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Headmen, shamans, and mothers: Natural and sexual selection for computational services

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ABSTRACT

Computer engineers face a dilemma. They must build systems with sufficient resources to solve the most complex problems the systems are expected to solve, but the systems will only need to solve such problems intermittently, resulting in inefficient use of expensive computational resources. This dilemma is commonly resolved with timesharing, networking, multitasking, and other technologies that enable computational resources to be shared with multiple users. The human brain, which evolved to acquire, store, and process information to make beneficial decisions in situations that were periodically complex, is likewise energetically expensive to build and maintain yet plausibly has idle capacity much of the time. We propose that humans evolved to use advantages in information or computational resources to provide computational services to others via a language-based "network" in exchange for payments of various sorts that helped subsidize the energetic costs of the brain. Specifically, we argue that with the Pleistocene transition of Homo to a niche in open habitats with a more meatbased diet, four major selection pressures for knowledge specialists began to act on the human lineage: (1) the need to resolve conflicts and maintain cooperation in larger multilevel societies, which lead to the rise of knowledge-based leaders as decision-making and conflict resolution specialists who were "paid" with increased mating success or resources; (2) the need for greater defense against zoonotic pathogens, which lead to the rise of shamans as medical knowledge specialists, who were "paid" with increased mating success or resources; (3) the greater complexity of mothering with shorter interbirth intervals and longer periods of juvenile dependency, which led to mothers as both decision-making and medical specialists, who were "paid" with increased inclusive fitness; and (4) the need to make more efficient use of an increasingly large and energetically expensive brain.

1. Introduction

Computational resources represent the capacity to solve problems of a given complexity. Problem complexity is measured in *time complexity* and *space complexity*—the number of steps and the amount of memory, respectively, required to solve the problem (Arora & Barak, 2009; Dasgupta & Gershman, 2021). Substantial computational resources are expensive to build and maintain, yet if a user only needs to solve complex problems intermittently, resource use will be inefficient. To increase efficiency, engineers designed time-sharing and multitasking systems that allow multiple users to interact concurrently with a single multimillion-dollar mainframe computer (Corbató, Merwin-Daggett, & Daley, 1962). In the early 1960's, Joseph Licklider, an employee at the United States Department of Defense Advanced Research Projects

Agency (ARPA), proposed another way to increase efficiency: enable researchers to access computational resources remotely. His proposal, which he wryly termed an "Intergalactic Computer Network", = (Licklider, 1963) launched development of ARPANET, the predecessor of the internet (Lukasik, 2010).

The invention of computer time-sharing, multitasking, and network technologies allowed multiple users to make much more efficient use of expensive computational resources. These technologies, combined with the ubiquity of the internet, have given rise to a wide array of cloud computing services, accessible with application programming interfaces (APIs). In one important class of services, customers upload data, such as images or queries, to a company that subjects it to complex computational processing, such as image recognition or database retrieval, and returns the output for a small fee. Computational service providers often

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develop the software and hardware for internal use as part of their primary business but then open up the service to others to help pay for the high costs of building and maintaining the computational infrastructure (Armbrust et al., 2010; Mell & Grance, 2011; Miller, 2016).

There are important analogies between expensive computer systems and the brain. First, nervous systems evolved to map information to actions that, on average, increased fitness; that is, they evolved to make "good" decisions (Hagen et al., 2012). As we explain later, some good decisions require extraordinary computational resources, yet circumstances requiring such decisions, however important, only occur intermittently, resulting in unused cognitive capacity much of the time. Second, nervous systems are expensive: human brain development takes over 15 years (Blakemore, 2012), and the total glucose used from birth through age 15 is equivalent to nearly half the total energy used for resting metabolism over this period (Kuzawa et al., 2014). See Fig. 1. In adulthood, the brain continues to consume about 20 % of basal energy (Herculano-Houzel, 2012).

Remarkably, brain metabolism is essentially fixed: the additional energy consumption associated with transitory cognitive demands might be less than 5 % of the baseline energy budget (Raichle, 2006, 2015). Even when asleep, brain energy consumption during the REM cycle is the same as when awake, and during the non-REM cycle only reduces to about 85 % of the waking value (DiNuzzo & Nedergaard, 2017).

1.1. Computational services

We draw an explicit analogy between the efficient use of expensive computing resources via electronic networks and the efficient use of energetically expensive nervous systems via a language-based "network." Human foragers, relative to great apes, have a much higher rate of energy acquisition (Kraft et al., 2021), leaving more time for activities such as childcare, socializing, manufacturing, innovation, exploration, defense, and importantly, collecting, processing, and disseminating information that might be valuable to others. We argue that throughout human evolution when individuals were not using their cognitive resources to make complex decisions for themselves, they could subsidize the substantial cost of building and maintaining a large brain by offering some of these valuable computational services to others via language in return for a "payment". In a co-evolutionary dynamic, more efficient use of the brain would have enabled the evolution of larger brains for individual benefit, which might have selected for improved capabilities to offer computational services.

Our model requires that, despite universal cognitive mechanisms (Barkow, Cosmides, & Tooby, 1992; Barrett, 2014; Boyer, 2018), there was marked individual variation in computational resources due to age (e.g., infants vs. adults), sex-specific competencies (Geary, 2020), developmental disruptions (Lanphear, 2015), injuries (Tsai et al., 2021), infections (Damiano et al., 2022; Townsend, Sewall, Leonard, & Hawley, 2022), heritable variation (Johnson & Barton, 2005; Zietsch, 2024), and greater investment in mastering one domain at the expense of others (Ericsson & Charness, 1994). Most individuals also possessed some proprietary information that would have been valuable to others, such as the location of transient resources or the existence of covert sexual affairs. Each of these would enable some individuals to provide better and/or faster solutions to certain important problems.

Througout we will use terms such cognitive abilities, intelligence, and knowledge somewhat interchangeably. As our timeframe is the 2.6 million years of the Pleistocene, during which brain size tripled in the human lineage, and our contemporary contexts include diverse



Fig. 1. A: Cumulative energy use from birth through age 15 in human males. B: Cumulative proportion of resting metabolism consumed by the brain from age 1 through 15 in males. Data from Kuzawa et al. (2014).

nonindustrial societies, we caution against equating these terms with the intelligence quotient (IQ), a construct developed to assess the cognitive development of children in industrialized societies. Instead, we mean the cognitive resources, including learned skills, needed to solve information processing problems relevant to fitness in the environment of evolutionary adaptedness (EEA) of the human lineage, which can be conceptualized as neural capital (Kaplan & Robson, 2002).

"Payments" for computational services could have been any of the forms of social interactions that increased inclusive fitness, such as helping kin or long-term social partners, or receiving resources. Providing useful information, for instance, inspires *epistemic gratitude*, a positive emotional response that increases the likelihood of future reciprocation (Karabegovic, Wang, Boyer, & Mercier, 2024). In some cases the payoff was mating success, leading to sexual selection for computational abilities, a key element of our argument (briefly sketched in previous publications, Garfield, Hubbard, & Hagen, 2019; Garfield, von Rueden and Hagen, 2019; Hagen & Garfield, 2019).

Predator alarm calls are a paradigmatic example of a computational service in non-human animals. Detecting a predator is an extremely computationally demanding task, involving rapid processing of high bandwidth visual, auditory and olfactory data channels (Pereira & Moita, 2016). An alarm call is a computational service whose "payment" is the survival of kin, i.e., increased inclusive fitness (Price et al., 2015; Seyfarth, Cheney, & Marler, 1980; Taylor et al., 2024).

Teaching is another important type of computational service (Castro & Toro, 2014). In social learning models, agents individually learn about environmental variation, such as toxic foods to avoid during pregnancy (Henrich & Henrich, 2010; Placek, Madhivanan, & Hagen, 2017), information that they can then transmit to others (Boyd & Richerson, 1985; Rogers, 1988). Providing information on, e.g., toxic plants or tool manufacture is valuable to most members of the population, and the information is typically valid for multiple generations. This computational service, which can be "paid" for via increased prestige and deference, plays a central role in theories of cultural evolution (Henrich & Gil-White, 2001).

Computational services extend far beyond facilitating cultural transmission, however, because much transmitted information is only useful for specific individuals at specific points in time, and this information is therefore not fodder for cultural evolution. Communicating useful information on transient environmental conditions, for instance, such as "that tree has ripe fruit", is a computational service that was probably one of the major selection pressures for the evolution of language (Pinker & Jackendoff, 2005), but this information is not fodder for cultural evolution.

Other valuable cognitive services employ rare or proprietary information, or involve complex weighting of factors that are specific to one individual at a single point in time. Conflict resolution, for instance, is subject to culturally evolved rules that typically apply to everyone. Nevertheless, resolving a particular conflict within these constraints can be difficult due to limited information and the need to weigh many factors. Leaders could offer valuable advice and counsel on resolving particular conflicts (e.g., Garfield, 2021) by drawing on their proprietary knowledge of the interests of the parties involved, their preferences, personalities, and past histories, along with potential bargaining chips. They could also draw on their individually learned heuristics of conflict resolution. But advice to one person would not necessarily be applicable to any other person, nor even to that same person in the future, and hence is not fodder for cumulative cultural evolution.

It would be difficult and perhaps impossible to reverse engineer many of these computational services by simply observing limited instances of their delivery, a task whose challenges are analogous to those of correctly inferring complex functions from limited samples of inputoutput pairs.

Finally, there are many services that require complex computations on the part of the provider, such as obtaining food and providing it to others, but that we do not conceptualize as computational because the primary benefit to the recipients is not informational or improved decision-making. In short, we restrict the concept of computational services to computations that could, in principle, be performed by the recipient's nervous system, like diagnosing illness, but are instead performed by the service provider's nervous system.

Our paper is organized as follows. We first argue that the Plio-Pleistocene transition to a more carnivorous dietary niche in open habitats intensified selection in the human lineage for cooperation in larger groups and for pathogen defense. We present shamans, a type of healer common in hunter-gatherer societies, as an important example of a computational service provider whose roles might have arisen in response to intensified pathogen pressure. We then conceptualize knowledge-based leaders as decision-making and conflict resolution specialists, computational services that might have arisen in response to intensified selection for cooperation in larger groups. Both roles (which sometimes were filled by the same person, Garfield, Syme, & Hagen, 2020) might have been subject to sexual selection for cognitive abilities, contributing to encephalization. Finally, we argue that healing and decision-making services might have initially been naturally selected in mothers, who provide numerous medical and computational services for their cognitively immature offspring who are not yet able to provide these services for themselves.

2. The transition to open terrestrial habitats and carnivory intensified selection for cooperation in larger groups and for pathogen defense

The Plio-Pleistocene transition of the human lineage from a partially arboreal, woodland niche with a plant-based diet (Almécija et al., 2021) to a committed terrestrial lifestyle in a more open habitat with a more carnivorous diet (Antón, Potts, & Aiello, 2014) likely increased selection for greater cooperation for predator defense (Willems & van Schaik, 2017), and for scavenging and hunting large herbivores (Domínguez-Rodrigo et al., 2021; Domínguez-Rodrigo & Pickering, 2017; Pobiner, 2020; Smith, Swanson, Reed, & Holekamp, 2012; Szilágyi, Kovács, Czárán, & Szathmáry, 2023). It also likely increased zoonotic spillover, increasing selection for physiological and behavioral immune responses to zoonotic pathogens (Hagen, Blackwell, Lightner, & Sullivan, 2023).

Although the timing for each is uncertain, the human lineage's new Pleistocene niche also involved the evolution of many other important traits, such as biparental and alloparental care (Burkart, Hrdy, & Van Schaik, 2009), multilevel social organization (Hamilton, Walker, Buchanan, & Sandeford, 2020), sophisticated symbolic communication (language) (Pinker & Jackendoff, 2005), and cumulative culture (Muthukrishna, Doebeli, Chudek, & Henrich, 2018; Richerson & Boyd, 2005). All of these were probably interrelated causes and consequences of the tripling of brain size over the course of the Pleistocene (Fig. 2) and the consequent increased energetic requirements of the human nervous system, whose fitness costs, we argue, could have been partially offset by offering computational services to others.

2.1. Predation increased selection for cooperation in larger groups

Plio-Pleistocene East African herbivore communities included numerous megaherbivores (>1000 kg) and the large (>100 kg) carnivores that preyed on them, such as giant hyenas, sabertooth cats, lions, and highly carnivorous bears (Faith, Rowan, & Du, 2019; Treves & Palmqvist, 2007). Many of these carnivores outweighed hominins, could outrun them, and hunted in packs (for a brief review, see Hagen, 2022). Extant primate species inhabiting open terrestrial habitats live in larger groups than those inhabiting wooded arboreal habitats, have more males in the group and greater sexual dimorphism, and the males frequently cooperate in counter-attacks against terrestrial carnivores. Chimpanzees and savanna baboons, two species that illustrate these patterns, often form groups with more than 100 individuals when far from the safety of trees, and the males engage in joint counter-attacks



Millions of years before present



against large carnivores, occasionally using stones or sticks (Willems & van Schaik, 2017). The hominin transition to open, terrestrial habitats would therefore have been possible only with joint predator defense provided by a large group of highly cooperative individuals who probably used weapons of some sort (Bickerton & Szathmáry, 2011; DeVore & Washburn, 1963; Pobiner, 2020; Treves & Palmqvist, 2007; Van Valkenburgh, 2001; Willems & van Schaik, 2017).

2.2. Carnivory increased selection for cooperation in larger groups

The relative importance of animal vs. plant foods for early *Homo*, and whether it was hunted or scavenged, are hotly debated (Crittenden & Schnorr, 2017; Domínguez-Rodrigo & Pickering, 2017; Pobiner, 2020). Nevertheless, evidence for early access to large herbivore carcasses, including those of megaherbivores, c. 1.8 million years ago with the appearance of *Homo erectus* and the transition from Oldowan to Acheulean stone tools, suggests that cooperative hunting was now part of the behavioral repertoire of the human lineage (Domínguez-Rodrigo et al., 2021; Domínguez-Rodrigo & Pickering, 2017), another selection pressure for cooperation in larger groups. The Pleistocene transition to a more carnivorous diet by *Homo* would also have increased its exposure to predators as it contested with them for carcasses, further selecting for cooperative predator defense (e.g., Daujeard et al., 2016; Van Valkenburgh, 2001; cf. Speth, 2024).

Finally, cooperative territorial defense is common in social carnivores (Smith et al., 2012), and well-documented in chimpanzees, a highly territorial species that cooperatively patrols and defends boundaries with hostile and sometimes lethal interactions between groups (Mitani & Watts, 2005). Bonobos, though much more tolerant of outgroups, nevertheless distinguish ingroup from outgroup members and occasionally exhibit hostility to outgroups (Langergraber, Watts, Vigilant, & Mitani, 2017; Samuni, Langergraber, & Surbeck, 2022). Some baboons and other primates and mammals live in multilevel societies, a relatively rare form of social organization, and engage in group-level cooperation against intruders (Grueter et al., 2020; Grueter, Matsuda, Zhang, & Zinner, 2012). Modern humans also live in

multilevel societies with cooperative and competitive relationships among groups (Dyble et al., 2016; Glowacki, 2024; Hamilton et al., 2020; Pisor & Surbeck, 2019; Rodseth, Wrangham, Harrigan, & Smuts, 1991). In ethnographically known foraging societies, territoriality ranges from essentially non-existent to cooperative physical defense of clearly defined boundaries (Codding, Parker, & Jones, 2019; Moritz, Scaggs, Shapiro, & Hinkelman, 2020). A reasonable supposition is that groups of early *Homo*, and maybe earlier hominins, might also have cooperated to defend their territories, perhaps in larger multilevel societies.

The upshot is that the transition to a committed terrestrial lifestyle in open habitats, coupled with increased scavenging and hunting of large herbivores and perhaps cooperative defense of larger territories, increased selection for cooperation within and between large groups in the human lineage. Larger groups would have increased within-group competition for food, however (Alexander, 1974; Wheeler, Scarry, & Koenig, 2013), and also increased the risk of free-riders and other barriers to collective action (Powers & Lehmann, 2016; Powers, van Schaik, & Lehmann, 2021). We will propose that knowledge-based leaders emerged to help solve these problems using exceptional computational resources.

2.3. Carnivory increased selection for pathogen defense

The transition from the plant-based diets of Australopithecines and other early hominins to greater meat-eating c. 2.6 million years in genus *Homo* ago likely increased zoonotic pathogen pressure (Hagen et al., 2023). Although plant foods are often contaminated with animal pathogens, e.g., in feces, the threat from plant pathogens themselves is relatively low due to the substantial differences between plant and animal cell walls and immune systems (Kim, Yoon, Park, Kim, & Ryu, 2020). Meat, on the other hand, would often have been infected with pathogens adapted to primates and other mammals that had a high risk of spillover into hominins. Most human infectious diseases indeed originate in non-human animals, hunting is associated with spillover into modern humans, and hunter-gatherers, bushmeat hunters, and veterinarians have increased zoonotic infections relative to others living in the same environments. Hunters and scavengers in the genus *Homo* would have had intimate, near-daily contact with mammalian prey and predators, and their pathogens and arthropod disease vectors (Hagen et al., 2023).

Pathogens are a primary selection pressure in humans (Fumagalli et al., 2011; Peros, Dasgupta, Kumar, & Johnson, 2021; Uricchio, Petrov, & Enard, 2019). Consistent with increased zoonotic pathogen pressure, the human lineage evolved a number of defenses that diverged from chimpanzees and other primates. These include: exceptionally low stomach pH compared to other primates, a pathogen defense that is closely related to carnivory; a loss-of-function mutation in the CMAH gene that arose c. 2 mya in the human lineage, radically changing cell surfaces, the point of entry for pathogens; exceptional human immune responses to lipopolysaccharide compared to other primates, suggesting greater costs of bacterial infections since divergence from chimpanzees; human-specific down-regulation of the ANTXR2 gene which would protect against increased exposure to zoonotic anthrax; and divergent APOE, which is linked, among other things, to meat-eating and pathogen exposure (Hagen et al., 2023).

We propose that selection intensified in *Homo* for the plant-based self-medication strategies already in place in apes and other primates (Huffman, 2003) for two major reasons. The first was the carnivory-related shift and perhaps increase in zoonotic pathogen pressure. The second was the challenge of defending a large body and brain from pathogens across what would eventually become one of the longest lifespans of any mammal (Hagen et al., 2023). We will argue that shamans and other healers arose as one solution to these challenges.

2.4. Increased pathogen pressure selected for increased reliance on plantbased self-medication

Plants are attacked by the same broad classes of pathogens and parasites that attack humans and other animals–viruses, bacteria, protozoa, fungi, helminths, and arthropods. In response, the plant kingdom has evolved a broad array of defenses, including toxins. Plants produce an estimated $10^5 - 10^6$ chemically unique structures, with 5000–15,000 structures per species, most of which comprise lineage-specific toxic compounds involved in defense against plant consumers (Li & Gaquerel, 2021).

There is increasing evidence that non-human animals have evolved to co-opt plant toxins to combat their own infections, a phenomenon termed self-medication (Boppré, 1984; De la Fuente, Souto, Albuquerque, & Schiel, 2022; de Roode & Huffman, 2024; de Roode, Lefevre, & Hunter, 2013; Erler et al., 2024; Huffman, 1997, 2017; Neco, Abelson, Brown, Natterson-Horowitz, & Blumstein, 2019; Rodríguez & Wrangham, 1993; Villalba & Provenza, 2007; Wrangham & Nishida, 1983; Yoshimura, Hirata, & Kinoshita, 2021). Self-medication has been reported in 71 mammalian species, including 46 primate species and 10 carnivore species. It involves, e.g., ingestion of whole leaves to expel parasites from the digestive system (mostly apes and elephants), rubbing fur with toxic plants (non-human primates), placement of bay foliage around the nest to reduce ectoparasites (rodents), and use of specific plants to attenuate negative effects of food ingestion (artiodactyls). Selfmedication in mammals evolved independently at least four times and is associated with greater body size, brain size, and longevity (Neco et al., 2019), traits that increased in the human lineage in the Pleistocene. There is also evidence for medicinal plant use by Neanderthals (Hardy, Buckley, & Huffman, 2013).

Thornhill and Fincher (2014) proposed that pathogen pressure increased selection for human behavioral immunity. We similarly propose that the human lineage, entering a niche that increased exposure to zoonotic pathogens, began to evolve cognitive mechanisms to more effectively utilize plant toxins to fight pathogens.¹ Due to the high cost of Western medicine, the majority of the world's population still relies on plant-based traditional medicine (Hagen et al., 2023).

3. Shamans and other healers as computational service providers

Intensified use of plant-based medicine likely required an increased cognitive ability to assess ambiguous symptoms in individuals of varying ages, sexes, exposures, and circumstances, to classify distinct illness conditions, to discover which plant substances were the most effective, and then to store and recall the solutions (memory). To illustrate the complexity of this task with a simple example, there are 175 unique combinations of 1-3 symptoms out of 10, i.e., up to 175 distinct illnesses, and 210 unique combinations of 1 or 2 substances out of 20, i.e., up to 210 treatments. To determine which combinations of local plant substances best treated which illnesses it would be necessary to sift through $175 \times 210 = 36,750$ matches of possible treatments to illnesses. Such an exhaustive search is intractable (Arle & Carlson, 2020). We are not proposing that humans evolved to test every combination of substances against every combination of symptoms, however, and remember each outcome. We are proposing that making good use of the local and continually evolving "pharmacy" of plant compounds against continually evolving pathogens, using both individual and social learning to enable cumulative cultural evolution, would have required substantial computational resources (processing and memory).

Ethnoscience and *ethnomedicine* refer to culturally varying, locally useful bodies of conceptual knowledge about the social and natural world (Lightner, Heckelsmiller, & Hagen, 2021b) and illness and health (Quinlan, 2011), respectively. We distinguish *products of knowledge*, which refers to observable applications of knowledge, from *know-how*, which refers to the underlying cognitive system or process that reliably yields a desired product. Importantly, although some types of knowhow, such as food preparation or tool use, can be reliably inferred from its products (e.g., observing the butchering of an animal), others cannot. Doctors know how to diagnose and treat illnesses, for example, but their patients do not gain this know-how by observing their doctors (Lightner et al., 2021b).

A study of ethnoscientific expertise in ethnographic records from 55 nonindustrial societies found that although there were many domains of expertise, medicine was by far the most common (Lightner et al., 2021b). See Fig. 3. This study also found two basic types of expertise. One involved easily-observed motor-based skills, such as woodworking and crafts, that are important for subsistence and other tasks performed by most community members on a daily basis. Experts in these domains had prestige and taught others, corresponding to influential theoretical models of prestige-biased cultural transmission (Henrich & Gil-White, 2001; for studies of learning and teaching in hunter-gatherers, see Garfield, Garfield, & Hewlett, 2016; Garfield & Lew-Levy, 2024). The other type of expertise, our concern here, involved providing solutions to uncommon but serious problems, such as illness. Knowledge in these domains, primarily medicine and divination, was typically restricted and proprietary. Experts, who competed for clients based on a reputation for efficacy, provided their medical and other services in exchange for some type of "payment", which we refer to as a market for specialists (Lightner et al., 2021b; Lightner, Heckelsmiller, & Hagen, 2021a).

Under our hypothesis, although increased carnivory led to increased zoonotic spillover and use of pharmacological plant substances in the population of early humans as a whole, individual infection by a large number of different zoonotic pathogens would have been rare. Furthermore, many zoonotic diseases, such as anthrax and rabies, do not

¹ for brevity, we will use the term "plant toxins" to also include defensive toxins produced by fungi, arthropods, and vertebrates



Fig. 3. Common domains of knowledge and skill in the ethnographic record. Vertices indicate domains that occurred in at least 10 ethnographic reports. Vertex size corresponds to the number of reports including that domain. Each edge indicates that a pair of knowledge/skill domains were both included in at least one report. Edge widths indicate the number of reports that included both domains. Graph layout by stress majorization. Data from Lightner et al. (2021b).

transmit from human to human. As a consequence, it might not have been worthwhile for all individuals to invest in acquiring the extensive medical knowledge needed for self-diagnosing and treating numerous illnesses that they might never acquire. But it could have been worthwhile for a few individuals to make a heavy investment and then cultivate a large clientele that would "pay" for their services when needed (Hagen et al., 2023; Lightner et al., 2021a, 2021b), a dynamic that could account for the appearance of ethnomedical experts that are commonly referred to as shamans or healers.

3.1. Shamans

In hunter-gatherer societies, whose characteristics provide insights into the conditions under which humans evolved, healing services are typically provided by shamans. A study of a global sample of huntergatherer societies found that 79 % had shamans, defined as a socially recognized part-time ritual intercessor, healer, and problem solver (Peoples, Duda, & Marlowe, 2016). Several societies categorized in this study as lacking shamans in fact have them, however, for a total of 88 % (Singh, 2018). There is also archaeological evidence for shamanism in prehistory, including in paleolithic foragers (Lewis-Williams, 2001; Price, 2001). Conversely, shamans in all societies provide healing services (Singh, 2018), hence our focus on them here.

The word shaman comes from the Tungus language group, spoken by, among others, the Evenk, nomadic Siberian reindeer herders (Harvey & Wallis, 2007). See Fig. 4. The etymology of the term has been debated for more than a century. A recent treatment concludes that the root word, *sar*, means knowing or understanding, and *shaman* means a wise man who knows everything (Guo & Liang, 2015).

Extensive fieldwork in Siberian and many other indigenous populations in the 19th and 20th centuries revealed a common pattern: in most hunter-gatherer and other small-scale societies there was a specialized role or status, often the only such one, that typically involved engaging in ritual behaviors to gain information and effect important outcomes, e.g., divination and healing (DuBois, 2009; Harvey & Wallis, 2007; Peoples et al., 2016; Winkelman, 2021a). This role also frequently entailed the consumption of powerful psychotropic substances and their administration to patients (Furst, 1972; Nyberg, 1992; Wilbert, 1987; Winkelman, 2021b). The men and women occupying this role have been dubbed shamans, and their practices as shamanism.

The literature on shamans and shamanism is as contentious as it is vast. Some scholars consider shamanism to be the world's oldest religion (Vitebsky, 2001), a framing that continues to dominate academic studies of shamanism (e.g., DuBois, 2009; Eliade, 1964; Lewis, 2002; Winkelman, 2021a), whereas others insist that the terms appropriately apply only to the nomadic Siberian cultures from which they derive, and to those circumpolar groups that could plausibly have acquired similar practices via cultural transmission (e.g., Kehoe, 1996, 2000). Yet others view shamanism as a "desiccated" and "insipid" category (Geertz, 1966, p. 122).

Nevertheless, definitions of shamans by a variety of scholars exhibit an undeniable family resemblance in which healing plays a central role (Lightner, 2023). Shamans are: medical and spiritual practitioners (Balzer, 1997); those who can engage in two-way communications with spirits, sometimes to heal (Grant, 2021); "a communally recognized professional who cultivates personal relations with helping spirits in



Fig. 4. "Een schaman ofte Duyvel-priester in't Tungoesen lant" (A Shaman or Devil Priest in Tungoesen land), from Noord En Oost Tartarye (Witsen 1692, 2024). Witsen was the mayor of Amsterdam and an amateur scholar. His book described what was known about remote areas of Inner Eurasia and the nomadic peoples who lived there. This engraving is the earliest known depiction of a Siberian shaman.

order to achieve particular ends for the community: generally, healing, divination, and/or the control of fortune" (DuBois, 2009, p. 6); those who "provide rituals for healing, divination, protection from spirits, hunting magic and sorcery, causing illness and death to others" (Winkelman, 2021a, p. 5); and "practitioners who enter trance to provide services" (Singh, 2018, p. 1).

We do not aim to provide a comprehensive theory of shamanism, and we set aside its close association with animism, and practices such as divination, trance, and control of fortune (for overarching theories of shamanism and religion, see Lightner & Hagen, 2022; Peoples et al., 2016; Singh, 2018; Winkelman, 2021a). We aim only to explain the diagnosis of patients and the prescription of psychoactive and other pharmacological plant substances to heal them in exchange for payments such as meat and other foods, tobacco, slaves, and sexual partners (Hagen et al., 2023; Singh, 2018).

Many psychoactive drugs used by Amazonian plant doctors have antiparasitic and antimicrobial properties and might have been selected for use in religious ceremonies for that reason (Rodriguez, Cavin, & West, 1982). Tobacco, which contains high levels of nicotine and is hallucinogenic at large doses (Elferink, 1983), is one such drug with demonstrated efficacy against endoparasites and ectoparasites (Iqbal, Lateef, Jabbar, Ghayur, & Gilani, 2006; Pavela, Canale, Mehlhorn, & Benelli, 2016; Roulette et al., 2014; Schorderet Weber et al., 2019). It was widely used across both American continents by shamans and commoners, with pipe residues providing direct evidence of smoking wild tobaccos and other plants by North American hunter-gatherers for thousands of years (Damitio, Tushingham, Brownstein, Matson, & Gang, 2021), and other archaeological evidence of use as early as the Pleistocene, c. 12.3 ka (Duke et al., 2021). Ethnographic evidence shows tobacco was consumed by drinking concoctions, inhaling snuffs, chewing, smoking large cigars and pipes, and, rarely, via enemas. In South America, it was often combined with coca or ayahuasca (Von Gernet, 2000; Wilbert, 1987; Winter, 2000), for which there is archaeological evidence of shamanistic use c. 1000 BP (Miller, Albarracin-Jordan, Moore, & Capriles, 2019). In Australia, pituri, a nicotine based drug made from *Duboisia hopwoodii* and/or tobacco species, was widely consumed and traded across the continent by Aborigines, with some evidence of shamanistic use (Watson, 1983).

Europeans observed South American shamans curing patients with tobacco as early as the 16th century (Wilbert, 1987). Tobacco shamans, themselves initiated into the profession with copious doses of tobacco, treated their patients by applying tobacco poulstices, powders, wet leaves, spit, and smoke directly to the skin, which readily absorbs nicotine (Wilbert, 1987). See Fig. 5. Given the efficacy of nicotine and other tobacco compounds against various *endo*- and ectoparasites (Iqbal et al., 2006; Pavela et al., 2016; Roulette et al., 2014; Schorderet Weber et al., 2019), these treatments undoubtedly provided genuine benefits in some cases.

The anti-infective and medicinal effects of many hallucinogens, such as *Amanita muscaria* (Fly Agaric), a mushroom used by Siberian shamans, are less clear (for an overview, see Ferreira Júnior, Cruz, Vieira, & Albuquerque, 2015). Many hallucinogens interfere with serotonin signaling (López-Giménez & González-Maeso, 2017), however, which is important in all parasitic helminths (Patocka, Sharma, Rashid, & Ribeiro, 2014). Ergot alkaloids, for example, some of which are hallucinogenic (Schiff, 2006), interfere with serotonin signaling and are promising antiparasitic compounds (Chan, Day, & Marchant, 2018).

The use of pharmacological substances extends far beyond hallucinogens (Fig. 6), and although shamans and healers typically have the greatest knowledge, plant medicines that treat a variety of conditions



Fig. 5. Brazilian Tupinambá curing by blowing tobacco smoke. André Thevet, La cosmographie vniuerselle, 1575.



Fig. 6. The numbers of psychoactive plant species used by ethnic groups in broad geographic regions, by their effects. Total species = 126. Median number of effects per species = 2. Data from Alrashedy and Molina (2016).

are widely known by community members. A study of Baka Congo Basin foragers, for instance, found that they could name 73–82 of the 90 plant species presented. In addition to plant uses for food and material culture, there were 61 uses for medical problems, such as problems with digestion, child illnesses, respiration, pregnancy, birth, and headaches. Medicinal knowledge was not distributed evenly, however: whereas informants had almost the same knowledge of plant uses for food and material culture, knowledge of medicinal plants was mostly different, and some individuals had markedly more knowledge than others (Hattori, 2020).

In summary, in hunter-gatherer and other small-scale societies, shamans and healers use proprietary knowledge to identify illness conditions from ambiguous symptoms and prescribe effective treatments, often powerful psychotropic or other toxic substances with demonstrated efficacy against pathogens, and receive valuable benefits in return. These individuals therefore serve as one of our paradigmatic examples of computational service providers.

4. Knowledge-based leaders as computational service providers

Increased predation pressure in open terrestrial habitats and a diet increasingly reliant on cooperative scavenging and hunting likely increased selection in the human lineage for cooperation in larger groups. Larger groups, however, would have increased the potential for conflict among group members due to resource competition and freeriding, jeopardizing group member fitness (Alexander, 1974; Powers & Lehmann, 2016). We will make the case that in humans, groupbeneficial decision-making and conflict resolution are especially computationally demanding and require high levels of knowledge, and can therefore be conceptualized as computational services that leaders provide to followers in exchange for various forms of payment. We will not provide a comprehensive account of leadership, however: high quality decision-making is a necessary skill for knowledge-based leadership, we argue, but not sufficient, and other factors like social and material capital often play important roles (Garfield, von Rueden, & Hagen, 2019; Glowacki & von Rueden, 2015).

4.1. Leadership, knowledge, and dominance in non-human animals

Leadership in humans and other animals involves a disproportionate influence over group decisions, whereas dominance involves increased access to contested resources and deference from others but not necessarily influence over group behavior (Kantner, 2010; Smith et al., 2016; Van Vugt, 2006; von Rueden, Gurven, Kaplan, & Stieglitz, 2014).

In some cases, such as mountain gorillas, leadership and dominance are synonymous (Fossey, 1972). In other cases, though, animal leadership is based on asymmetries in information rather than dominance. A model of the emergence of leadership among nonhuman animal groups, for instance, demonstrates that large groups of individuals can achieve consensus in direction of movement relying exclusively on the movements of relatively few knowledgeable leaders (Couzin, Krause, Franks, & Levin, 2005). Social learning biased towards older, experienced individuals plays a role in some avian migration (Berdahl et al., 2018; Mueller, O'Hara, Converse, Urbanek, & Fagan, 2013). Among elephant species, older matriarchs with special knowledge and experience are the primary decision-makers in the group (Payne, 2003). Among killer whales, post-reproductive females lead foraging movement, especially during times of limited food resources, presumably due to their superior ecological knowledge (Brent et al., 2015). Chimpanzee leaders can effectively communicate information on the location, quality, and quantity of resources to the group (Menzel Jr., 1971). Chimpanzees also appear to defer towards and preferentially learn from experienced individuals (Horner, Proctor, Bonnie, Whiten, & de Waal, 2010; Kendal et al., 2015). This suggests that elements of knowledge-based leadership might have been present in the last common ancestor of humans and chimpanzees, which lived more than 6 million years ago (Besenbacher, Hvilsom, Marques-Bonet, Mailund, & Schierup, 2019; Chapais, 2015).

4.2. Leadership, knowledge, and dominance in humans

Humans, like many social species, form social hierarchies that regulate access to resources (Durkee, Lukaszewski, & Buss, 2020; Hawley, 1999; Qu, Ligneul, Van der Henst, & Dreher, 2017). In some cases, these hierarchies are based on individual and coalitional formidability, and are therefore probably homologous to non-human primate dominance hierarchies (Barkow, 1989; Chapais, 2015; Henrich & Gil-White, 2001; Tiger & Fox, 1997). Leadership involving aggression, punishment, and fear is well-supported in the ethnographic record (Garfield, Hubbard, & Hagen, 2019; Garfield, von Rueden and Hagen, 2019; Garfield et al., 2020). Nevertheless, small-scale societies, especially mobile huntergatherers that are thought to be the best analogs of ancestral human societies, tend to be relatively egalitarian, i.e., there are limited differences in access to resources and political influence among adults (Boehm, 1999; Leacock, 1978; Lee & Daly, 1999; Woodburn, 1982).²

Most explanations of egalitarianism depend on aspects of huntergatherer social organization that differ from our close primate relatives and that sharply limit the scope of individuals to benefit by physically threatening others. These explanations include the unpredictability of hunting and the need to pool risk via widespread sharing within and across groups (Cashdan, 1980, 1985; Lee, 1968; Washburn & Lancaster, 1968; Wiessner, 1982); the inability to store resources, which hampered the accumulation of wealth (Borgerhoff Mulder et al., 2009; Woodburn, 1982); the high risk of injury from hunting large prey and defending kills from other predators, which required individuals to act prosocially to accumulate sufficient social capital for their care during extended periods of disability (Gurven, Allen-Arave, Hill, & Hurtado, 2000; Sugiyama, 2004); the possession of lethal weapons by all adult men, and the ability to form coalitions, which reduced the ability of stronger individuals to physically dominate others (Bingham, 2000; Boehm, 1993, 1999; Gintis, van Schaik, & Boehm, 2015; Isaac, 1987; Woodburn, 1982); and the option, in residential groups that expand, contract, and shift according to resource availability, to join relatives in other groups, or to form new ones (Bettinger, Garvey, & Tushingham, 2015; Grove, 2009, 2010; Grove, Pearce, & Dunbar, 2012; Hamilton, Buchanan, & Walker, 2018; Kelly, 1983, 1995; Shaw & Stock, 2013; Tallavaara, Eronen, & Luoto, 2018), which allowed individuals to vote with their feet and avoid domination (Chapais, 2009; Lee, 2018).

It is critical to our argument that in egalitarian societies, unlike stratified societies, there are few if any formal leadership positions, and there is typically no requirement to follow or obey leaders nor to assume a leadership role. Hence, individuals who follow leaders, and those who assume a leadership role, must construe it to be in their interests to do so. The typical pattern is that in community discussions, the opinions of some individuals carry more weight than others. Given the constraints on physical domination and coercion, these individuals have gradually acquired and maintained influence with a lifetime of beneficial contributions to their communities (Boehm, 1993; Fried, 1967; Henrich, Chudek, & Boyd, 2015; Henrich & Gil-White, 2001; Macfarlan, Remiker, & Quinlan, 2012; Price & Van Vugt, 2014; Service, E. R, 1964; Woodburn, 1982).

As in many animal species, human leadership and status in both egalitarian and stratified societies appears to depend, in part, on asymmetries in information. Theoretical and empirical studies propose that individuals gain influence and respect for their knowledge and expertise in culturally valued skills, such as procuring resources, parenting, oration, politics, religious and ritual activities, and warriorship (e.g., Barkow, 1989; Cavazotte, Moreno, & Hickmann, 2012; Connelly et al., 2000; Henrich et al., 2015; Henrich & Gil-White, 2001; Judge, Colbert, & Ilies, 2004; Roscoe, 2007; Van Vugt & Kurzban, 2007; Wilson, Near, & Miller, 1996).

In a study of 1212 ethnographic records on leadership traits from a probability sample of 60 cultures in the Human Relations Area Files (HRAF), which included both egalitarian and stratified societies, "knowledgeable/intelligent" and "experienced/accomplished" were the second and third most commonly mentioned traits, each appearing in

² For arguments that some Late Pleistocene societies were larger and more stratified, see Jochim (1987), Moreau (2020), and Singh and Glowacki (2022). For evidence of permanent wooden structures in the Middle Pleistocene, suggesting some sedentism, see Barham et al. (2023). Ancient and modern DNA evidence, indicates, however, that the effective population size of Upper Paleolithic foragers was small, and that their social and reproductive behavior was similar to modern day foragers (Sikora et al., 2017).

about 80 % of cultures (high status was the most common trait). These qualities characterized leaders in social contexts ranging from subgroups within communities to multi-community groups. See Table 1. The three most common functions of leaders were resolving conflict, organizing cooperation, and providing counsel and direction. In aggregate, numerous qualities and functions indicated that many (but not all) leaders were prosocial. Both leaders and followers obtained material, social, and mating benefits (Garfield et al., 2020). Leaders in hunter-gatherer societies also play a central role in teaching social norms (Garfield & Hagen, 2024). We term leaders in this mold *knowledge-based* leaders.

4.3. The computational challenges of decision-making

Humans make innumerable decisions every waking moment: when to move, and where: what to look at: what to eat: which individuals to engage with: what to say: and what tasks to perform. Over human evolution, there was strong selection to discriminate decision options that produced benefits from those that incurred costs. Many decisions were both frequent and consequential. Ancestral mobile foragers, for instance, would have needed to assess the net payoff of each possible destination: its quantities of food and water minus costs such as the abilities of adults, children and the ill to travel the necessary distance, and competition with other bands and predators. A poor choice of destination could have been disastrous. Other decisions, such as who to marry, occurred much less frequently but were especially consequential. Such decision-making can be extraordinarily computationally complex, so much so, we propose, that individuals who were good at it offered it as a computational service. Combined with other traits, such as prosociality and having allies (Garfield, von Rueden, & Hagen, 2019; Glowacki & von Rueden, 2015), some such individuals eventually rose to become knowledge-based leaders with community-wide influence.

In decision theory, the individual agent has a set of decision options; a function that for each decision either specifies the outcome or the probability distribution over the set of outcomes; a utility function that specifies the utility of each outcome; and an ability to determine the decision(s) with the highest utility, or, in the case of probabilistic outcomes, the highest expected utility (Savage, 1954). In some evolutionary models, utility is biological fitness, and strategies are optimized by natural selection. In other evolutionary models, computational machinery evolves under natural selection to make decisions that maximize a proxy of fitness, such as the rate of energy intake (Hagen et al., 2012).

Here we focus on evolved decision-making machinery that (approximately) maximizes a fitness proxy, which can be surprisingly computationally complex. The famous traveling salesman problem (TSP), for example, one of a large class of discrete combinatorial optimization problems, involves finding the shortest path through a set of fixed locations, which has obvious relevance to optimal foraging theory (Trapanese, Meunier, & Masi, 2018). To determine the shortest path through only 10 locations, a forager using brute-force search would have to calculate the lengths of $10! \sim 3.6 \times 10^6$ paths, and for $20, 20! \sim 10^{18}$ paths,³ which is computationally intractable. The dinner party problem involves taking a list of *n* acquaintances and a list of all pairs of them who are not on speaking terms, and determining the maximum number of acquaintances that can be invited to a party without inviting any two that are not on speaking terms. The complexity of this problem, which has obvious relevance to forming cooperative groups, grows as 2^n , and is thus computationally intractable for large n (Arora & Barak, 2009). Planning an optimal sequence of actions to achieve a goal is likewise often computationally intractable, as is optimal diagnosis and treatment of illnesses (Arle & Carlson, 2020; Blondel & Tsitsiklis, 2000; Geffner,

Table 1

Representative quotes from the ethnographic record on leaders in huntergatherer cultures that were coded as knowledgeable and intelligent in Garfield, Hubbard, and Hagen (2019) and Garfield et al. (2020). Parts relevant to knowledge and intelligence indicated in bold. These quotes also illustrate other important leader qualities and functions.

Hunter- gatherer culture	Quote	Reference
Blackfoot	The young man ambitious of [achieving chiefdomship] sought to be conspicuous for energy and daring in war, intelligence in council , and liberality in giving feasts and providing tobacco for the guests of his lodge. The exhibition of these qualities in more than ordinary degree would win him the respect and confidence of one after another of his band, who were ready to follow his guidance and accept his council.	Ewers (1955)
Pawnee	Bravery, wisdom , and personal popularity were the important factors in acquiring and retaining influence and authority[T]he man chosen to [become chief] had to demonstrate humility, generosity, and sagacity , because a jealous or aggressive temperament was considered unbefitting a chief.	Grinnell (1889); Murie (1989)
Bororo	That knowledge is highly valued among the Bororo is substantiated by the fact that the chief of a village is always the most knowledgeable man. Social status and functions are connected with particular lineages and transmitted matrilineally, but the true influential leaders and authorities are the men who excel in knowledge.	Levak (1973)
Mbuti	This respect for age, and for the opinions of wise old men , is the basis of pygmy governmentbut as some of the old men are considered eccentrics and freaks, little attention is paid to them.	Putnam (1948)
Copper Inuit	Ikpakhuak himself professed no shamanistic powers, yet his personal dignity, his sagacity , and his prowess as a hunter won him the most prominent place among the natives of this region.	Jenness (1922)
Andamans	Age factor is not very vital for headmanship. The man who is physically sound and considered active and witty is picked up. The members of the group start considering his views and regard the same as more than those given by any body else. The headman's views carry weight and are attended accordingly.	Mann (1979)
Ojibwa	Within a hunting group, the senior male member was most often recognized as headman of the group. His leadership was based on his age, knowledge and skills as a hunter, perhaps also on his reputation as a shaman, and he fulfilled his role as leader through his ingenuity , personality and his enjoyment of the group's approval.	Hansen (1987)
Mataco	But although a Toba may inherit the chieftainship from his father, he must always display certain prominent qualities to be approved of by his people. These qualities are valour, skill, and experience in making war, as well as intelligence and eloquence	Hansen (1987)
Tlingit	Other important criteria for selecting the incumbent's successor included leadership potential, eloquence, high morality, wisdom, and the knowledge of the sacred traditions of his own and other matrilineal groups.	Kan (1989)

³ There are *n* possible locations to visit first, n - 1 to visit second, n - 2 to visit third, and so forth. The number of possible paths is therefore *n*!, the factorial of the number of locations, which increases very rapidly with *n*.

2013).

Herbert Simon recognized early on that optimal decision-making was sharply bounded by limits on information and computing capacity. He introduced bounded rationality, the idea that real decision-makers use heuristics to solve optimization and other computationally challenging problems, often drawing on the structure of information in the environment (Simon, 1955, 1972). Simon and many others have attempted to create formal frameworks of bounded rationality, including satisficing (Simon, 1956), aspiration adaptation theory (Selten, 1990, 1998), Modeling Bounded Rationality (Rubinstein, 1998), simple, or fast and frugal heuristics (Gigerenzer & Selten, 2002; Gigerenzer & Todd, 1999) and the related term ecological rationality (Goldstein & Gigerenzer, 2011), fixed parameter tractability (Van Rooij, 2008), and resource rational analysis (Lieder & Griffiths, 2019). Although some have sparked fruitful research programs, none have gained widespread acceptance. For recent reviews, see Gershman, Horvitz, and Tenenbaum (2015), Bossaerts and Murawski (2017), Bossaerts, Yadav, and Murawski (2019), Van Rooij, Blokpoel, Kwisthout, and Wareham (2019), and Lieder and Griffiths (2019).

4.4. Joint utility improvement: Knowledge-based leaders as decisionmaking specialists

With the transition to a more carnivorous dietary niche in more open habitats, human fitness increasingly depended on close cooperation in larger groups; and groups, like individuals, must make decisions. Group decision-making differs from individual decision-making, however, because although group members benefit by belonging to a group, they pay a consensus cost when the group decision differs from their optimal outcome, as it often will when there are conflicts of interest. High consensus costs for some, in turn, can precipitate group fissioning (Conradt & Roper, 2007; Davis, Crofoot, & Farine, 2022), which, compared to resolving conflicts and maintaining cooperation, reduces the fitness of all. Based on patterns in contemporary foragers, human groups comprised a complex mix of biological kin, affinal kin, and unrelated individuals (Fig. 7), likely as a consequence of sexual egalitarianism and strong pair bonds (Dyble et al., 2015). Group members therefore had many inherent conflicts of interest that could jeopardize cooperation.

In all human communities, this complex mix of individuals is organized into multiple, overlapping groups. Although some anthropologists deny that hunter-gatherers have levels of social organization between the band and population levels, emphasizing instead wide-ranging social networks among individuals (e.g., Bird, Bliege-Bird, Codding, & Zeanah,

2019), most researchers have identified a modular or nested structure. The reproductive group (i.e., family) typically comprises a pair-bonded male and female who both invest in their joint offspring. Several reproductive units are nested within a subsistence or residential group (e.g., a hunter-gatherer band) that cooperates to acquire food (e.g., social hunting) and raise children (alloparenting). Multiple subsistence groups are nested within one or more larger groups that periodically aggregate to forage, exchange information, trade material goods, exchange marriage partners, and defend territory; these groups, in turn, usually, but not always, belong to an ethnic population that speaks a common language (Binford, 2001; Birdsell, 1958; Hill et al., 2011; Kaplan, Hill, Lancaster, & Hurtado, 2000; Murdock, 1949; Rodseth et al., 1991; Roscoe, 2009). The hierarchical structure of huntergatherer groups has a branching ratio of about 4: individuals are organized into families of about 4, which are organized into bands of about 4 families, which are organized into macrobands of about 4 bands, and so forth, with about 2 more levels, resulting in a regional population of around 1000 individuals (Hamilton, Milne, Walker, Burger, & Brown, 2007)

There are conflicts of interest at each level of the nested hierarchy, including within-family sibling competition over parental investment, parent-offspring conflict, and spousal conflict over levels of parental investment; within-group competition over resources and access to mates; and between-group competition over territory, game, and possibly mates (Chagnon, 1988; Codding et al., 2019; Moritz et al., 2020; Parker, Royle, & Hartley, 2002). See Fig. 8.

In one model of decision making, there is a tradeoff between reward and cognitive cost, such that more complex decision rules yield greater rewards, but incur greater cognitive costs (Lai & Gershman, 2024). Individuals with greater computational resources could therefore identify decision options yielding greater rewards. We propose that knowledgebased leaders rise to their positions, in part, by using their exceptional decision-making abilities and knowledge to resolve group conflicts, organize cooperation, and provide counsel and direction in ways that benefit most group members. Alliances and conflicts among bands, especially lethal conflict (warfare, Glowacki, 2024), might have posed especially strong selection pressures on decision-making abilities because individuals at the high end of the decision-making spectrum were competing with their counterparts in other groups (Alexander, 1990; Bowles, 2009; Chagnon, 1988; Choi & Bowles, 2007; Flinn, Geary, & Ward, 2005; Gavrilets & Fortunato, 2014). In a study of settled huntergatherers, perceived conflict resolution skills were indeed associated with perceived decision-making expertise and intelligence (Garfield & Hagen, 2024), and in an ethnographic sample of 59 largely



Fig. 7. Co-residence patterns across modeled and observed egalitarian populations. Chart area represents the proportion of all dyads across nine categories of relatedness for the egalitarian model (left), Agta (middle left), Mbendjele (middle right), Ache (bottom right), and Ju/'hoansi (top right). Ache and Ju/'hoansi data redrawn from Hill et al. (2011). Figure and caption from Dyble et al. (2015).



Fig. 8. A typical hunter-gatherer band. There are potential intra- and inter-familial conflicts over parental investment, mates, and resources. Siblings compete over the investment from parents (sib competition). Offspring have different interests from their parent(s) over investment (parent–offspring conflict). Where both parents invest, they are in conflict over the amount each should give (sexual conflict). Members of different families cooperate within bands, but nevertheless compete over resources, and adult members compete over access to mates. Bands cooperate and compete over territory and game. Figure and caption modified from Parker et al. (2002).

nonindustrial societies, evidence for conflict resolution by leaders was similarly associated with representing the group in between-group interactions and providing counsel to followers (Garfield, 2021).

The Meat Fight (Marshall, 1974), a film of!Kung foragers resolving a dispute, illustrates conflict resolution by a skilled mediator. A young hunter shot a large antelope, but then lost track of it. It was found by a hunter from another band, who distributed the meat to his group. Although the second hunter had rights to some meat, he did not have the right to distribute it, which belonged to the owner of the arrow that killed the animal. An angry confrontation between the hunters ensued, drawing in members of their respective bands. At this point, each actor had many decision options, such as verbal or physical attacks, taking meat, providing further justifications, backing one party or the other, or walking away, each with substantive consequences for their future relationships, and each interacting with those of the other actors, creating a large combinatorial space of possible outcomes. A respected individual from a third band then stepped in, confirming ownership of the arrow, but also offering a compromise that was accepted by all: the first hunter would get his share of meat and the father of the second hunter would distribute the rest according to established norms.

We conceptualize such decision-making that discovers an option benefiting both the decision-maker and fellow group members as a computational service we term *joint utility improvement* (JUI).

5. Payment: Sexual selection of leader and shaman traits

James Neel, a major figure in twentieth century genetics, observed that in small-scale societies leaders are often polygynous and have more children than other men (Neel, 1980; Neel & Salzano, 1967; Neel, Salzano, Junqueira, Keiter, & Maybury-Lewis, 1964). Neel reasoned that if this pattern characterized most human societies during our evolution, there would have been strong sexual selection for the trait(s) that predisposed men to ascend in social rank and become community leaders. What traits would men value in other men? Leaders are often skilled hunters, warriors, orators, and masters of tribal lore. Neel therefore argued that although physical strength is an asset in campaigns for leadership in small-scale societies, *mental agility* is even more critical, i. e., that there was social and sexual selection on cognitive abilities (Neel, 1980; Neel & Salzano, 1967), an early version of what would later be known as the social intelligence hypothesis. Because sexual selection often results in exaggerated traits, this could explain the dramatic increase in human cranial capacity in the genus *Homo* (Fig. 2).

The contributions of Neel and colleagues have been largely forgotten, yet the problem of human encephalization remains unsolved, and popular explanations, such as social intelligence (e.g., Byrne & Whiten, 1988; Humphrey, 1976; Whiten & Byrne, 1997), extractive foraging (Kaplan et al., 2000; Milton, 1988), and social learning and culture (Boyd & Richerson, 1985; Boyd, Richerson, & Henrich, 2011) ignore the possible role of reproductively successful leaders. (For recent treatments of influential hypotheses for encephalization, see Ashton, Thornton, & Ridley, 2018; DeCasien, Williams, & Higham, 2017; Gonzalez-Forero & Gardner, 2018; Muthukrishna et al., 2018; Powell, Isler, & Barton, 2017; Rosati, 2017; Street, Navarrete, Reader, & Laland, 2017).

Male reproductive skew is observed in many non-human species (Kokko, 2003; Shen & Reeve, 2010; Vehrencamp, 1983). In non-human primates, for example, the association between male status and reproductive success (RS) is r = 0.80 (Cowlishaw & Dunbar, 1991). There is ethnographic evidence for mating benefits for leaders in about 50 % of cultures but mating benefits for followers in only about 10 % of cultures (and in the remaining cultures, simply a lack of evidence, Garfield et al., 2020). A meta-analysis of the association between male status and various indices of reproductive success (RS) in 33 non-industrial societies that included hunter-gatherers, pastoralists, and agriculturalists found a mean effect size of r = 0.19, which did not vary among societies of different subsistence types (von Rueden & Jaeggi, 2016).

There is also limited evidence for the greater reproductive success of shamans and other healers. Of 131 married Ju/'hoansi (!Kung) men, for example, all 7 who were polygynous were also healers, and 5 of the 7 had reputations as the strongest and most effective healers in the area. The wives of these 5 expressed pride in their husbands' abilities, and were themselves among the strongest singers in the all-night healing dances (Lee, 1993). A !Kung shaman stated, "The women really did like the healers. Whenever I see one who is getting num [healing energy], I say, 'Think of the sex the guy's going to get!''' (Katz, 1982, p. 186; quoted in Singh, 2018). A survey of ethnomedical and ethnoscientific experts similarly found a cluster of cases with increased access to, or provisioning of mates (Lightner et al., 2021b; see also Singh, 2018).

Genetic evidence indicates that ancestral human societies also exhibited male reproductive skew. Comparisons of variation in mtDNA (inherited from mothers only) to non-recombining Y chromosomal regions (inherited by sons from fathers only) in large multi-regional samples of genomes found that, prior to the migration of modern humans from Africa, female effective population size was consistently larger than that of males, i.e., relatively fewer males reproduced (Karmin et al., 2015; Lippold et al., 2014). This could indicate either a long evolutionary history of polygyny, sex-specific migration, and/or matrilineality (Oliveira et al., 2018). A comparison of levels of neutral genetic variation on the X-chromosome and autosomes, which can be used to infer joint effects of historical changes in life history and population size, likewise suggests (albeit with many caveats) that prior to the Out-of-Africa bottleneck, ancestral human populations were highly polygynous (Amster, Murphy, Milligan, & Sella, 2020).

It is not clear whether male reproductive skew in contemporary small-scale societies or in ancestral populations is primarily a result of male-male competition (Puts, Carrier, & Rogers, 2023), female choice (Barkow, 1989), some combination of the two, or other processes, such as parental choice (Apostolou, 2017). Evidence that women find prestigious men to be sexually attractive (Schmitt, 2014) suggests that female choice played some role. Evidence that women were mating with a subset of adult men, however, does not indicate which male traits, if any, were shaped by sexual selection.

Furthermore, depending on the precise mechanism, sexual selection can have positive or negative effects on population fitness. High male investment in a trait that increases mating success, for instance, would reduce the ability to invest in offspring, or the trait can be detrimental when expressed in females (intralocus conflict) (Rowe & Rundle, 2021). Unfortunately, Neel did not explain how intelligence enabled men to achieve leadership roles or acquire multiple mates. Such men could be preferred as mates because they are able to provide more resources (Barkow, 1980, 1989; Barkow et al., 1975), or have higher genetic quality (Miller, 2000), which are plausible hypotheses, but neither explain why such men would achieve status with other men. Influential theories of male status and prestige (Gavrilets & Fortunato, 2014; Henrich & Gil-White, 2001; Hooper, Kaplan, & Boone, 2010; Price & Van Vugt, 2014; Van Vugt & Kurzban, 2007), on the other hand, fail to explain mating success. We refer to this disjunct as the conundrum of prestige (Garfield, Hubbard, & Hagen, 2019).

Although the conundrum of prestige can be resolved in many ways (e.g., both sexes value good hunters), we highlight one. Because human reproduction occurred in highly cooperative groups known as families, women valued knowledgeable and intelligent men for largely the same reasons other group members did: such men were more likely to make good decisions that benefited their families (JUI). Moreover, their influence would align group decisions with the interests of their families, reducing consensus costs.

Families, which can take diverse forms (Sear, 2021), are universally organized around a long-term pair-bond between a man and a woman cooperating to raise their joint offspring (Chapais, 2013; Kramer, 2021; Quinlan, 2008; Quinlan & Quinlan, 2007; Schacht & Kramer, 2019). Polygyny is permitted in most societies, including most hunter-gatherers (Marlowe, 2000). Long-term mateships, especially those involving two or more wives, are similar to other cooperative groups that benefit from leadership abilities: they involve cooperation by two or more unrelated individuals to raise their joint offspring over a period of perhaps 20 years or more, but who also have numerous potential conflicts over, e.g., investment in offspring from the current and previous mateships, investment in one wife vs. others, investment in genetic kin vs. affines, and other mating opportunities. Divorce is expected when the costs of a mateship outweigh the benefits, and divorce rates are indeed high in some small-scale societies (Blurton Jones, Marlowe, Hawkes, & O'Connell, 2000; Hewlett, 1991). Those, like knowledge-based leaders, who are adept at finding JUI solutions, thereby avoiding costly conflicts such as divorce, and enjoying better outcomes, would be especially valued. Indeed, there is increasing evidence that fathers provide their children with valuable computational services like education and conflict resolution, and that children in families with less conflict have better outcomes (Gettler, Boyette, & Rosenbaum, 2020).

In our model, in addition to increasing male mating success, male investment in energetically expensive brain tissue would have directly benefited females. Moreover, as we argue next, expression of the relevant alleles in females would also have benefitted females, thus aligning sexual and natural selection (Rowe & Rundle, 2021).

6. Mothers as archetypal leaders and healers

Humans live in multilevel societies, e.g., families are nested within residential groups, which are nested within supracommunity political groups, and there are often leaders at each level. Across cultures, although women certainly play important political roles at each level, almost all leaders identified in the ethnographic record are men, and almost all of these are at the residential (community) level or above (Garfield et al., 2020; Garfield, Hubbard, & Hagen, 2019; Low, 1992). We propose that knowledge-based leaders at the family level, however, are usually women.

Compared to other primates, hominids (humans and other great apes) have exceptionally large brains that take many years to fully develop (Gómez-Robles, Nicolaou, Smaers, & Sherwood, 2024; Rilling, 2014). Consequently, hominid infants require substantial postnatal care. We and others propose that key components of this care are the computational services that mothers provide to their cognitively immature offspring that their offspring cannot yet provide for

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themselves (Humphrey, 2010; Piantadosi & Kidd, 2016). These services include rapid detection of threats in highly dynamic socioecological conditions, choices of food, and transmission of learned information (Garfield et al., 2016; Hayashi & Matsuzawa, 2017; Hrdy, 1999; Matsuzawa et al., 2001; Otali & Gilchrist, 2006). The computational complexity of these services increases dramatically when infants are capable of moving independently of the mother (cf. Piantadosi & Kidd, 2016). In short, mothers are making good decisions for their children, and hence can be conceptualized as knowledge-based leaders of the family.

6.1. Uniquely human mothering challenges

Women in forager populations have relatively short interbirth intervals (~3 years) compared to chimpanzees (~4 years), and their children require provisioning for up to 20 years, compared to 5 years for chimpanzees (Davison & Gurven, 2021; Davison & Gurven, 2022). Human mothers are therefore simultaneously raising multiple offspring of different ages with different needs, unlike chimpanzee mothers who typically care for one dependent offspring at a time, and unlike species with large litter sizes whose offspring are the same age and have the same needs. Human mothers must develop, maintain, and update a cognitive model of each child, supplying a constant stream of childspecific computational and other services, most of which require accurate inferences about many aspects of the offspring's state, e.g., hungry, sick, scared, happy, interested, or bored, capabilities termed theory of mind and perspective-taking (Lamm, Batson, & Decety, 2007; Martin & Santos, 2016; Premack & Woodruff, 1978; Schaafsma, Pfaff, Spunt, & Adolphs, 2015; Underwood & Moore, 1982).

Moreover, unlike chimpanzee mothers who provide all food for themselves and their nursing infants, human mothers invest heavily in their dependent offspring in exchange for provisions from the father, grandparents, and others (Davison & Gurven, 2021; Davison & Gurven, 2022) in a sexual division of labor (Kelly, 2013), an arrangement that supplies high levels of energy but requires greater coordination and cooperation. See Fig. 9. Much of this maternal investment involves provisioning their children with informational resources like ecological, social, subsistence, and language skills, and social norms and cultural values (Garfield et al., 2016; Jang et al., 2024).

Because a woman and her children are only related by r = 0.5, their interests are not perfectly aligned (Mock & Parker, 1997; Royle, Smiseth, & Kölliker, 2012; Trivers, 1974). A decision that might optimize an outcome for a child, such as providing it more food or attention, might not optimize the outcome for the mother, who might benefit more by providing the food and attention to a needier child. Mothers constantly face the challenge of making decisions for cognitively immature offspring that improve child outcomes while at the same time improving their own outcomes, an example of JUI that is similar to the decision



Fig. 9. Net productivity of female chimpanzees and human foragers in kcals by age. Female data from Davison and Gurven (2021), Davison and Gurven (2022). Hadza male surplus value from Kraft et al. (2021). Gaussian kernel smoothing applied to noisy female human data for ages above 39.

making services provided by knowledge-based leaders at the community level. See Fig. 8.

Mothers also employ traditional medicine related to pregnancy, childbirth, lactation, and childcare (Deb & Emdad Haque, 2011; Placek et al., 2017; Shewamene, Dune, & Smith, 2017; Sibeko & Johns, 2021; Sibeko, Johns, & Cordeiro, 2021; Towns, Mengue Eyi, & van Andel, 2014), which requires the same cognitive abilities as shamans and other healers (who in small-scale societies are predominantly men, Singh, 2018). In a group of Congo Basin foragers, for example, mothers with higher medicinal plant use scores had healthier children (Salali et al., 2016). More generally, autonomous decision making by mothers and maternal status are both positively associated with better nutritional outcomes in offspring (Alami et al., 2020; Engle, 1991; Starkweather & Keith, 2018).

Finally, humans rely heavily on alloparental care (Hrdy, 1999, 2011), much of it provided by older siblings (Kramer, 2010). Human mothers are therefore typically supervising and training multiple dependent offspring, and managing the alloparenting of their younger children by their older children, while also managing the social relationships that are essential to obtain resources, all of which increase the complexity of the computational challenges they must solve relative to other apes. This perspective is supported by the emerging literature on mental labor, also termed cognitive, mnemonic, or invisible work/ labor, or sometimes prospective memory, which focuses on the cognitive dimensions of mother's unpaid domestic work and childcare (and is distinct from emotional labor, which involves fostering others' wellbeing). Mental labor involves information encoding, storage, processing, and retrieval, and decision-making in the service of monitoring, managing, planning, organizing, instructing, and delegating for the benefit of mothers' families and communities (Weeks & Ruppanner, 2024). Mental labor often entails high cognitive load, i.e., high levels of multitasking and utilization of working memory (Haicault, 1984; for review, see Reich-Stiebert, Froehlich, & Voltmer, 2023).

In summary, we propose that there has been long-standing natural selection in females, most of whom were mothers, for the cognitive abilities necessary for conflict resolution, organizing cooperation, providing counsel, diagnosis, treatment, and other abilities underlying knowledge-based leadership and healing at the family level. In parallel, there has been sexual selection for the same cognitive abilities in the fewer polygynous male leaders and healers at the community level.

7. Adaptations for computational services

We propose that the cognitive adaptations underlying computational services are analogous to key capabilities underlying modern day cloud computing services. We highlight two: a "network protocol" capable of sharing complex information, and the ability of applications to serve many users, processing user-specific information. We also propose one adaptation—joint utility improvement (JUI)—related to leadership, and one—identification of pharmacological plant substances—related to healing.

Language: Although we are not offering a comprehensive theory for the evolution of language (for reviews of such theories, see Corballis, 2017; Everaert et al., 2017; Fedorenko, Piantadosi, & Gibson, 2024; Fishbein, Fritz, Idsardi, & Wilkinson, 2019), the potential fitness benefits from computational services would have been a selection pressure for improvements in communicating complex information, which, in turn, would have increased the scope for profitable computational services. We therefore propose a synergistic coevolution of language and the psychological adaptations underlying computational services.

Context switching: The nervous system provides individuals with an enormous number of information processing capabilities, universal in the species, which, to generate fitness benefits, must nevertheless take into account individuals' current *state*, such as their age, sex, hunger, acute and chronic illnesses and injuries, physical location, and social environment – in other words, all the fitness-relevant factors that might vary from one person to another. We refer to the values of these factors as individuals' *state vectors*. A primary theoretical contribution of the computational services model is the hypothesis that humans evolved the ability to substitute the state vectors of *others* for their own state vector, thereby enabling their CNS circuitry to compute outcomes, such as optimized decisions, as if they were another person. As noted earlier, there is increasing evidence for such capabilities, e.g., theory of mind and perspective-taking (Lamm et al., 2007; Martin & Santos, 2016; Premack & Woodruff, 1978; Schaafsma et al., 2015; Underwood & Moore, 1982). Individuals with more computational resources or information could potentially offer "clients" better assessments, decisions, and other computed outcomes than the clients could provide themselves.

Joint utility improvement (JUI): Classic game theory models of optimal decision-making, such as the prisoner's dilemma, typically involve a few agents with a few decision options (e.g., two agents with two options). Reality is more complex. Computational services provided a means for providers to influence the behavior of clients in ways that benefitted the providers. Yet this avenue of influence required that clients benefitted too. As providers in small-scale foraging societies context-switched to evaluate client options, many of which would have had downstream impacts on the provider, they must also have evaluated the implications for their own fitness. Jointly improving fitness likely required specialized cognitive mechanisms to search a large combinatorial space of options to (hopefully) discover a few mutually beneficial ones.

Plant pharmaceutical identification system: The human plant nutrient identification system involves numerous specialized taste receptors and other nutrient-sensing proteins (Efeyan, Comb, & Sabatini, 2015; Raka, Farr, Kelly, Stoianov, & Adeli, 2019), combined with individual and social learning based on intricate gut-brain feedback systems (Li et al., 2022; Mayer, Nance, & Chen, 2022; McDougle et al., 2024; Olsson, Knapska, & Lindström, 2020). We propose an analogous evolved system specialized to identify pharmacological plant compounds that would be effective against human pathogens yet be reasonably non-toxic to humans. Pathogens are among the strongest and most ancient selection pressures, driving the evolution of elaborate immune systems across the tree of life, with some human immune modules likely evolving prior to the divergence of eukaryotes from prokaryotes, billions of years ago (Bernheim, Cury, & Poirier, 2024). The increasing evidence that vertebrates and invertebrates self-medicate infections with toxic plants (de Roode & Huffman, 2024) suggests the early evolution of innate pharmaceutical identification systems, which in some species might also involve individual and social learning. In humans, for example, the chemosensory qualities of botanical drugs (e.g., taste, smell) predict their therapeutic uses (Leonti, Baker, Staub, Casu, & Hawkins, 2024).

Our proposed system would be grounded in the extensive interactions among the immune system, brain, and gut (Agirman, Yu, & Hsiao, 2021). The gut contains communities of prokaryotes, eukaryotes, viruses, and (in many populations) helminths (Pfeiffer & Virgin, 2016) that interact with consumed plants on a daily basis (Collins & Patterson, 2020; Maurice, Haiser, & Turnbaugh, 2013). This gut microbiome, in turn, interacts extensively with the immune and central nervous systems (Sasso et al., 2023), and could therefore serve as a natural laboratory for the proposed system to determine which plant substances might be effective against pathogens.

8. Related evolutionary theories and concluding remarks

It is important to clarify what our theory is not. It is not a comprehensive evolutionary theory of leadership (many of which posit compensating benefits for costly leadership, Garfield, Hubbard, & Hagen, 2019; Garfield, Rueden, et al., 2019; Garfield et al., 2020; Pietraszewski, 2020; Price & Van Vugt, 2015), or of shamanism (instead, see, e.g., Lightner & Hagen, 2022; Peoples et al., 2016; Singh, 2018; Winkelman, 2002), or of mothering (instead, see, e.g., Hrdy, 1999, 2011), or of human encephalization (instead, see, e.g., Burkart et al., 2009; Gonzalez-Forero & Gardner, 2018; Kaplan et al., 2000; Muthukrishna et al., 2018; Navarrete, van Schaik, & Isler, 2011). Rather, our theory proposes that when there were asymmetries in information or computational resources, many of the diverse cognitive adaptations that evolved to benefit the individual could have been deployed as computational services to benefit others in exchange for various payments, thereby helping subsidize the large fixed energetic cost of maintaining the brain. Such services might help explain the emergence of leaders and shamans, key social roles in hunter-gatherer societies.

The computational services model is most closely related to theories of collective intelligence, collaborative problem solving, and divisions of cognitive labor. These theories generally propose that each agent solves part or all of a group- or population-level problem and then, as in our computational services model, provides that solution to others towards a collective solution (Couzin, 2009; Graesser et al., 2018; Hamilton, 2022; Henrich & Muthukrishna, 2023; Kemp, Kline, & Bettencourt, 2024; Krause, Ruxton, & Krause, 2010; McMillen & Levin, 2024; Momennejad, 2022; Muthukrishna & Henrich, 2016; Rabb & Sloman, 2024; Whiten, Biro, Bredeche, Garland, & Kirby, 2022). Swarm intelligence models, which are based on analogies with social insects, involve a large number of agents executing a simple algorithm that leads the swarm to a good solution (Krause et al., 2010). Collaborative problem solving models involve interdependent groups of individuals performing different cognitive tasks to solve novel problems (Graesser et al., 2018). Cultural evolution models involve agents individually acquiring socioecological information and skills that they socially transmit to others, increasing population-level knowledge and skills, which potentiates further individual innovation (Henrich & Muthukrishna, 2023; Muthukrishna & Henrich, 2016); in some versions there are guilds of specialists, which can increase overall population-levels of knowledge and skills but with increased risk of cultural loss (Ben-Oren, Kolodny, & Creanza, 2023).

Our computational services model encompasses these types of distributed cognition. Shamans and healers, for instance, acquire their valuable expertise from other shamans and healers, and our survey of the ethnographic record found extensive evidence for collaboration among knowledge specialists (Lightner et al., 2021b), similar to specialist guilds (Ben-Oren et al., 2023). But our model also includes cases where proprietary expertise is exchanged for payments: where single individuals provide good solutions to computationally complex problems, such as those involving combinatorial optimization, to give one example, or where asymmetries in knowledge and/or computational resources are stark, such as mothers making good decisions for their young children. Our individual-level approach also naturally admits extensions like biological markets (Hammerstein & Noë, 2016) for computational services, cultural production (André, Baumard, & Boyer, 2023), interdependence (Aktipis et al., 2018; Lightner, Pisor, & Hagen, 2023; Roberts, 2005; Syme & Balliet, 2024; Tomasello, Melis, Tennie, Wyman, & Herrmann, 2012), and related proposals that group members will invest in those who provide valuable services to the group (Gurven et al., 2000; Sugiyama, 2004; Sugiyama & Sugiyama, 2003; Tooby & Cosmides, 1996).

In conclusion, we highlighted four major selection pressures that likely began to act on the human lineage near the beginning of the Pleistocene with the transition to a more meat-based diet in open terrestrial habitats with greater exposure to predators: the need to resolve conflicts and maintain cooperation in larger multilevel societies; the need for greater pathogen defense; the greater complexity of mothering with shorter interbirth intervals, longer periods of juvenile dependency, and a sexual division of labor; and the need to make more efficient use of an increasingly large and energetically expensive brain. We argued that each of these selected for the cognitive abilities to provide computational services to others, usually via, and perhaps helping select for, an increasingly sophisticated vocal signaling system that would eventually evolve into language.

The computational services model provides several insights. First,

headmen and similar respected leaders in small-scale societies can be conceptualized, in part, as specialists in decision-making and conflict resolution, which are often computationally demanding, and who can provide decision options that benefit most group members, including themselves, while minimizing consensus costs. Second, shamans and other healers can be conceptualized, in part, as specialists in diagnosing and treating illness, which are also often cognitively demanding yet highly valuable to group members. Pathogen defense thus emerges as a selection pressure for encephalization, in addition to the widely recognized selection pressures of extractive foraging and sociality. Cognitively demanding leadership and healing services, which are typically compensated in some way, are also valuable within families, resulting in sexual selection for the underlying cognitive abilities in fathers and contributing to encephalization. At least as important, if not more so, these cognitive abilities were also subject to natural selection in mothers caring for multiple, highly dependent offspring, thus contributing to encephalization. Mothers can therefore be conceptualized as familylevel leaders and healers, contrary to the prevailing view that these roles were mostly occupied by men.

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Edward H. Hagen: Writing – review & editing, Writing – original draft, Conceptualization. Zachary H. Garfield: Writing – review & editing, Conceptualization. Aaron D. Lightner: Writing – review & editing, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

No new data was generated for this article. Data are available from the cited sources.

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