognition, a deep mammalian pattern, are central aspects of complex primate behavior (Steklis and Lane, 2013; Porges, 2003). Physiological correlates of emotional responses, for example heart rate, skin conductance, and pupil mimicry, are shared across primates, reflecting a deep evolutionary history (Nieuwburg et al., 2021). Emotional contagion is apparent across primates, and multiple primate species are documented to have the cognitive ability to infer emotional meaning from facial and bodily expressions (Romero et al., 2010; Preston and de Waal, 2002; Nieuwburg et al., 2021; Townrow and Krupenye, 2025). There is also anecdotal evidence for cognitive empathy in targeted helping within apes (Koski and Sterck, 2010).

How contemporary humans process and interpret emotional information can significantly impact social interactions, relations, interpretation of events, and decision-making (Dolcos and Denkova, 2014). Like other mammals, human infants are primed to elicit care, and as adults we respond to signals of needing care from infants (Decety, 2010, Hrdy and Burkart, 2022). Emotional responses with phylogenetically deep roots still play a key role in behavior patterns, albeit mediated by conscious or unconscious thought processes (Adriaense et al., 2020). Human developmental patterns of secure or insecure attachment influence not just the emotional connections of close social relationships and the tendency to be genuinely altruistic (Mikulincer and Shaver, 2005), but also elements of experience and decision making as diverse as human experience of pain (Davies et al., 2009), confidence to explore (Feeney and Van Vleet, 2010), and capacity to solve problems creatively or reliably infer the motivations of others (Mikulincer et al., 2011).

Empathy and compassion—often assumed to be uniquely human—have their roots in mammalian heritage (Carbonell and Mosquera, 2006; deWaal, 2009; but see Adriaense et al., 2020). More complex social emotions in humans, such as shame or gratitude, depend not just on affective empathy but also on its integration with theory of mind (Emmons, 2004). Guilt and shame depend on an understanding of social expectations. These emotions are building blocks of human social functioning. The human ability to hold an awareness of emotional states within rational thought— or emotional self-awareness (Steklis and Lane, 2013) —depends on conscious awareness. Emotional self-awareness is essential to living complex social lives with multiple levels of social interaction without simply responding to 'instinct'. Equally distinctive, yet built on common mammalian roots, is the human capacity for social surrogacy (Gabriel and Schneider, 2024); the capacity to derive a sense of belonging from and with non-human or non-living agents.

Perhaps the most significant evolutionary development in human emotional cognition was one of least cognitive complexity: a human capacity to make deep seated emotional commitments to others' wellbeing (Nesse, 2001). It is this capacity which allows the substantial give and take seen in close human relationships, something fundamental to the sharing of knowledge, behavior, materials, food, etc. which makes distinctively human hunting and gathering lifestyles possible. Emotional commitments of this kind depend on abilities to make judgements of trust made over many instances of behavior, something not seen to the same extent in other animals (Adriaense et al., 2020; Nesse, 2001; Spikins, 2022).

All of these human emotional characteristics are biocultural developments, emerging within a relationship between our mammal biological systems (Porges, 2003, 2022), individual biological responses (such as empathy, Decety, 2010, 2015), and a sociocultural context (Fuentes, 2016). Guilt and shame are expressed physically in blushing and crying for example (Evans, 2002), while social surrogacy depends on alternative cultural mechanisms to fulfil a sense of belonging. Some even argue that language developed to foster emotional regulation rather than for more practical communication (Hobson, 2004). Even 'rational' thought itself, whilst often studied in isolation, relies upon emotions (Damasio, 1994).

It also follows from an understanding of evolutionary dynamics as laid out here that there may have been different branches of emotional cognition within a general human (or hominin) pattern. Small-brained *Homo naledi*, for example, may have had a developed sense of social and emotional connection, with enlarged social and emotional processing areas of the brain, with less emphasis on analytical skills (Fuentes et al., 2025). Neanderthals may have had a subtly different and more intragroup focused emotional cognition (Slimak et al., 2024; Spikins, 2022). We suggest that the examination of complex human emotional cognition should be a central focus of hominin evolution studies, particularly in the latter half of the Pleistocene.

6. Material evidence and the inference of biocultural evolution with a role for emotional cognition in the pleistocene

It is one thing to conceptualize that the behavior of Pleistocene hominins was shaped by social networks using social and emotional cognition. It is something else to recognize these processes in the material evidence from the archaeological and fossil record. Whilst we may agree that complex emotional cognition evolved among Pleistocene hominins, understanding when and where these emerged, and identifying the correlations of emotional cognition in material remains, is in its very early stages. Many relevant behaviors do not leave material traces. Even when traces do occur, natural and cultural processes can interfere with archaeologists' attempts to recover or recognize them. Still, there are multiple domains within which we can use archaeological and skeletal evidence from the Pleistocene to infer dynamics involving social relations and social and emotional cognition.

In the context of human evolution, we argue that the progressive capacity to regulate emotions was a significant development that provides a core focal point for the examination of emotional cognition from the Pleistocene material and behavioral record. Some of the earliest examples of an integration between emotions and rational thought come from stone toolmaking. Since tool making is pleasurable in non-human animals, it is likely to have been pleasurable in humans (McCoy et al., 2019). However, more significantly, the creation of bifaces, involving an imposition of form on stone (rather than simply following a sequence of actions), also involves a notable element of tolerance of frustration (Spikins, 2012; Green and Spikins, 2020). In many ways this frustration tolerance is similar to the frustration tolerated in using language to communicate involving deliberate construction of sentences (Stout et al., 2008). Overcoming notable frustration likewise involves a certain element of emotional regulation and integration with rational awareness.

Below, we provide three examples of how emotional cognition may be identified in the paleoanthropological record: care of vulnerable members of the community, mortuary behaviors, and childcare practices. Each shows aspects of the emotional regulation and self-awareness described above.

Healthcare practices: Empathy and compassion have been argued to be reflected in evidence of care for ill, injured or otherwise vulnerable individuals (Spikins et al., 2019; Spikins, 2022). Healthcare provisioning is a form of sharing (of health) in much the same way as food sharing or sharing of infant care and reflects the human capacity to make deep seated emotional commitments to others' wellbeing (Nesse, 2001). Care practices for adults made vulnerable through illness or injury is a process whereby healthy individuals invest time and effort in improving those with poor health, in the knowledge that they themselves will receive similar future help. Care for ill and injured individuals has direct evolutionary benefits in certain contexts (Spikins et al., 2019). For this reason, we see such care in African wild dogs, for example (Spikins, 2022). In humans, the broader pattern of mammalian empathy has been extended beyond infants to include empathy for adult members of the group, and plays a key role in prompting care (Adriaense et al., 2020; Decety, 2015). In situations with high injury rates, such as risky hunting or even active scavenging, care practices maintain healthy adults in the population who are able in future to return to being active contributors, bringing in resources. Cases of care over the long-term necessarily involve empathy and emotional regulation, and in many cases emotional regulation within collaborative goals.

Care for incapacitated and largely immobilized individuals, begins at least one and half million years ago, as evidenced by cases such as KNM ER 1808; Walker et al., (1982), likely incapacitated for several weeks due to hypervitaminosis. By half a million years ago, we see care for several different individuals at Sima de Los Huesos, including a child with craniosyntosis and an adult with limited mobility (Spikins et al., 2019). Within Neanderthal populations, there are more than thirty possible cases of care (Spikins et al., 2019). Some are contentious, such as a mandible with tooth loss from Bau de L'Aubesier or La Quina 5 with atrophy of the left humerus (Spikins et al., 2019). Others are far more uncontroversial such as La Chapelle aux Saints (an adult Neanderthal male, 25–40 years at death, who suffered from a range of ailments, including extensive tooth loss and severe osteoarthritis; Tilley, 2015) or Shanidar I (an adult Neanderthal male, 35–50 years at death whose multiple traumatic injuries resulted in limb disfigurement and likely partial blindness; Trinkaus and Zimmerman, 1982). Care practices are also evident in later Pleistocene human populations such as Ohalo 2 (Trinkaus, 2018). The existence of largely uncontroversial cases of complex care demonstrate that care likely included an integration of feeling (empathy) with rational thought and a shared intentionality required for complex planning. Such care also has a cultural component and requires sharing of information and practice. Most obviously this is seen in terms of knowledgeable care practices, such as use of antimicrobials or analgesics (Hardy, 2018, Hardy, 2021). However, care also sets a visible social and cultural context, that sits within emotional cognition, of trust and safeness which itself promotes altruism and sharing (Spikins et al., 2018).

The biological imperative for care and its evolutionary context and the cultural context of care have co-evolved. The archaeological record documents only the most extreme examples of care, where injuries or illnesses have left skeletal evidence. Nonetheless, a clear pattern is evident. Whilst individual cases can be debated, the overall chronological pattern of increasing time and investment in care is clear. The earliest cases of care, such as KNM ER 1808; Walker et al., (1982), consist of assistance which is similar to that provided to healthy infants, such as food, water shelter and protection, which might be provided by a single individual, and over a relatively short period of weeks, and direct empathetic responses. Later cases such as the aforementioned Shanidar 1 or La Chapelle aux Saints involve much more complex care, likely involving many members of the group, integration and discussion of emotional motivations, cultural practices, and long timescales (Spikins et al., 2018). This increasing time, investment and knowledge shows how biologically-mediated empathy has co-evolved with its cultural context (Hrdy, 2009, 2024; Rosenberg, 2021; Spikins et al., 2019; Spikins, 2022; Conde-Valverde et al., 2024). Directly empathetic responses can drive dyadic and immediate care, however emotional regulation, self awareness and the integration of emotions within decision-making is necessary for collaborative, long term and medically informed care practices.

*Mortuary behavior***:** The archaeological and paleoanthropological record of mortuary behavior also provides case-studies for tracing the role of social and emotional cognition in hominin biocultural evolution. Mortuary practices occur in social contexts with strong emotional valence, and they function to enable social groups to manage shared experiences of grief. Simplistic equivalence of the presence of formal burial with the emergence of "cognitive/behavioral modernity" has been replaced with a broader framework of 'evolutionary thanatology' (Anderson et al., 2018; Pettitt, 2018) that examines the development of mortuary behavior more broadly—and its relationship with cognition and social collaboration—across the hominin lineage. The distinction within evolutionary thanatology between "mortuary activity" as a face-to-face interaction with the corpse, and "funerary activity" which extends these interactions spatially and temporally and incorporates an element of active commemoration, marks an important transition in hominin mortuary behavior that emerges within a context of increasingly strong emotional bonds, bringing at the same greater potential emotional rupture when these are broken, alongside changing cognitive capacities and social relations.

The Pleistocene archaeological record suggests a clear complexification and elaboration of mortuary behavior (or at least those behaviors that leave a material trace) through time. Pettitt (2018) places the aforementioned transition between "mortuary activity" and "funerary activity" somewhere in the Mid-Late Pleistocene with archaic *Homo*, perhaps necessitated by increases in the size and/or complexity of social groups, which made face-to-face mortuary activity unfeasible. The deliberate placement of at least 28 early Neanderthal individuals into the Sima de los Huesos (Atapuerca, Spain) more than 400 kya (Carbonell and Mosquera, 2006) represents a clear case of the association of the dead with specific places in the landscape. A similar inference can be made from the *H.naledi* individuals from the Dinaledi chamber of the Rising Star Cave system ~300 kya (although the depositional mechanisms here are a source of ongoing debate; Berger et al., 2025; Foecke et al., 2025). If one accepts the Hadar AL 133 *Australopithecus afarensis* remains, at over three million years ago, as the first possible evidence of some form of mortuary activity (Pettitt, 2010), these behaviors need not involve any emotional responses beyond unregulated grief. However, in both the Sima de los Huesos and the Rising Star cases, a significant behavioral, communicative, and we would argue emotional, suite of relations and actions were needed to create the material remains discovered (Carbonell and Mosquera, 2006; Fuentes et al., 2025); a biocultural dynamic encompassing cultural (in terms of collective practice) and cognitive-emotional elements (in terms of allowing the bringing into conscious awareness and so management of, feelings of grief). The cultural agreement of a place to bring the dead, and collective action to transport corpses to that location (and emplace them in specific manners) may mark a significant transition -to a shared set of behavior (a ritual), functioning as a means of regulation of feelings of grief and related emotions through interpersonal co-regulation and collective action. Social responses to grief can explain the earliest mortuary practices, but more complex and collective mortuary practices result from emotional regulation, self-awareness and integration in collective decision making. Transformations in the emotional complexity of both healthcare provisioning and mortuary practices appear at similar chronological stages, as we might expect.

Childcare practices: In terms of childcare practices, much of the empathetic care involved in successful survival of vulnerable young is implied indirectly in the evolution of extended childhoods, within the context of an understanding of alloparenting in primates more broadly. However, the development of more socially complex and multifaceted emotional relationships between caregivers and young—elements of what Hrdy and Burkart (2020) labeled "emotional modernity"— offers a wider range of possibilities for the emergence of the range of relational, social dynamics evident in the later hominin niche. Much parental and alloparental care involves immediate nurturing and empathetic responses. However, given the primary importance of successfully raising infants to adulthood, often within an environment with high rates of predation and the necessary development of a diverse set of social relations, evolutionary pressures would be placed on abilities to integrate emotional motivation to care for young within decision making and forward planning (Bogin et al., 2014, Zollikofer et al., 2024). Both bipedalism and reduction in hair thickness place pressures on effective baby carrying technology for example (Suddendorf et al., 2020, see also Gettler, 2010). Once again, later stages of the archaeological record document the clearest integration between conscious self-awareness of emotions motivating care and collaborative decision making. For example, the creation of space to learn and to play, as seen in apprentice knapping spaces (Assaf et al., 2016; Forte et al., 2023) and children's play spaces (Langley, 2020), involves an awareness of emotional motivations to provide a sense of protection and safety, collaboratively integrated into spatial behaviors.

In sum, across all these elements as they are reflected in the archaeological record, some of the earliest examples can be seen as representing a direct influence of empathy or other interpersonal emotions (such as grief) on behaviors. Later examples illustrate a progressive transition to an integration of emotions such as empathy, compassion, or grief or feelings such as pleasure with explicit cognitive process one might term as rational thought, as well as necessarily collaborative decision making. Other areas of archaeological evidence, such as fire (MacDonald et al., 2021), pigment use (Dapschauskas et al., 2022; MacDonald et al., 2024), and personal ornamentation (Baker et al., 2024) may also involve a similar transition between early direct influence of emotions on behaviors, and later regulation within social collaboration. However, in these cases the evidence is more difficult to interpret.

7. Social and emotional cognition in pleistocene hominin evolution as a biocultural framework for inquiry

Multiple scholars have provided a range of theory and method well suited to assessing, analyzing, and interpreting the archaeological and fossil record via a biocultural framework that includes a focus on social and emotional cognitions (e.g. Burkart et al., 2025; Colagè and d'Errico, 2020, 2025; Spikins et al., 2021; Fuentes 2017a, Sterelny and Hiscock, 2014; Schultz, 2009; Read, 2011; Kissel and Fuentes, 2018, 2021, French, 2021; Whiten and Erdal, 2012; Wadley, 2013; and many others). However, there has been little connection across many of these scholars and projects nor is there always explicit attention to clearly outlining the methodological and theoretical framings and commitments in relation to a biocultural approach. Here, we have tried to combine a number of sources and highlight specific contributions to develop a common framework to facilitate a broader and more integrative interest in investigating social and emotional cognition as a key component of the niche(s) of Pleistocene hominins.

What this work proposes is a framework for understanding Pleistocene hominin evolution, integrating archaeological and paleoanthropological evidence with contemporary evolutionary theory and insights from studies of humans and other primates. While there are challenges applying this framework where archaeological and skeletal data are sparse, a growing record with higher resolution of patterning at multiple sites have brought this perspective, and a focus on emotional and social cognition, within closer reach. The available evidence points to increasingly diverse and sophisticated cultural behaviors, some of them in unanticipated contexts. When viewed alongside analyses of socio-emotional cognition in humans and other animals, particularly primates, these findings challenge a traditional concentration of models upon analytic cognition and technical problem-solving as the primary drivers of hominin evolution. Instead, the central role of interpersonal relationships in shaping cultural materials and relations, coupled with the intricate social structures and communication they imply, highlights the significance of emotional cognition. Given the deep ties between social behaviors, emotional states, and their neurobiological underpinnings within the hominin niche, these elements may be just as critical—if not more so—than brain size or ascribed rational capacities when exploring the evolutionary story of our ancestors.

CRediT authorship contribution statement

Agustín Fuentes: Writing – review & editing, Writing – original draft, Investigation, Funding acquisition, Conceptualization. **Jennifer C. French:** Writing – review & editing, Writing – original draft, Investigation. **John Hawks:** Writing – review & editing, Writing – original draft, Investigation. **Marc Kissel:** Writing – review & editing, Writing – original draft, Investigation. **Penny Spikins:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Agustin Fuentes reports financial support was provided by John Templeton Foundation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Authors AF, JF and MK, were supported, in part, by funding from the John Templeton Foundation (Grant # 61924) during the writing of this manuscript.

Data availability

All information in this manuscript is drawn from published studies. No new data are presented or discussed.

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