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# The Meanings and Dividends of Man the Hunter

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ABSTRACT

The phrase Man the Hunter is associated with disparate meanings across communities of scholars, journalists, and the public, which has led to unnecessary scientific disagreement and popular misunderstanding. In this paper, we ask: what does Man the Hunter mean? We distinguish three historical meanings of Man the Hunter. First, in the early-to-mid 20th century, popular writers propagated ideas of human evolution that focused on hunting, men, aggression, rigid sexual divisions of labor, and immutable sex differences. These ideas gained widespread acceptance in popular circles and continue to be influential, but were rejected by anthropologists as early as the 1950s. Second, the *Man the Hunter* conference (1966) and resulting volume (1968) brought together hunter-gatherer scholars to synthesize how contemporary hunter-gatherers inform human prehistory. Third, Man the Hunter has referred to the field of hunter-gatherer behavioral ecology that studies how human behavior has adapted to local environmental contexts, and has offered a critical foundation for present-day knowledge about hunting and gathering lifeways and human origins, which we summarize. In the final section of the paper, we trace the historical development of these three meanings of Man the Hunter, situating their origins in evolutionary biology, ethnology, feminist studies, ethology, genetics, and other disciplines. While the latter two meanings were strongly intertwined, there was little intellectual exchange, and mostly antagonism, between these two and the earlier but still influential popularized meaning. Based on these disparate histories, conflating the three meanings of Man the Hunter should be avoided. We offer suggestions for improving scientific and popular discourse regarding Man the Hunter.

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## 1. Introduction

*In anthropology, as elsewhere, progress will never result from destroying what has been previously achieved but rather from incorporating the past of our science into its present and future, enriching the one with the other and turning the whole process into a lasting reality.*

- Claude Lévi-Strauss, concluding remarks at the *Man the Hunter* conference in 1966 (Lévi-Strauss, 1968)

*Man the Hunter's and UNESCO man's unmarked (and unremarkable) gender were part of the solution to one kind of racism at the inherited cost of unexaminable, unintentional, and therefore particularly powerful, scientific sexism.*

- Donna Haraway (1989, p. 201)

The phrase Man the Hunter has long been a flashpoint in the social sciences. An early critique condemned it as "a theory that leaves out half the human species" (Slocum, 1975). Today it is perhaps more controversial than ever. For instance, a recent series of academic articles exploring anatomical and physiological (Ocobock & Lacy, 2023), archaeological (Haas et al., 2020; Lacy & Ocobock, 2023) and ethnographic (Anderson, Chilczuk, Nelson, Ruther, & Wall-Scheffler, 2023) evidence for women's hunting have sought to revise established paradigms concerning gendered divisions of labor in the present and past. These papers have each been framed as critiques of Man the Hunter, labeling it a "myth" (Anderson et al., 2023, p.1) (Slocum, 1975) and a "paleo-fantasy"[1] (Lacy & Ocobock, 2023, p. 1). Associated media coverage, some of it written by professional anthropologists, declared that Man the Hunter has been killed, debunked, or dismantled (Gibbons, 2020; Aizenman, 2023; Alex, 2023; Criado, 2023; Flam, 2023; Lacy & Ocobock, 2023; Miller, 2023).

To others, however, Man the Hunter has a different meaning. The modern era of hunter-gatherer studies, one pillar of the science of human evolution that we will summarize here, began with the *Man the Hunter*[2] conference, held at the University of Chicago in 1966, and the eponymous conference volume that followed two years later (Lee & DeVore, 1968). This title emphasizing men's hunting obscured the diversity and breadth of views expressed at the conference and in the volume. Bringing together dozens of experts conducting research among hunter-gatherer (or forager) societies with diverse geographic specializations and theoretical perspectives, *Man the Hunter* synthesized existing knowledge and revolutionized the scientific and public conceptions of hunter-gatherers, presenting them as fully human masters of complex socioecologies who, ironically, often depended heavily on plant foods gathered by women (Lee, 1968). This meeting laid the foundation for decades of subsequent quantitative hunter-gatherer research (Kelly, 2013), including critiques of the original volume (Dahlberg, 1981; Tanner & Zihlman, 1976; Fedigan, 1986; Sterling & Zvelebil, 2014). According to one authority, *Man the Hunter* represented a "20th century watershed for knowledge about foragers" (Kelly, 2013, p. 9).

How do we explain these conflicting interpretations of Man the Hunter? We contend that terminological imprecision plagues the concept of Man the Hunter, perpetuating inaccurate conceptions about the beliefs of contemporary anthropologists and leading to false stereotypes, and resulting in the miscommunication of scientific findings (Aizenman, 2023; Alex, 2023; Criado, 2023; Flam, 2023; Lacy & Ocobock, 2023; Miller, 2023). It is now time to ask: what is the meaning of Man the Hunter (hereafter, MTH) and how has it impacted the science of human evolution?

To answer these questions, this paper explores critical interpretations of MTH in the context of older literature from the anthropological and archaeological sciences - including the prominent 'hunting hypothesis' - as well as popular science theories. This historical perspective enables us to delineate three distinct meanings of MTH, outlined below, and to argue that the term MTH, though a convenient shorthand, conflates different sets of scientific assumptions, empirical findings, and popularizations. Specifically, it 1) conflates different, even mutually incompatible theories; 2) misrepresents the position of past scholars, including the ~75 contributors to the 1968 MTH volume (Lee & DeVore, 1968), who held diverse views; and 3) miscommunicates findings from the contemporary anthropological sciences about hunter-gatherers and human evolution to broader public audiences. Our aim here is to disentangle distinct views, not to evaluate them. Critiquing controversial topics in the anthropological sciences is necessary and valuable, and looking back on the nuanced history of MTH can help scholars do so more accurately and carefully.

Finally, we argue that the most important dividends of MTH are the results of the nearly six decades of research that the conference and volume inspired. Conference organizers, their students, and other contributors launched multiple research projects to realize their vision of integrating paleoanthropology, primatology, and hunter-gatherer studies to help answer questions raised by MTH. We summarize their work that now provides a clearer view of human evolution.

## 2. Critical Interpretations of Man the Hunter

The idea that hunting - generally done by males - shaped human nature goes back centuries, if not millenia (Cartmill, 1992, 1995). In this broadest sense, MTH is an ancient theme. Cartmill, a prominent biological anthropologist, describes the closely related hunting hypothesis (HH) as "the first truly Darwinian explanation of human origins" because Darwin (1876), though not using the HH phrase, postulated that bipedalism, large brains, and tool use were shaped by hunting and arose in concert (Cartmill, 1996).

Across the 20th and 21st centuries, anthropologists and popular writers have employed the phrases MTH and HH to describe several different but related concepts. Perhaps most commonly, they refer to the idea that humans evolved from an australopith "man"-ape with aggressive instincts for both hunting and homicide, and that this heritage was a driving force in human evolution. Advocated most notably by South African anthropologist Raymond Dart (1953), and later by popular writer Robert Ardrey (1976), this version of the HH is often called the 'killer ape' theory (Cartmill, 1992, 1995; Sussman, 1999; Washburn & Lancaster, 1968).

Cartmill (1996) takes the HH's central proposition to be "that hunting and its selection pressures had made men and women out of our apelike ancestors, instilled a taste for violence in them, estranged them from the animal kingdom, and excluded them from the order of nature." MTH has also been applied (Sussman, 1999) to the idea that humans have inherited a propensity for violence from our last common ancestor (LCA) with chimpanzees because chimpanzees are one of relatively few species that also engages in war-like behaviors (Wrangham & Peterson, 1996). Similarly, MTH has been interpreted to mean early humans were fearless, bellicose apex predators, rather than prey (Hart & Sussman, 2008).

MTH has also been applied to the idea that contemporary hunter-gatherers have strong sexual divisions of labor (Conkey & Spector, 1984; Lacy & Ocobock, 2023). In this interpretation "the 'Man the Hunter, Woman the Gatherer' hypothesis" describes a "sexual division of labor where women were excluded from hunting" (Lacy & Ocobock, 2023, p. 2)

[1] The origin of the term 'paleofantasy' has been attributed to anthropologist Leslie Aiello. Speaking to journalist Michael Balter (Balter, 2008) about research on the evolution of human intelligence and geneticist Richard Lewontin's views about it, Aiello said that new research can "get us beyond the paleofantasy that Richard Lewontin is talking about."

[2] We use the italicized *Man the Hunter* when referring to the 1966 conference or 1968 publication. We do not use italicizations when discussing Man the Hunter in the more general sense.

or a "sexual division of labor with females as gatherers and males as hunters" (Haas et al., 2020). Elsewhere, MTH references the idea that there are "sex-specific gender roles" and "separate subsistence roles for females and males" (Anderson et al., 2023, p. 1), including the notion that "females engage in the majority of child-rearing activities"(Anderson et al., 2023, p. 1), that "men hunted, fought, and provided; women gathered, raised the kids, and tended the hearths" (Fuentes, 2017, p. 39) and that "men hunt big game while women procure vegetable foods and small game"(Panter-Brick, 2002, p. 627). Pontzer (2025, p. 193) wrote: "The traditional 'Man the Hunter' view, led these days by the Paleo bro contingent, paints a picture of macho cavemen hunting woolly mammoths and fighting over nurturing, plant-loving females. Those conditions, in their telling, led to the evolution of massive sex differences in bodies and behavior that are real and innate—differences that progressive, woke society foolishly or unfairly tries to extinguish. As with most pop-psych evolutionary storytelling, this view takes a kernel of biological reality and extrapolates it into fantasy, often to excuse (or encourage) men being jerks."

MTH is also taken to imply that an entrenched sexual division of labor extends to the deep past (Fuentes, 2017, p. 39; Lacy & Ocobock, 2023, p. 2), to "Prehistoric Man the Hunter" (*sensu* Lacy & Ocobock, 2023, p. 2): "the persistent assumption that Paleolithic foragers practiced a widespread deep sexual division of labor" and the associated assumption "that the sexual division of labor in the Pleistocene must have been extreme". To uncritically extend contemporary patterns of the division of labor into prehistoric contexts represents "a misapplication of modern forager studies to the past" (Lacy & Ocobock, 2023, p. 2). The repeated natural extension of this version of MTH is that women do not or cannot hunt (Anderson et al., 2023, p. 1; Hoffman, Farquharson, & Venkataraman, 2023), and that in today's societies, gender differences in domestic labor reflect gender differences in capabilities and preferences rather than differences in power and institutionalized sexism (Solnit, 2015). A future publication by our group will provide an in-depth evaluation of scientific theories and empirical evidence for and against the evolution of a sexual division of labor.

**Fig. 1.** A. The 1968 Man the Hunter conference gave rise to hunter-gatherer studies. B. Playwright Robert Ardrey's book *The Hunting Hypothesis* was based on Raymond Dart's Killer Ape Theory and proposed that humankind descended from vicious predatory apes. C. Desmond Morris's, 1967 *The Naked Ape* advanced a similar thesis to Ardrey's. Both accounts minimized the role of women in human evolution. D. Popular media from the mid-20th century reflected the ideas advanced by Ardrey and Morris. This cigar advertisement is from 1959. E. Stanley Kubrick's *2001: A Space Odyssey*, from 1968, was inspired by Robert Ardrey's writings and engaged the Killer Ape Theory in its depiction of human origins.

Relatedly, MTH has been associated with the notion that men and women have evolved rigid, strongly differentiated 'natural' gender roles that are biologically fixed and genetically based (Fuentes, 2017, p. 39; Sussman, 1999). This carries along "the persistent myth of 'male biological superiority'… in interpretations and reconstructions of human evolution" (Ocobock & Lacy, 2023, p. 1). In short, many critics have used the phrase MTH to object to what they see as evolutionary justifications in both the scientific literature and in popular culture for modern day aggression, violence, patriarchy, and sexism (Gould, 2011; Fig. 1).

These above framings of MTH each have textual bases, either in 20th century anthropology or popular science. Quite often, however, they are directly sourced to the MTH conference and volume (Lee & DeVore, 1968). For instance, Fuentes (2017) links the MTH volume to aggression and leadership: "Men who were better hunters became leaders, and hunting and the aggression associated with it became a central aspect of the human evolutionary story" (p. 51). Anderson et al. (2023) link the MTH volume with the notion of gendered traits including that men are "less emotional and more aggressive, while human women tend to demonstrate more nurturing behavior" (p.1). Lacy and Ocobock (2023) write that the MTH volume "focused on the role hunting played in driving human evolution, both by adding a nutrient-dense food to the diet and by giving males an opportunity to show off for potential female mates."[3] Sear (2021, p. 2) writes, "'Man the Hunter' was an influential conference and subsequent book in the 1960s which promoted a vision of an evolutionary past in which hunting by men and provisioning of women and children was of key importance in human evolution." However, these examples overemphasize a genuine but minority sentiment of the conference and volume, when in fact conference contributions ran the gamut and pursued patterning and diversity in all aspects of forager life, from demography, to land-use, to marriage practices, and more.

We will argue that such portrayals of MTH conflate different concepts and misrepresent the history of discourse in the discipline, painting a falsely black and white picture that distracts from genuinely useful empirical and theoretical discussions over evolved sex differences, men's and women's hunting and other subsistence practices in the present and past, and the reasons underlying sexual divisions of labor. To address some of these confusions, there is a clear need to disambiguate the phrase MTH and how it has been used and understood in historical context.

In the following sections of the paper we propose three distinct framings of MTH, each of which pertains to gender, hunting, and human evolution (Fig. 2). In Section 3, we highlight how the theories of Raymond Dart, amplified by popular writers such as Robert Ardrey and Desmond Morris, promoted the idea of a violent and male-centric human past. In Section 4, we discuss the MTH conference and volume (Lee & DeVore, 1968), in which contributors held a range of views on topics including subsistence, patriarchy, aggression, sexual divisions of labor, and evolved sex roles. We review key areas of consensus and disagreement at the MTH conference and argue that MTH promoted diverse views that would shape subsequent research programs in the years to come.

In Section 5, we tackle the current science of human evolution. We address the scientific legacy of the MTH conference and volume, whose contributors emphasized the importance of integrating evidence from an evolutionary perspective from fossils and archaeology, non-human primates, and contemporary foragers, and who helped launch research projects in these areas. We summarize what these projects have revealed about human evolution over the past six decades. We highlight major

[3] The idea that males hunt to 'show off' for females does not appear in the MTH conference volume. In fact, this idea came to prominence in anthropology in the 1980s and 1990s (e.g., Hawkes 1991), later incorporating theoretical insights of biologist Amotz Zahavi (Hawkes & Bird, 2002; Zahavi, 1975).

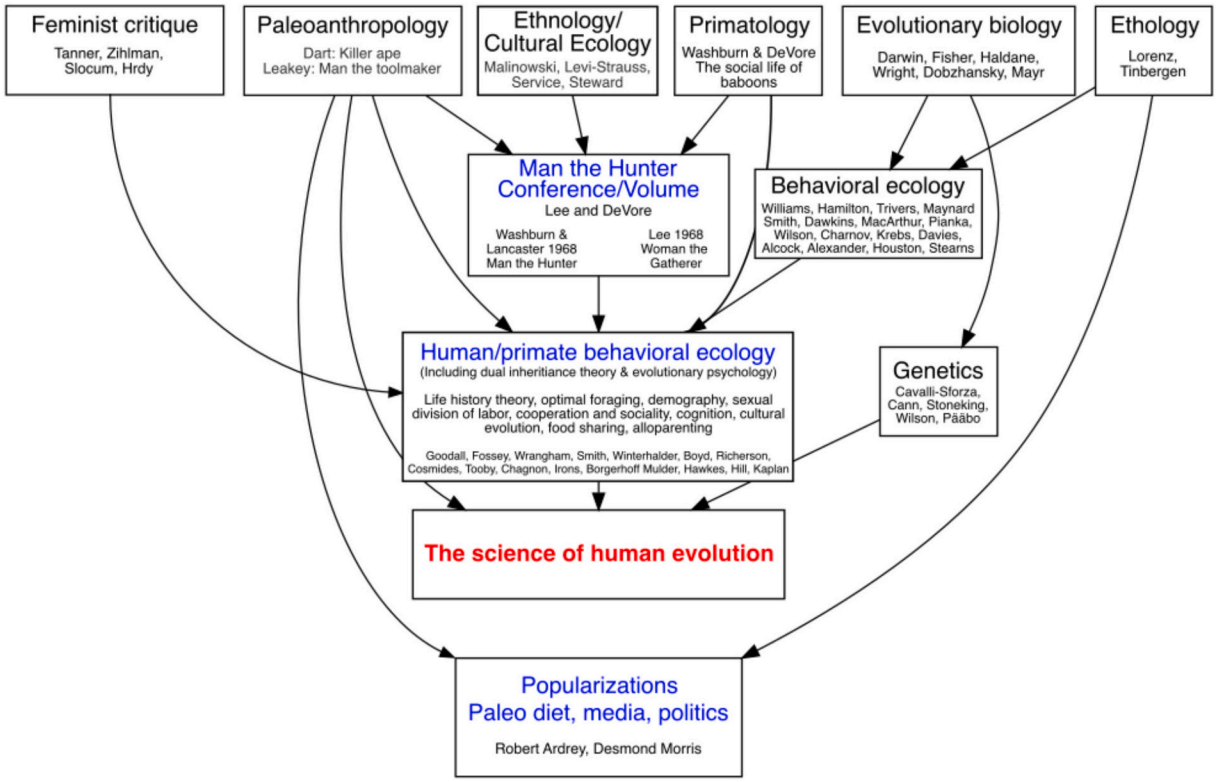


**Fig. 2.** Proposed influences on Man the Hunter, Human Behavioral Ecology, the science of human evolution, and popularizations. The MTH conference and volume contained more viewpoint diversity than commonly realized. Participants at the MTH conference advocated multiple scenarios of human evolution, ranging from an emphasis on hunting to an emphasis on gathering, with diverse views on aggression, territoriality, and sex differences. Modern scholarship on foragers relies on systematic ethnographic methods, combined with theoretical insights from the evolutionary biology of social behavior. This has resulted in the tripartite division of behavioral ecology, cultural evolution, and evolutionary psychology. Contemporary theoretical and empirical approaches to the study of foragers are a result of the MTH conference and its legacy of immersive ethnography, the feminist response to MTH, and the 1960s revolution in an evolutionary understanding of social behavior. This is a far different trajectory than that of the popularized MTH, which owes its heritage to paleoanthropology and various popularizers who were independent from mainstream anthropology, including Robert Ardrey and Desmond Morris. These writers combined insights from paleoanthropology (Dart and later LB Leakey) and ethology (Tinbergen and Lorenz) to arrive at a highly gendered and aggressive view of human evolution, which is still influential today. Washburn and Lancaster's (1968) contribution in the MTH volume proposed hunting as a driver of human adaptation and was largely independent of Dart's ideas. These insights were used sparingly by popular authors but nevertheless reinforced male-dominated narratives.

areas of consensus and disagreement, arguing that the most important contribution of the MTH conference and volume has been its inspiration for 60 years of subsequent research. Although we can only speak for ourselves, we will outline a contemporary view of human evolution that we hope most of our colleagues would agree with, which we will refer to as the "rough consensus."

In Section 6 and 7, we ask: to what extent are there intellectual connections between these various framings of MTH? Using historical evidence, we argue that there is little connection between the Dart/Ardrey version of MTH and that of the MTH conference, as well as later work by behavioral ecologists working with contemporary hunting and gathering communities. We also examine the complex legacy of anthropologist Sherwood Washburn, who played a leading role in the development of the latter two framings of MTH. Finally, we suggest avenues for fruitful discussion of MTH in the future, proposing that more precise use of the phrase MTH is warranted to avoid inaccurate caricatures of anthropological theory.

## 3. Man the Hunter in the Early-to-Mid 20th century

In the mid-20th century, paleoanthropologist Raymond Dart began to advance theories of hunting and violence that would come to shape popular notions of human evolution (Fig. 1). Based on his decades-long paleontological work in South Africa, which included the first discovery of an early hominin (*Australopithecus africanus*), Dart proposed that the human lineage originated in Africa and theorized that bipedalism preceded encephalization. These claims were wrongly dismissed by many experts at the time (Rowan & Wood, 2024). Dart further hypothesized that our early ancestors were predaceous 'ape-men' who wielded bones as weapons, expressing an 'osteodontokeratic' (bone, tooth, and horn) culture. Dart remarked in 1953 that "it was the ape-man's instinct for violence, and his successful development of lethal weapons, that gave him his dominance in the animal world from the very beginning. Those instincts are with us today." This notion is now known as the Killer Ape Theory (Dart, 1953).

Yet, despite its popularity and influence, Dart's Killer Ape Theory was challenged by contemporary anthropologists in the 1950s. Washburn (1957) was among the first to critique Dart, arguing that early hominins were more likely to be prey than predator. Later, archaeologist CK Brain showed that hominins at the South African sites of Sterkfontein, Swartkrans, and Kromdraai had evidence of being preyed upon by large carnivores (Brain, 1981).

While Dart's Killer Ape Theory was dismissed by many professional anthropologists of the time (but supported by some others; see Wolberg, 1970, and commentaries), it persisted in the popular imagination in large part due to Robert Ardrey, a Hollywood and Broadway screenwriter and playwright. Ardrey met Dart in 1955 and was taken by his ideas. In his four-part book series, *The Nature of Man*, Ardrey brought these ideas to the public eye. The books in this best-selling series included *African Genesis* (1961), *The Territorial Imperative* (1966), *The Social Contract* (1970), and *The Hunting Hypothesis* (1976).

In these books, Ardrey stridently promoted Dart's aggressive

interpretation of human nature: "…most significant of all our gifts, as things turned out, was the legacy bequeathed us by those killer apes" (Ardrey, 1961, p. 1). Ardrey posited an inherent disposition toward violence in humans, one manifestation of which was hunting. Meat provisioned by men was of prime importance, with plant foods playing little role. In this telling of human evolution, the lives of women were devoted to reproduction, as "sexual specialists to counteract the tendency of social males to be preoccupied with activities other than reproduction" (Ardrey, 1961, p. 17). Ardrey proposed his own causal model of the 'cultural consequences' of the shift toward carnivory in australopiths: "food-sharing, the male role of provider, the bipolar society in part sexually segregated, the female role of defender of the home-site" (Ardrey, 1976, p. 93). Desmond Morris, the ethologist-turned-writer who authored the mega-bestsellers *The Naked Ape* and *The Human Zoo*, thought similarly: "Because of the extremely long period of dependency of the young and the heavy demands made by them, the females found themselves almost perpetually confined to the home base" (Morris, 1967, p. 33).

Popular depictions of human evolution and behavior developed in the Cold War era (Milam, 2019) followed Dart's theorizing, including depictions of cavemen and highly gendered depictions of prehistoric life (Lacy & Ocobock, 2023). One notable example comes from *2001: A Space Odyssey*, Stanley Kubrick's memorable meditation on humanity's dark evolutionary trajectory that was explicitly influenced by Ardrey (Weidman, 2011). Coarse notions of MTH still hold sway over popular conceptions of the human past, exemplified by the popularity of "Paleo diets"[4] and lifestyles (Lavi, Rudge, & Warren, 2024), the ideologies of some online communities that may promote misogynistic commentary (see Bachaud, 2024; Bachaud & Johns, 2023; Bachaud et al 2025), and museum displays that reduce women's contributions in prehistoric foraging societies to domestic work alone (Gifford-Gonzalez, 1993; McDowall, 2025). These ideas also inform critical characterizations of hunter-gatherer research by some anthropologists (Fuentes, 2017; Ocobock & Lacy, 2023).

What views, then, were actually expressed by participants in the MTH conference and volume?

## 4. The Man the Hunter conference and publication

The MTH conference gathered ~75 anthropologists at the Center for Continuing Education at the University of Chicago from April 6-9, 1966. The conference was the brainchild of Sol Tax, a professor at the University of Chicago. Following a symposium organized by Tax in 1965 - also at the University of Chicago - called *The Origin of Man*, Tax encouraged a follow-up conference on hunting and gathering societies. Richard B. Lee and Irven DeVore, two graduate students of Sherwood Washburn at Berkeley, were the main organizers of the 1966 meeting, alongside Tax. Attendees were chosen according to geographic and topical expertise, which spanned biological anthropology, cultural and linguistic anthropology, and archaeology. Many had lived among hunter-gatherers around the globe and conducted systematic research on material culture, behavior, religion, subsistence, and gender roles. There was a mix of established and emerging scholars, and the participant pool was notably male-dominated.[5]. In total, 28 papers were presented at MTH, covering hunter-gatherer ecology and economics, social and territorial organization, marriage, demography and population ecology, prehistory, and relevance to human evolution, with 12 discussion sessions and 10+ hours of open debate. Papers were distributed in advance, enabling the organizers to limit talks to 10 minutes. Lee and DeVore significantly condensed these discussions for the subsequent volume (Lee & DeVore, 1968; Venkataraman & Lee, 2025).

The motivations for the MTH conference were manifold. There were two reasons explicitly stated in the MTH volume. The first was that so much new data had emerged about foragers that reassessment of "our concept of Man the Hunter" (Lee & DeVore, 1968, p. 7) was necessary. This applied not only to social anthropology but also to archaeology, which was quickly adopting ethnographic data to contextualize archaeological findings. Second, participants recognized that the subsistence-based lifestyles of many hunter-gatherer groups were rapidly disappearing and the opportunity to study certain traditional lifeways would soon vanish.

A broader motivation of MTH was to re-introduce evolutionary models into anthropology (Venkataraman & Lee, 2025), which had waned in popularity after the cultural evolutionary stage models characteristic of 19th-century anthropology were discredited (e.g. Morgan's, 1877 model of 'savagery, barbarism, and civilization'), and as the Boasian revolution, which emphasized particularistic studies over synthetic research, took hold (Stocking, 1966). MTH represented an opportunity to recontextualize hunter-gatherers in modernized cultural ecological and evolutionary frameworks, free from discredited stage models, and to show that careful and situated study of hunter-gatherer societies, integrated with evidence from paleoanthropology and primatology, could inform theories of human prehistory (Venkataraman & Lee, 2025). Contributors to MTH used some form of the word "evolve" over 160 times, "Pleistocene" over 100 times, "prehistoric" over 100 times, "paleo" over 70 times, "primate" over 60 times, "baboon" over 30 times, "hominid" over 25 times, and "chimpanzee", "gorilla", and "fossil" each over 10 times. For other commonly used terms, see Figure 3.

The word 'man' in the conference title — off-key to the modern ear and to younger conference attendees at the time (see Venkataraman & Lee, 2025)— referred to 'humankind' broadly. Indeed, the MTH conference followed the *Origin of Man* symposium, where the word "Man" was a synonym for "human". As MTH co-editor Richard Lee explained (Venkataraman & Lee, 2025): "The term "Man" was a shorthand for a humanistic worldview, specifically to counter creationism and God-centered world views. In that respect, it was considered an enlightened use of the word, not a sexist one." The eponymous conference volume starts with the sentence: "Cultural Man has been on earth for some 2,000,000 years; for over 99 percent of this period he has lived as a hunter-gatherer" (Lee & DeVore, 1968, p. 3). As explained in the Introduction to the MTH volume, the term "hunters" was defined by participants as synonymous with foragers (both men and women): "It was also generally agreed to use the term 'hunters' as a convenient shorthand, despite the fact that the majority of peoples considered subsisted primarily on sources *other than meat* [their italics] - mainly wild plants and fish." (Lee & DeVore, 1968, p. 4). The title *Man the Hunter* was chosen by Sherwood Washburn, a leading academic and the doctoral supervisor of both Lee and DeVore (Venkataraman & Lee, 2025). Despite several MTH participants expressing reservations about the title on sexist grounds, Lee felt in no position to overrule his advisor (Venkataraman & Lee, 2025).

There was significant viewpoint diversity at the MTH conference, which was highlighted by Lee and DeVore (1968) in their introduction

[4] For a revised scientific version of a paleo-diet by two of its original proponents, see Konner and Eaton (2023).

[5] In his plenary, Lévi-Strauss remarked on the young pool of participants. This was only partly intentional on the part of the organizers. For example, Elman Service was invited but declined. Richard Lee does not recall whether Marvin Harris or Leslie White were invited (pers comm). Lee and DeVore had speculated that Service declined because it was becoming clear by the time of the MTH conference that Service's patrilocal model was no longer sustainable in light of new evidence. Julian Steward was invited but did not attend due to ill health, but he did submit a paper that is included in the final volume.

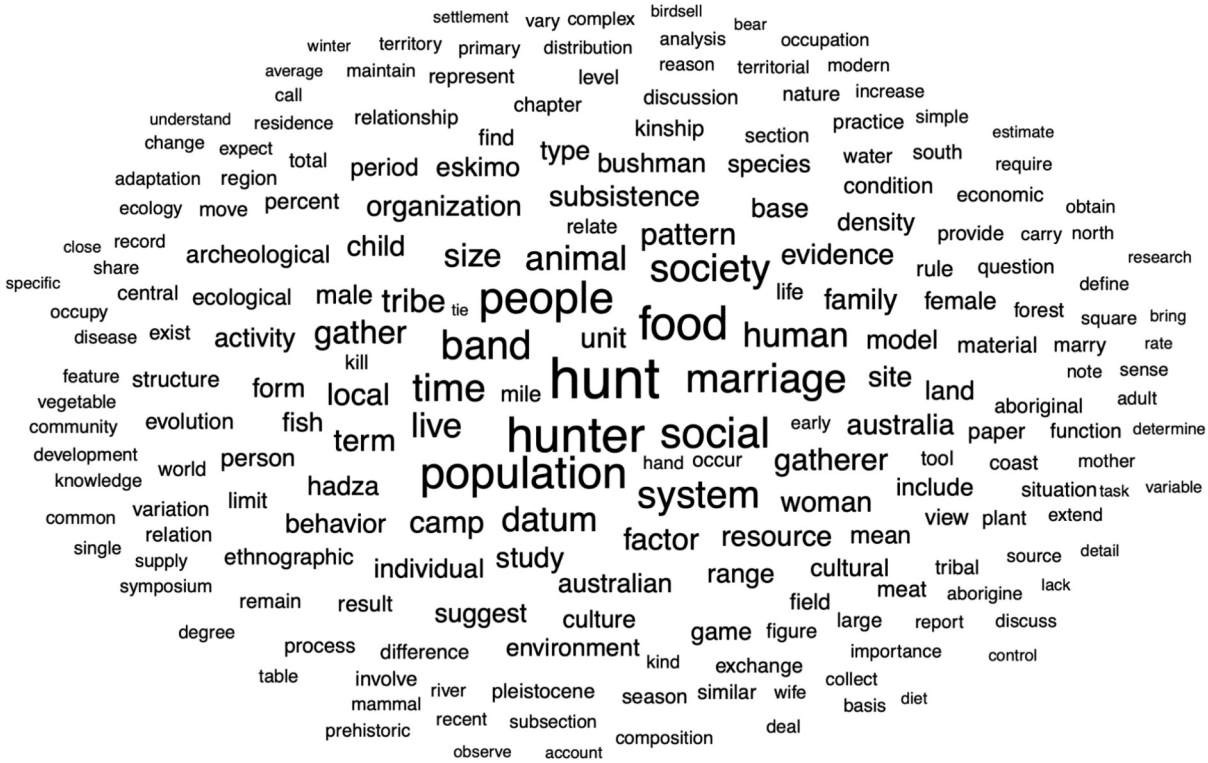


**Fig. 3.** Word cloud of the 200 most common words in the entire text of the MTH volume (minus stopwords, i.e., common words like "and" or "the"). Words were first lemmatized. Word size is proportional to word frequency in the text. Some form of the word "hunt" appeared about 835 times.

to the volume[6], but which subsequent scholars rarely acknowledge. One exception is Hawkes, O'Connell, and Jones (2018), who wrote: "As discussions in *Man the Hunter* show, participant opinion was complex and divided about whether any particular observations of hunter-gatherers in one time and place could do more than expand the descriptive record of human experience." Despite this diversity of opinion, it has been common for the contribution of Washburn and Lancaster (1968), as well as that of Laughlin (1968), both of which articulated strong versions of the HH, to be taken as emblematic of the conference as a whole (i.e., Domínguez-Rodrigo, 2002; Fuentes, 2017; Speth, 2010), perhaps because they most closely reflect the volume's title. Overall, numerous topics were debated at length during the MTH conference, including subsistence, aggression, territoriality. In the rest of this section, we outline key findings from MTH and highlight areas in which diverse views were expressed.

### 4.1. Subsistence

Subsistence has long been central to theories of human origins. Some contributions at MTH strongly emphasized male hunting, such as William Laughlin's chapter, which proposed hunting as "the master behavior pattern of the human species" (Laughlin, 1968, p. 304). Washburn & Lancaster's chapter[7], entitled *The Evolution of Hunting* (Washburn & Lancaster, 1968), connected (putatively) evolutionarily unique attributes of the human species (i.e., tool use, extensive male cooperation, and the pair bond) to hunting, and argued for habitual hunting behavior in hominins at the origin of the genus *Homo*. Interestingly, this chapter was a later contribution, not presented or discussed at the meeting (Venkataraman & Lee, 2025). Washburn and Lancaster's (1968) version of the HH was much more comprehensive than Darwin's and has been labeled an articulation of the 'original' hunting hypothesis (Binford, 1987).

In contrast to these male hunting-centric views, some anthropologists at the MTH conference focused on the role of plants and women's gathering. Richard Lee, marshaling data from the !Kung, showed that women's plant gathering provided 60-80% of the diet by weight, more than previously assumed (Lee, 1968). Through a comparative sample of foragers, Lee demonstrated that gathering, on average, was more important calorically among foragers, and the relative importance of hunting versus gathering depended on ecology and geography (Lee, 1968). This latter demonstration was replicated by archaeologist Lewis Binford's widely cited research on hunter-gatherer settlement (Binford, 1980) and other comparative studies on hunter-gatherer dietary variation (e.g., Roscoe, 2004). Ironically, Lee's contribution on the critical importance of women's gathering is widely considered by many anthropologists and science communicators to be the most enduring result of the MTH conference. Lee later remarked that *Man the Hunter* could just as easily have been called *Woman the Gatherer* (Lee & Leacock, 1982), which, in fact, became the title of two later books (Dahlberg, 1981; Slocum, 1975).

The MTH conference radically transformed the prevalent view that

[6] From Lee and Devore (1968, p.4): "A number of divergent viewpoints are represented in this volume and many of the issues to be raised remain unsolved. As both editors and partisans, it is our task to point out areas of general agreement while trying to avoid glossing over real differences where they occur. Considering the many points of view presented at the symposium, it would be impossible to touch on all of the interesting material. We make no apologies for our selection but offer it as a partial guide to the papers and discussions."

[7] Laughlin employed a stricter definition of hunting than Washburn and Lancaster, whose chapter defines hunting as something closer to the hunting and gathering 'way of life.' We are grateful to Fabian Abriani for this clarification.

hunter-gatherers were constantly on the edge of starvation (Braidwood, 1975). Building on Lee's (1968) time allocation data with the !Kung, which showed that they worked <40 hours per week, Marshall Sahlins formulated the idea of the 'Original Affluent Society', later elaborated in *Stone Age Economics* (Sahlins, 1972). Sahlins argued that hunter-gatherers lived lives of leisure, or "Zen affluence", and were not constantly toiling. Though subsequent work has since challenged the theoretical and empirical basis of the Original Affluent Society (Kaplan, 2000; Kelly, 2013; Kraft et al., 2021; Venkataraman, 2023; Winterhalder, 1993), it remains a prominent cultural product of the MTH conference (Suzman, 2017).

### 4.2. Sex differences and the sexual division of labor

Washburn and Lancaster (1968) proposed strong biological sex differences, including sex differences in aggression. They argued that "men enjoy hunting and killing, and these activities are continued as sports" and that "basic biological differences are reinforced in man[kind] by a division of labor" (p. 300). These ideas have continued to influence reconstructions of the past (e.g., Lovejoy, 1981, 2009). Here again, however, the MTH conference volume was not primarily concerned with the question of sex differences, a topic on which contributors had different opinions and reached different conclusions. Watanabe (1968, p. 74), for instance, argued: "Sex differences in physiology and psychology alone would not be sufficient to explain" sexual divisions of foraging labor, and that hunting among many societies "is, in fact, a woman's occupation".

Contributions to the MTH conference described sexual divisions of labor with varying degrees of rigidity. For instance, Rose (Rose, 1968, p. 201) described Australian aboriginal relations as a reciprocal economic exchange with "the man primarily providing the meat and the woman the vegetable food-stuffs for themselves and her children". In the discussion of nomadic hunter-gatherers as a cultural type, Lee (1968, p. 11) highlighted that hunter-gatherer economies were typically based on "males hunting and females gathering", while Murdock (Murdock, 1968, p. 335) stated "there is a strikingly uniform division of labor… the women gather; the men hunt". Elsewhere in the volume, Watanabe (1968) stated that "the consistent allocation of hunting to males and collecting to females" is a "problem" (p. 74), and he described women's frequent pursuit of small game, and participation in communal large game hunts among the Ainu, Mbuti, and Copper Inuit.

### 4.3. Reconstructing prehistory by ethnographic analogy

One of the central goals of the MTH conference was to reconstruct Paleolithic behavior based on ethnographic analogy. Part of the volume was specifically devoted to the exploration of foragers as models for human evolution (e.g., see Binford, 1968; Clark, 1968). For example, Washburn and Lancaster (1968) drew on ethnographic data to construct an evolutionary model "where males hunt and women gather" and "where the results are shared and given to their young" (p. 301). On the other hand, Freeman (1968) strongly critiqued the use of ethnographic analogy, concluding that "reasoning from modern behavior must be kept to a minimum in the construction of models of past cultural systems (p. 265). Glynn Isaac remarked that "Anthropological interest in peoples that subsist solely on hunted and foraged foodstuffs has long been heightened by the notion that these people are in some sense survivors from the primitive condition of all mankind. Today this hypothesis — like the hunting peoples themselves — is so hedged about by reservations and restrictions, that it no longer has much value" (Isaac, 1968, p. 253). Similarly, Clark (1968, p. 280) remarked: "Most of the hunting and gathering groups existing today are living in some of the least favorable habitats and have for long been in contact with more complex societies and technologies. They can, therefore, no longer be considered 'typical' or useful for any direct comparison with prehistoric populations of optimum and favorable, or even of the marginal, ecological zones." Sally Binford (1968, p. 274) argued that "there can be no valid assumption that living hunter-gatherers are relics of the Pleistocene." Sol Tax (p. 345) noted that we should be interested in the persistence of foraging populations in the face of change. Washburn, despite being an older and more conservative scholar in many respects, did not see hunter-gatherers as relict populations living in the past (Venkataraman & Lee, 2025). Summarizing the MTH conference, Hawkes et al. (2018) wrote: "Participants recognized the errors of previous scholars who had tried to equate particular modern human populations with those that left specific archaeological records dated to the Pleistocene. For many, the question wasn't whether observations of modern foragers are relevant to understanding the past, but how to use them." (Hawkes et al., 2018, p. 777)

### 4.4. Aggression, warfare, and territoriality

There was a tremendous diversity of opinion at the conference about the importance of aggression and territoriality among foragers. Washburn and Lancaster (1968) argued that the importance of hunting in human evolution has led humans, including foragers, to be naturally aggressive. This aggression manifests in a tendency both to kill for pleasure and also to wage war: "The extent to which the biological bases for killing have been incorporated into human psychology may be measured by the ease with which boys can be interested in hunting, fishing, fighting, and games of war" (Washburn & Lancaster, 1968). However, MTH participants disagreed over the importance of forager aggression and territoriality. Colin Turnbull took issue with Washburn and Lancaster's (1968) portrayal of foragers as aggressive and argued that most foragers rarely engage in warfare and raiding (Lee & DeVore, 1968, p. 341). David Schneider argued that if aggression and warfare was important in human evolution, it should be seen among contemporary foragers (Lee & DeVore, 1968, p. 341). James Woodburn noted that "The Hadza do not often come into conflict with their neighbors" (p. 157). Others pointed to the fact that hunter-gatherers surrounded by other hunter-gatherers, like the Indigenous Australian Tiwi, are more likely to make war than the more well-known Mbuti and !Kung who are surrounded by non-hunter-gatherers, a claim supported by recent scholarship (Wrangham & Glowacki, 2012). In short, there was no consensus among the participants over the importance of aggression (an area of active debate, see Glowacki, Wilson, & Wrangham, 2020), with most seeming to acknowledge that many foragers lacked war, or that it consisted primarily of inter-family feuds.

The question of whether foragers defend territory was less debated. Les Hiatt, writing about Indigenous Australians, argued against Radcliffe-Brown's published works stating that territorial trespass was a cause of violence. Hiatt argued that many Australian societies allowed others to access territory and there was too much cultural variation for a generalizable rule (Hiatt, 1968, p. 100). Turnbull argued that the Mbuti worked to ensure that territorial boundaries are well-known in order to avoid conflict due to trespass (Turnbull, 1968, p. 135). Steward and Lee both acknowledged that foraging groups might claim territory but fighting to defend it was "very uncommon" (Steward, 1968, p. 334). In sum, it was acknowledged that many foragers recognized territory (cf. Woodburn, 1968), but that the responses to trespass and poaching were varied or under-researched.

### 4.5. Summary

Participants at the MTH conference held strong disagreements about foundational questions in human evolution and hunter-gatherers, aggression, division of labor, hunting, and subsistence. Other prominent areas of disagreement at the conference - beyond the scope of this paper - included marriage practices, post-marital residence patterns, infanticide, and social complexity. These divisions among the participants makes it impossible to point to any specific hypothesis or agenda that the conference participants supported. It is fair to say, however, that

all supported ongoing research in hunter-gatherer societies to help illuminate the human condition, in the present as well as the past.

## 5. The dividends of MTH: Integrating paleoanthropology, primatology, and the human behavioral ecology of hunter-gatherers to elucidate human evolution

> Man the Hunter *raised more questions than it answered…*
> -Lee and DeVore (1968), Introduction to *Man the Hunter*

> *The most instructive primates are the chimpanzees, gorillas, and baboons, for they have received greatest attention and are most similar to hominids in several respects.*
> - Julian Steward (1968)

> *[A]lthough the record is incomplete and speculation looms larger than fact, for those who would understand the origin and nature of human behavior there is no choice but to try to understand "Man the Hunter."*
> -Washburn and Lancaster (1968)

The scientific dividends of MTH are not its title, talks, or chapters, but instead the empirical framework and the many research projects it inspired. In the century prior to MTH, anthropologists and other scholars developed, and then rejected, unilineal theories of social evolution (Morgan, 1877; Stocking, 1966). As we noted earlier, MTH sought to reintroduce evolutionary thinking into anthropology based on the recognition that humans evolved from an ape ancestor in Pleistocene Africa, and new data from paleoanthropology, primatology, and contemporary hunter-gatherers.

Much subsequent research aimed to understand contemporary hunter-gatherer lifeways on their own terms, often within a cultural ecology framework and without necessarily any implications for human evolution (e.g., Barnard, 1983; Bird-David, 1992; Hayden, 1981; Headland & Reid, 1989; Hewlett and Fancher, 2014; Sahlins, 1972; Testart, 1982: Woodburn, 1982). Congo Basin foragers, for example, have been extensively studied by Japanese, French, and American teams. Whereas the Japanese and Americans were explicitly interested in elucidating human evolution, the French focused more on ethnolinguistics, ethnomusicology, and rich descriptions of the cultures of these forest peoples (Hewlett & Fancher, 2014; Ichikawa, 2020). Because recent criticisms of MTH have focused on the Washburn and Lancaster (1968) chapter, however, and its account of human evolution and the implications for human nature, here we take stock of almost six decades of hunter-gatherer and nonhuman primate research inspired by MTH that, integrated with paleoanthropology and genetics, now provides several plausible, but by no means definitive, scenarios for the evolution of that "uniquely unique species" (Alexander, 1990), *Homo sapiens*.

By the mid-20th century evidence had accumulated that hominins — the human clade — first emerged in Africa. Organizers of MTH, including Sherwood Washburn, Irven DeVore, and Richard Lee, along with paleoanthropologists Louis and Mary Leakey and other anthropologists, launched research projects to better understand human evolution with evidence from three mostly African sources: fossils; primate behavior research, especially among chimpanzees, gorillas, and baboons; and contemporary human foragers research. James Neel, Napoleon Chagnon (a participant in MTH), and their collaborators launched similar research efforts among Amazonian horticulturists (Chagnon & Hames, 1979; Hames & Vickers, 1982; Neel & Chagnon, 1968; Neel, Salzano, Junqueira, Keiter, & Maybury-Lewis, 1964). This ongoing work, which now includes genetic evidence from many ancient and contemporary populations, aims to shed light on human evolution from the time of our divergence from African apes at the end of the Miocene, 6-9 million years ago (Almécija et al., 2021), up to the origins of agriculture at the end of the Pleistocene, 11-12 k.y.a (Bergström, Stringer, Hajdinjak, Scerri, & Skoglund, 2021), with some research on recent positive selection in Holocene populations (Gao, 2024), as well as cultural evolutionary analyses of the dramatic increase in social and technological complexity (e.g., Sheehan et al., 2023).

Given intrinsic limits on inferring behavior from the fossil record, contributors to MTH repeatedly noted the importance of data from living non-human primates and human foraging societies to reconstruct our evolutionary history, in addition to perspectives from other non-primate mammals, especially social carnivores (Bartholomew & Birdsell, 1953; Schaller & Lowther, 1969). Washburn, a primatologist, and his students Irven DeVore (an organizer of MTH) and Shirley Strum initiated projects to study baboons, which lived in savannah environments similar to those inhabited by early hominins (DeVore, 1963). Leakey, a paleoanthropologist who helped discover important early hominin fossils in East Africa, and who had met with Washburn and DeVore early on, recruited Jane Goodall, Dian Fossey, and Birutė Galdikas to study chimpanzees and gorillas and orangutans, respectively, our closest relatives.

Washburn's student Richard Lee, sobered by the complexity of foraging lifeways revealed in MTH, expanded the Kalahari Project to include specialists in demography, child development, archaeology, population genetics, medicine, and nutrition (Lee, 1979). DeVore launched the similar Ituri Project to study Congo Basin foragers in the northeast of the Democratic Republic of Congo (Bailey & DeVore, 1989). Others, like Washburn's student Adrienne Zihlman, DeVore's student Sarah Hrdy, and Kalahari Project team member Marjorie Shostak, were instrumental in highlighting the important role of women in foraging societies, and by extension, human evolution (Hrdy, 1981; Shostak, 1981; Zihlman, 1998), compared to the relative neglect of women in MTH. These efforts coincided with efforts in anthropology to link cultural variation to ecological variation (cultural ecology; Steward, 1955; Murdock, 1940), as well as with major theoretical advances in the evolution of behavior (e.g, Hamilton, 1964; Maynard Smith & Price, 1973). These disparate approaches to understanding the genetic and cultural evolution of human behavior have, over the last 25 years, together come to be known as human behavioral ecology (HBE, which we use as a blanket term also encompassing dual inheritance theory and evolutionary psychology).

Behavioral ecology is the discipline that investigates the evolved strategies of species across the tree of life. It has its roots in the works of Darwin (e.g., Darwin, 1871), later ethologists (Lorenz, 1963; Tinbergen, 1951; von Frisch, 1967), and theoretical developments in evolutionary biology in the 1960's and 1970's (Hamilton, 1964; Williams, 1966; Maynard Smith & Price, 1973; Trivers, 1971, 1972, 1974; Stearns, 1976; Alexander, 1974; Wilson, 1975; Charnov, 1976). Theories in behavioral ecology typically consider the behavioral strategies and physiological traits that optimize fitness in particular socioecological conditions (the phenotypic gambit; Grafen, 1991). It is important to emphasize that what is "fixed" are not particular behaviors or social roles, but instead a limited number of mechanisms that lead populations toward adaptive behaviors and other traits in particular socioecological contexts. The optimizing process could be natural selection, but often involves individual or social learning (which likewise evolved by natural selection), and the optimized quantity is often a proxy for fitness, such as energetic returns or offspring survival (Bettinger, Garvey, & Tushingham, 2015; Borgerhoff Mulder, 1988; Borgerhoff Mulder & Schact 2012; Cronk, 1991; Frankenhuis, Panchanathan, & Barto, 2019; Nettle, Gibson, Lawson, & Sear, 2013; Ready & Price, 2021; Winterhalder & Smith, 2000). These theories are then tested in both naturalistic and laboratory conditions (Alcock, 2009; Koster, Scelza, & Schenk, 2024; Krebs & Davies, 2009; Winterhalder & Smith, 2000). Each of the millions of species can potentially serve as a natural experimental test of a theory,

an approach termed the comparative method[8].

The attributes of any animal species largely comprise its anatomical, physiological, and behavioral strategies for reliably extracting energy from often hostile plant and animal sources, and then allocating it to growth, maintenance (e.g., immunity, cellular turnover), activity levels, and reproduction so as to maximize the number or the quality of its offspring or other close genetic relatives that themselves survive to reproduce (inclusive fitness). Given the high energetic costs of pregnancy and lactation, theories of subsistence and social strategies in primates and other mammals center on females and their access to and competition for food, with males competing for females (Thompson, 2013; Wrangham, 1980). Even though the strategies of primates and other organisms have evolved to overcome abiotic and biotic challenges such as droughts, toxins, pathogens, predators, and competition with conspecifics, most individuals that have ever lived have failed to reproduce, the observation of Malthus that so inspired Darwin.

In humans, the behavioral ecology framework (HBE) is applied in diverse settings, ranging from archaeological and ethnographically studied hunter-gatherer populations (Bettinger et al., 2015; Borgerhoff Mulder, 1988; Borgerhoff Mulder & Schact 2012; Codding & Kramer, 2016; Cronk, 1991; Frankenhuis et al., 2019; Hill & Hurtado, 1996; Nettle et al., 2013; Ready & Price, 2021; Winterhalder & Smith, 2000) to industrialized nation states (e.g., Rosenbaum, Kuzawa, McDade, Bechayda, & Gettler, 2022), and to diverse problems, ranging from immunity (Blackwell, 2022) to the demographic transition (Borgerhoff Mulder, 1988) to pop culture (Dubourg & Baumard, 2022). We will focus on the integration of paleoanthropology, primatology, and HBE to help reconstruct human evolution, using chimpanzees and bonobos as models of our last common ancestor (LCA), baboons as models of Pliocene hominins, and contemporary foragers as models of Pleistocene hunter-gatherers, acknowledging the many limitations of these analogies. In Table 1, we present a sampling of field studies of hunter-gatherers that were conducted using the HBE framework.

Since the MTH conference, the role of ethnographic analogy in archaeology has been vigorously debated and has only become more nuanced, with the use of behavioral ecological theory to make predictions about hunter-gatherer behavior in archaeological contexts (Bettinger et al., 2015; O'Connell, 1995), an approach that has generated important insights (Lupo & Schmitt, 2024; Morin & Winterhalder, 2024; Speth, 2025; Speth & Morin, 2022). Some scholars have argued against the so-called 'tyranny of ethnography' (e.g., Wobst, 1978). In the 1980s, scholars debated the antiquity of the cultures and foraging practices of some modern-day foragers, as seen in the Kalahari Debate (Sadr, 1997; Solway et al., 1990; Wilmsen, 1989), the Wild Yam Debate (Headland, 1987b), and the Bow vs. Net Hunting Debate (Bailey & Aunger, 1989). Others argued that colonialism profoundly reshaped Indigenous societies (e.g., Leacock, 1983). Yet others investigated whether, as many claimed, contemporary hunter-gatherers occupied marginal habitats compared to Paleolithic populations, which may impact inferences about the forms of Paleolithic social organization (Cunningham, Worthington, Venkataraman, & Wrangham, 2019; Porter & Marlowe, 2007; Singh & Glowacki, 2022; Venkataraman, 2022). Still others evaluate the relevance of ethnographic analogy for inferring the behaviors of Neanderthals (French, 2018). In other words, contemporary scholars have diverse and nuanced views on these topics and most tread carefully when drawing ethnographic analogies.

Our aim here is not to provide a comprehensive model of human evolution from the LCA to the present (for that, see, e.g., Foley & Gamble, 2009; Chapais, 2010; Hrdy, 1999; and other references at the

[8] This is not to be confused with the 19th century comparative method, most often associated with Sir John Lubbock's, 1865 *Prehistoric Time*, which simply drew direct links of descent (not mere analogies) between ancient and living foragers, e.g., between Upper Paleolithic reindeer or red deer hunters of Europe and the caribou hunting Inuit.

**Table 1**
Representative studies of historically described hunter-gatherer societies conducted in the behavioral ecological (and adjacent) traditions. The list is not exhaustive. Instead, it is intended to show the diversity of field studies around the world and to highlight commonalities between research programs which afforded robust cross-cultural comparison. Notably, despite dozens of forager societies now having been studied in some depth, this accounts for but a small proportion of the (likely underestimated) ~300 ethnographically documented foraging societies (Binford, 2001).

| Population and location | Topic(s) | Representative studies and reviews | Connection to MTH conference/ volume |
|---|---|---|---|
| !Kung San (Botswana and Namibia) | Foraging ecology, social organization, ethnoarchaeology, sexual division of labor, child development | Marshall, 1976<br>Lee & DeVore, 1976<br>Shostak, 1981<br>Yellen, 1977<br>Draper, 1976<br>Tanaka, 2014<br>Wiessner, 1982 | One of the earliest studied populations. MTH featured research from the Marshall Family Expeditions, and the Harvard Kalahari Project. |
| Hadza (Tanzania) | Foraging ecology, energetics, sexual division of labor, costly signaling, cooperation, evolutionary psychology, ethnoarchaeology | Woodburn, 1968<br>Hawkes, Connell, & Blurton Jones, 1991<br>Crittenden, Conklin-Brittain, Zes, Schoeninger, & Marlowe, 2013<br>Marlowe, 2010<br>Pontzer et al., 2012<br>Stibbard-Hawkes, Attenborough, Mabulla, & Marlowe, 2020<br>Smith & Apicella, 2020 Apicella, Marlowe, Fowler, & Christakis, 2012 | The young Woodburn, a prominent MTH participant, inaugurated decades of subsequent Hadza research. |
| Alyawara, Mardu, Meriam (Australia) | Foraging ecology, costly signaling, ethnoarchaeology | Bird & Bird, 2008<br>Meggitt, 1962<br>Hart & Pilling, 1960<br>Bird, Bird, Smith, & Kushnick, 2002<br>Bird & Power, 2015<br>Smith & Bird, 2000<br>Codding, Zeanah, Bird, Parker, & Bird, 2016 | Australian Aboriginals were a heavy focus of discussion at MTH, setting the foundation for later research |
| Batek, Semaq Beri (Malaysia) | Foraging behavior, religion, determinants of reproductive success, | Endicott & Endicott, 2008<br>Kraft, Venkataraman, Endicott, & Endicott, 2020<br>Venkataraman et al., 2017<br>Kraft, Venkataraman, Tacey, Dominy, & Endicott, 2019<br>Kuchikura, 1988 | The Batek, classified under the labels of Malayan Negrito, or Semang, were discussed at MTH but not yet studied by anthropologists in the late 1960s. Endicott's and later studies were inspired by Lee's quantitative methods to measure foraging returns |
| Ache (Paraguay) | Foraging behavior, optimal foraging theory, life history, | Kaplan & Hill, 1985<br>Hill & Hurtado, | This project was inspired by the Kalahari, Ituri, |

(*continued on next page*)

**Table 1** (*continued*)

| Population and location | Topic(s) | Representative studies and reviews | Connection to MTH conference/ volume |
|---|---|---|---|
| | technology, demography | 1996 Hawkes, Hill & O'Connell, 1982 | and Hadza projects |
| Hiwi (Venezuela) | Foraging behavior, demography, life history | Hurtado & Hill, 1987 Gurven, Hill, Kaplan, Hurtado, & Lyles, 2000 Hill, Kaplan, Hawkes & Hurtado, 1987 | This project was inspired by the Kalahari, Ituri, and Hadza projects |
| Pumé (Venezuela) | Foraging ecology, sexual division of labor, life history, child learning, social networks | Kramer & Greaves, 2017 Kramer, Schacht, & Bell, 2017 Kramer, 2021 Hackman & Kramer, 2022 | This project added to the limited sample of South American foragers, and reconsidered the complementary subsistence roles of men, women and children in a savanna ecology |
| Nukak (Brazil) | Foraging, demography, ethnoarchaeology | Politis, 2016 | MTH heavily cited in Politis, 2016 |
| Cree, Ojibwa, Inuit, Montagnais-Naskapi (North America) | Foraging ecology | Winterhalder, 1977 Ready & Power, 2018 Binford, 2012 Leacock, 1955, 1958 Smith, 1985, 1991 | The Indigenous peoples of North America were a common discussion point at MTH; Smith and Winterhalder inspired by MTH conference |
| Western (e.g., Aka, Baka, BaYaka) and Eastern (e.g., Mbuti, Efe); Congo Basin foragers | Social learning, foraging ecology, parenting, development, fatherhood | Bailey, 1991 Bahuchet, 2017 Hewlett & Fancher, 2014 Turnbull, 1961 Kitanishi, 1995 Bailey & DeVore, 1989 Ichikawa, 2020 Lew-Levy et al., 2020b Jang, Janmaat, Kandza, & Boyette, 2022 Salali et al., 2019 Gettler, Redhead, Dzabatou, & Lew-Levy, 2023 | Congo Basin foragers were prominently discussed at MTH, most notably by Colin Turnbull, inspiring future research in the region |
| Agta (Philippines) | Foraging ecology, alloparenting, demography, health, multilevel sociality, life history | Headland, 1987a Page et al., 2019 Migliano et al., 2020 Migliano, Vinicius, & Lahr, 2007 | Referred to as a Negrito tribe in the MTH volume, but received little attention because of their extent of agricultural practice |
| Mikea (Madagascar) | Foraging, life history, ethnoarchaeology | Tucker & Young, 2017 Kelly, Poyer, & Tucker, 2005 | Initiated by Kelly and continued by Tucker, the research was inspired by MTH, in part because game hunted by the Mikea were so small and limited |
| Lamalera (Indonesia) | Cooperation, kinship | Alvard & Nolin, 2002 Nolin, 2012 | Alvard's research was inspired by MTH (pers comm) |
| Global sample of hunter-gatherers | Coding of ecological, socioeconomic, and demographic variables from numerous source ethnographies | Binford, 2001 Murdock, 1940 Ember, 1978 Kelly, 2013 Marlowe, 2005 Kirby et al., 2016 | Murdock presented ongoing work on cross-cultural analysis at MTH |
| Western native North Americans | Coding of ecological, socioeconomic, and demographic variables from numerous source ethnographies | Jorgensen, 1980 | The Indigenous peoples of North America were a common discussion point at MTH |

end of this section). Instead, we aim to illustrate the scientific legacy of MTH by highlighting key findings of fossil, primate, and human research inspired directly and indirectly by MTH and its contributors.

The human lineage has undergone complex changes in body morphology, diet, and behavior since the LCA. Compared to *Pan* (chimpanzees and bonobos), human hunter gatherers have larger body sizes, longer lifespans, shorter interbirth intervals, longer juvenile periods, more body fat, and bigger brains, and exploit more diverse habitats with larger range sizes (Antón, Leonard, & Robertson, 2002; Davison & Gurven, 2021; Zihlman & Bolter, 2015). In addition, unlike chimpanzees, hunter gatherers form long-term pair bonds, inhabit multilevel societies, cooperate in obtaining food and raising offspring, maintain lifelong relationships with both paternal and maternal kin, have a long female post-reproductive period (but see Wood et al., 2023), and develop and transmit complex culture via language, a uniquely rich signaling system (Chapais, 2010; Foley & Gamble, 2009; Hrdy, 1999). As we will briefly sketch, these distinctive traits are all linked to a distinctive ability to extract large amounts of energy from the environment compared to chimpanzees (Kraft et al., 2021).

Popular discussions of human evolution often fail to specify a time period. To facilitate discussion we therefore distinguish five major phases in the evolution of *Homo sapiens* from the LCA with *Pan*.

**Phase I: The LCA (6-9 mya).** Forty years after MTH, over 40% of primatologists could trace their academic lineage to Washburn (Kelley & Sussman, 2007), who believed "that the study of the nonhuman primates may be used to illuminate the nature of man" (Washburn, 1973, p. 177). In this regard, research has confirmed that humans share key behavioral and life history traits with other primates, which, relative to other mammals with the same body size, mature later, live longer, have bigger brains, and have fewer offspring, patterns that are apparent in great apes and might be related to variability in availability of fruit, a key food source (Jones, 2011). Almost all primate species, including humans, live in groups, which range in size from two to 50 or more (Dunbar & Shultz, 2021), a strategy commonly attributed to defense against predators and infanticidal males (Opie, Atkinson, Dunbar, & Shultz, 2013; Shultz, Opie, & Atkinson, 2011).

The LCA, which evolved in the late Miocene c. 6-9 mya, was some type of great ape. Extant African great apes are largely terrestrial and subsist primarily on fruits and leaves (Almécija et al., 2021; Pontzer & Wood, 2021). Although vertebrate meat is not an important source of either energy or protein in any extant non-human primate, meat-eating is nevertheless widespread in primates, with the most common prey species being birds (including eggs), reptiles, amphibians, mammals, and fish (Watts, 2020). The LCA was therefore probably a terrestrial frugivore that occasionally ate some vertebrate meat (but an LCA that more closely resembled extinct apes with markedly different locomotor and other behaviors cannot be ruled out, Almécija et al., 2021).

Chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), our closest relatives, are the most popular models of the LCA. Although many of their behaviors and other traits differ dramatically from

humans, such as females prominently signaling estrous and mating with most males in the group (Thompson, 2013), chimpanzees resemble humans in many other respects, such as living in multimale, multifemale communities. More strikingly, the discoveries that chimpanzees hunt, use tools, have cultural traditions, and engage in lethal war-like behaviors overturned early claims that these traits distinguish humans from apes and other animals (Goodall, 1988; Wilson, 2021). Later studies of bonobos revealed less hunting and tool use (Wilson, 2021), and higher levels of aggression than chimpanzees within groups (Mouginot, Wilson, Desai, & Surbeck, 2024) but more tolerant interactions between groups with no evidence of lethal attacks against other groups (Samuni & Surbeck, 2023), further complicating our understanding of the last common ancestor (LCA) of genus *Homo* and genus *Pan* (overviews of African great ape research projects include Boesch et al., 2019; Thompson, Muller, Machanda, Otali, & Wrangham, 2020; Wilson, 2021; Furuichi, Idani, Kimura, & Ihobe, 2023).

**Phase II: Pliocene hominins (5.3-2.58 mya)**. As African forests diminished, grasslands expanded and seasonality intensified, increasingly terrestrial and bipedal hominins with ape-sized brains emerged and steadily inhabited drier and more open terrestrial environments. Their suite of traits, such as large teeth and jaws, as well as stable isotope analyses, indicate a shift to a tough, plant-based diet with a mix of C3 and C4 vegetation (e.g., fruits and leaves, and grasses and underground storage organs, respectively). Considerable uncertainty remains in dietary reconstruction, however (Daegling et al., 2013; Lacruz et al., 2019; Lüdecke et al., 2025; Quinn, 2019; Sponheimer et al., 2013; Wynn et al., 2016). In some early hominins, including *Australopithecus afarensis*, a possible human ancestor, males were about twice as large as females, suggesting male defense against predators and/or intense male-male competition for mates and possibly a polygynous social organization (Plavcan & van Schaik, 1997; Willems & van Schaik, 2017); yet modest canine dimorphism raises questions about these interpretations (Alemseged, 2023).

MTH organizers and contributors focused on baboons as animal models of Pliocene hominins (Devore & Washburn, 1963), although studies of savanna chimpanzees are also informative (Izawa & Itani, 1966; Lindshield et al., 2021). Baboons (*Papio* spp.) and their close relatives (e.g., *Theropithecus*) appear in the fossil record at approximately the same time and place as Pliocene hominins and early *Homo* (Gilbert, Frost, Pugh, Anderson, & Delson, 2018), and resemble them in a number of respects. They occupy similar mixed woodland and grassland environments, exhibit a combination of arboreal and terrestrial locomotion, are relatively large and sexually dimorphic, and subsist on sedges, grasses and their seeds, and occasionally fish. Hamadryas baboons, in particular, share a combination of social traits with humans that is very rare in other primates: they form long-term sexual relationships, live in multilevel societies in which males in the same lowest-level group have a leader-follower relationship and males in different groups cooperate in defense against outsiders, and both sexes interact with genetic kin throughout their lives. Increased predation pressure (Willems & van Schaik, 2017) and patchy resource distribution in a more open, drier, and more seasonal environment might therefore help select for a more human form of social organization (Swedell & Plummer, 2019; see also Alberts & Altmann, 2012; Cheney & Seyfarth, 2007; King, 2022).

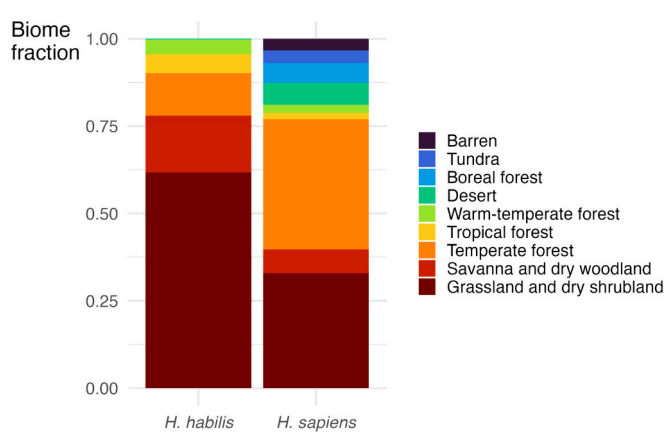


**Fig. 4.** Biome diversity of early *Homo* in Africa (left) versus *Homo sapiens* in Pleistocene Africa and Eurasia (right). Biome preferences were calculated by taking an age-weighted average of the biome occurrences, derived from a transient 3-million-year earth system-biome model simulation, at the grid point closest to the hominin specimen. Values from Zeller et al. (2023).

**Phase III: Early and Middle Pleistocene *Homo* (2.58 mya to 200-300 kya)**: The earliest fossil evidence of our genus, *Homo*, appears in Africa as high amplitude climate variability strongly impacted African vegetation and herbivore communities, creating more open, arid, and seasonally variable environments (Couvreur et al., 2021). See Fig. 4 and Fig. 8. The biomass of a new food source, medium-sized herbivores grazing on expanding C4 grasslands, increased (Bibi & Cantalapiedra, 2023). Herbivore prey and C4 foods such as underground storage organs were energy rich but difficult to acquire, and in the case of game animals, studies in contemporary societies indicate that hunting returns would have been highly variable (Koster et al., 2020). Nevertheless, a range of evidence, including stone tool cut marks on bones, leaves little doubt that vertebrate meat, much of it from megaherbivores, grazers, and other herbivore prey, was an expanding component of *Homo* diets (Aiello & Wheeler, 1995; Antón, Potts, & Aiello, 2014; Ben-Dor, Sirtoli, & Barkai, 2021; Domínguez-Rodrigo, Baquedano, & Organista, 2021).

Much theorizing that aims to connect Pleistocene climate change to *Homo*'s shift in diet toward hunting and gathering, and to changes in its morphology and behavior, is based on research among contemporary forager populations conducted or inspired by contributors to MTH (see Table 1). Early *Homo*, which soon expanded into Eurasia, had somewhat bigger brains and bodies than those of australopithecines (Antón et al., 2014), but was less sexually dimorphic, albeit more so than modern humans (e.g., Semaw et al., 2020; Villmoare, Hatala, & Jungers, 2019). Reduced sexual body dimorphism appears to be due to an increase in female body size rather than a reduction in male body size, suggesting an increased ability to acquire energy (Aiello & Key, 2002). Use of stone tools by *Homo,* and perhaps other hominins, to process plants and butcher animals is evident by the end of the Pliocene and onset of the Pleistocene (Braun et al., 2019; Plummer et al., 2023).

A rough consensus among researchers is that during this and the following phase (Phases III and IV), the human lineage evolved a synergistic suite of anatomical, physiological, and cognitive traits enabling it to exploit diverse habitats with energy-rich plant and animal resources (Fig. 4, Fig. 5). These traits include stone tool manufacture and use, larger brains to master the necessary complex foraging and manufacturing skills, and a longer juvenile period to acquire them via individual and social learning; reduced adult mortality and a longer lifespan to profit from heavy investment in skills; a new thermoregulatory system (sweating) to dissipate heat from high activity levels, potentially including endurance hunting (Morin & Winterhalder, 2024); and more body fat and food sharing to buffer variation in food supply. The prevailing view is that *Homo* evolved as a diet generalist, able to flexibly adapt to different trophic levels as conditions required.

As a flexible strategy for adapting to local ecological conditions, a division of labor likely emerged to increase efficiency at the group level (Bird & Codding, 2015). Females likely specialized in acquiring plant foods—such as underground storage organs, fruits, and leaves—as well as small game, which were less variable and more compatible with childcare, while males more often pursued large game and honey, which provided higher energy yields but were more unpredictable and carried greater risks of injury and death (Bird & Codding, 2015). We emphasize that such specialization was unlikely to be fixed, but rather, responded to specific environmental demands (but see ongoing debates, below). Use of fire and cooking further increased energy extraction. A modern

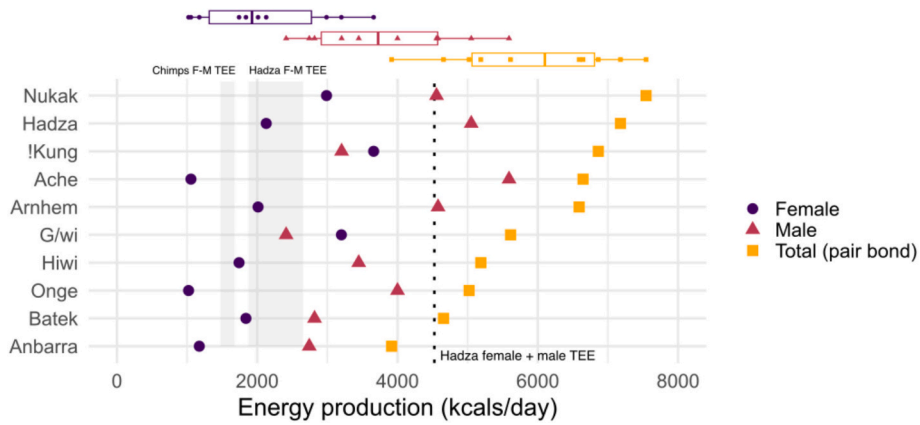


**Fig. 5.** Daily per capita adult energy production by contemporary hunter-gatherer females and males across ten populations. Boxplots in the top panel indicate the distributions of female, male, and total production depicted in the bottom panel. Total (pair bond): average production of one adult female plus one adult male. Grey bars indicate the range of average female (lower) to male (higher) total energy expenditure (TEE) for chimpanzees (left) and adult Hadza (right) measured using doubly labeled water. Dotted line indicates total TEE for one Hadza female + one male. Chimpanzee energy production is assumed to equal total energy expenditure (i.e., no surplus production other than for lactation). Data from Kraft et al. (2021) and Pontzer et al. (2015).

take on Sahlins' Original Affluent Society, based on decades of research in diverse foraging and great ape populations, is that hunter-gatherers expended a lot of energy to acquire a lot of energy in a short period of time compared to other apes, leaving more time for other activities (Kraft et al., 2021; Venkataraman, 2023).

The greater energy acquired via these traits then enabled increases in the size of the body and energetically expensive brain, along with shorter interbirth intervals. The latter, combined with a long juvenile period during which offspring were unable to fully meet their own energy needs, created a more complex parenting environment in which multiple offspring depended on steady adult surplus production (see Figs. 5 and 6), perhaps in the context of long-term pair bonds. This mode of subsistence in open, variable habitats required close cooperation within residential groups among kin and non-kin for hunting large game, predator defense, and child rearing (alloparenting), and between groups for access to mates, access to information and resources in other regions, and territorial defense. It might also have selected for an unusual female post-reproductive phase (menopause), during which investment was redirected from future children (e.g., pregnancies) to current children and/or grandchildren. For theory and evidence from paleoclimatology, paleoanthropology, primatology, evolutionary biology, and HBE supporting this rough consensus, see Aiello and Key (2002), Antón et al. (2014), Bird and Codding (2015), Boyd and Richerson (2009), Chapais (2010), Crittenden and Schnorr (2017), Foley and Gamble (2009), French (2024), González-Forero and Gardner (2018), Gurven and Hill (2009), Hamilton, Milne, Walker, Burger, and Brown (2007), Hart & Sussman (2008), Hawkes (2003), Henrich (2016), Hrdy (1999, 2009), Kaplan, Hill, Lancaster, and Hurtado (2000), Kaplan et al. (2009), Koster et al. (2020); Kraft et al. (2021), Pisor and Surbeck (2019), Pontzer and Wood (2021), Potts (2013), Richerson and Hames (2017), Rodseth et al. (1991), Schacht and Kramer (2019), Sievert (2025), Kramer and Russell (2015), Kramer (2010), Kramer and Ellison (2010), Kramer (2018), Tooby and Cosmides (1992), Van Schaik (2016), Wrangham (2009), Yegian et al. (2024), Zeller et al., 2023, and Zeller and Timmermann (2024).

**Phase IV: *Homo sapiens* (250-300 kya to 11.7 kya)**[9]: The first fossil evidence of *Homo sapiens* appears in Africa with brain sizes now approximately three times larger than apes and early hominins, clear evidence for the frequent controlled use of fire (MacDonald, Scherjon, van Veen, Vaesen, & Roebroeks, 2021), and with material culture, such as sophisticated stone tools, personal ornamentation, and art, that increasingly resembles that of contemporary humans, and probably indicates the emergence of a full-blown capacity for language, social learning, and cumulative culture (Powell, Shennan, & Thomas, 2009; Langley & Suddendorf, 2022; Kelly, Mackie, & Kandel, 2023; Scerri & Will, 2023; but see Stibbard-Hawkes, 2024). In contrast to 19th century theories in anthropology depicting hunter gatherers as a "savage" stage in human evolution, MTH initiated the modern conception of Upper Paleolithic hunter-gatherers as fully modern humans able to adapt to diverse environments (Hallett et al., 2025; Scerri & Will, 2023).

After an apparent expansion out of Africa c. 250 kya and interbreeding with Neanderthals that did not leave any modern human descendants (Harris et al., 2023), *Homo sapiens* again expanded out of Africa sometime after 80 kya, interbred with Neanderthals and Denisovans, and replaced them by the end of the Pleistocene (Bergström et al., 2021). Humans, who now occupied diverse habitats (Fig. 4), reached the Americas 15-25 kya (Pigati et al., 2023; Willerslev & Meltzer, 2021). Genetic evidence indicates that the effective population sizes of modern humans in Pleistocene Africa and Eurasia were small, in the few tens of thousands or less (Fan et al., 2023; Sikora et al., 2017).

**Phase V: The Holocene shift to agriculture (11.7 kya-present)**. In the Holocene, a period of rapid global warming and sea level rise, human populations began a relatively swift transition to permanent settlements and a reliance on domesticated plants and animals, leading to massive population growth (Stephens et al., 2019; Stoneking et al., 2023). Thus, with the important exception of the Indigenous peoples of Australia, who did not practice agriculture prior to European contact, all ethnographically known foragers have a long history of direct or indirect interaction with farmers and/or pastoralists. See Figure 7. Remote horticultural populations, studied by MTH participant Chagnon and others, serve as models of these early Neolithic farmers (e.g., Chagnon, 1996). Interactions between foraging and horticultural populations, their integration with state-level markets, and the subsequent health and social consequences, have been an important focus of much HBE research (Blackwell, Pryor III, Pozo, Tiwia, & Sugiyama, 2009; Gurven et al., 2017; Hart, 1978; Hill & Hurtado, 1996; Neel, 1977; Stagnaro, Stibbard-Hawkes, & Apicella, 2023; see also Table 1).

These five phases are not equal with respect to the potential of natural selection to shape morphology, physiology and behavior. Phases II and III were each more than two million years long, ample time for natural selection to act, and both phases involved substantial changes in ecological niche and morphology. Phase IV was only about one tenth as long, 0.2-0.3 million years, but likely witnessed the emergence of a full-blown capacity for language and cumulative culture. Phase V was only

[9] Unlike our other phases, which are defined by geological time periods, this phase is defined by the first appearance of our species in the fossil record.

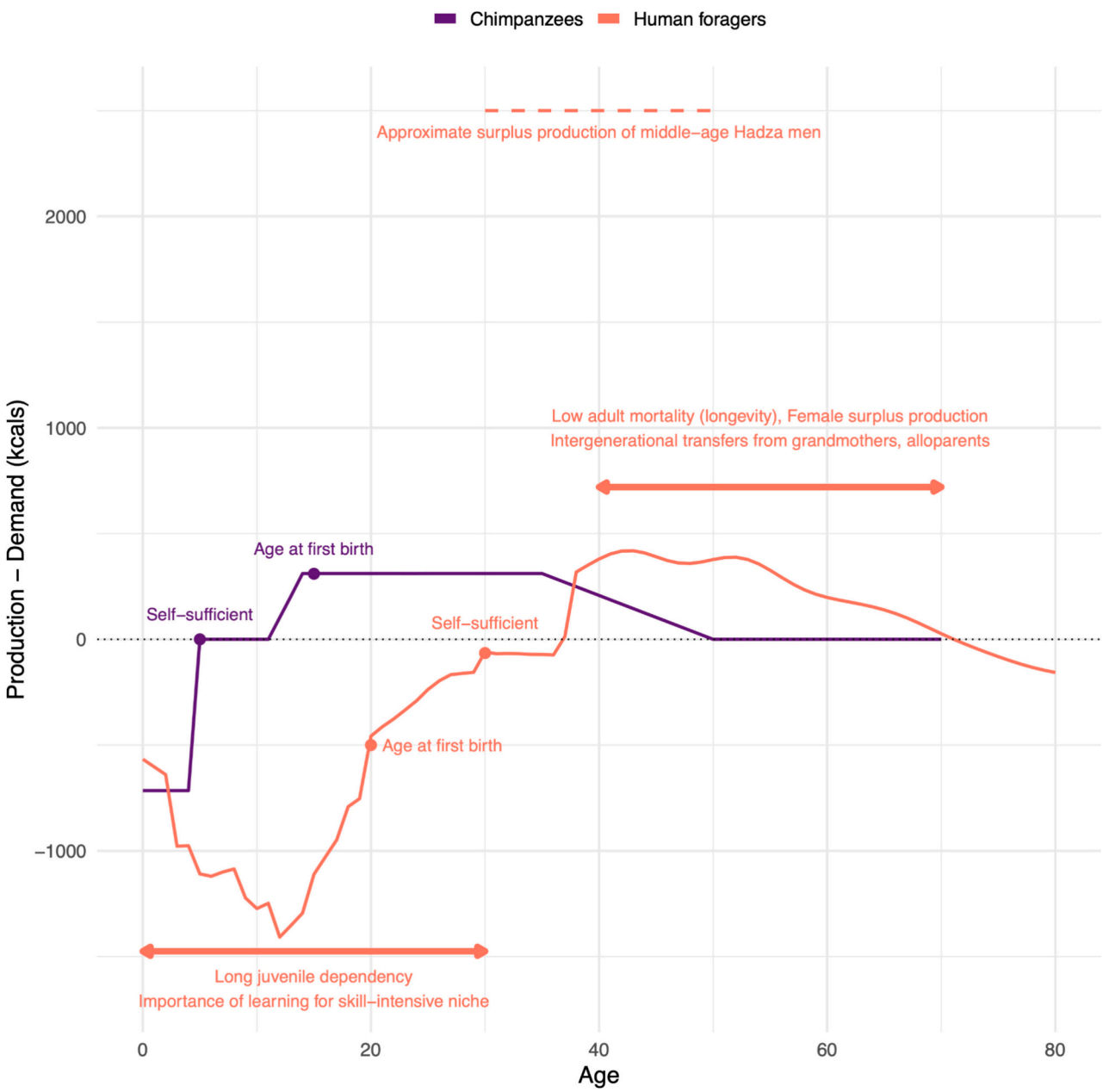


**Fig. 6.** Net calorie production of contemporary hunter-gatherers and chimpanzees by age. Female data (solid lines) from Davison and Gurven (2021, 2022). Hadza male surplus value (dashed line) from Kraft et al. (2021). Gaussian kernel smoothing applied to noisy human female data for ages above 39. Figure from Hagen, Garfield, and Lightner (2025). For a more thorough investigation of energy balance in hunter-gatherer families, see Hagen (2026).

0.01 million years, but involved substantial changes in subsistence and population size. See Figure 8.

### 5.1. Ongoing debates

There is a broad consensus that humans evolved to exploit an energy-rich but complex and variable extractive foraging niche that relied heavily on both plant and animal foods, demanded substantial learning, and required extensive cooperation within and between the sexes to obtain food and raise offspring. However, a number of issues remain heavily debated. These include identification of hominin taxa and their phylogentic relationships (Martin, Leece, Baker, Herries, & Strait, 2024; Wood & Boyle, 2016); when, why, and how bipedalism evolved (Almécija et al., 2021; Raichlen & Pontzer, 2021; Stamos & Alemseged, 2023); the relative importance of hunting (Domínguez-Rodrigo et al., 2021) vs. scavenging (Mateos et al., 2025; Pobiner, 2020), and animal (Ben-Dor et al., 2021) vs. plant foods (Crittenden & Schnorr, 2017; Pontzer & Wood, 2021) and their differing nutritional values (Konner & Eaton, 2023); whether men's hunting and food sharing benefited their own offspring (Kaplan et al., 2000; Kaplan et al., 2009; Wood & Marlowe, 2013) or were instead a means to acquire mating opportunities (Hawkes & Bird, 2002; Hawkes, O'Connell, Jones, Alvarez, & Charnov, 1998); whether the sexual division of labor evolved in the Pliocene (Lovejoy, 1981), early Pleistocene (Aiello & Key, 2002), late Pleistocene (Kuhn & Stiner, 2006), or Holocene (Lacy & Ocobock, 2023), and the extent to which it involved cooperation or conflict between the sexes (Bird & Codding, 2015; Gurven & Hill, 2009); whether hunter-gatherers were largely egalitarian and nomadic, or potentially sedentary and stratified, for much of human evolutionary history (Boehm, 1999; Woodburn, 1982; Price & Brown, 1985; Jochim, 1987; Shultziner et al., 2010; Singh & Glowacki, 2022; Barham, Duller, & Candy, 2023); the evolutionary mechanisms stabilizing cooperation in groups of various

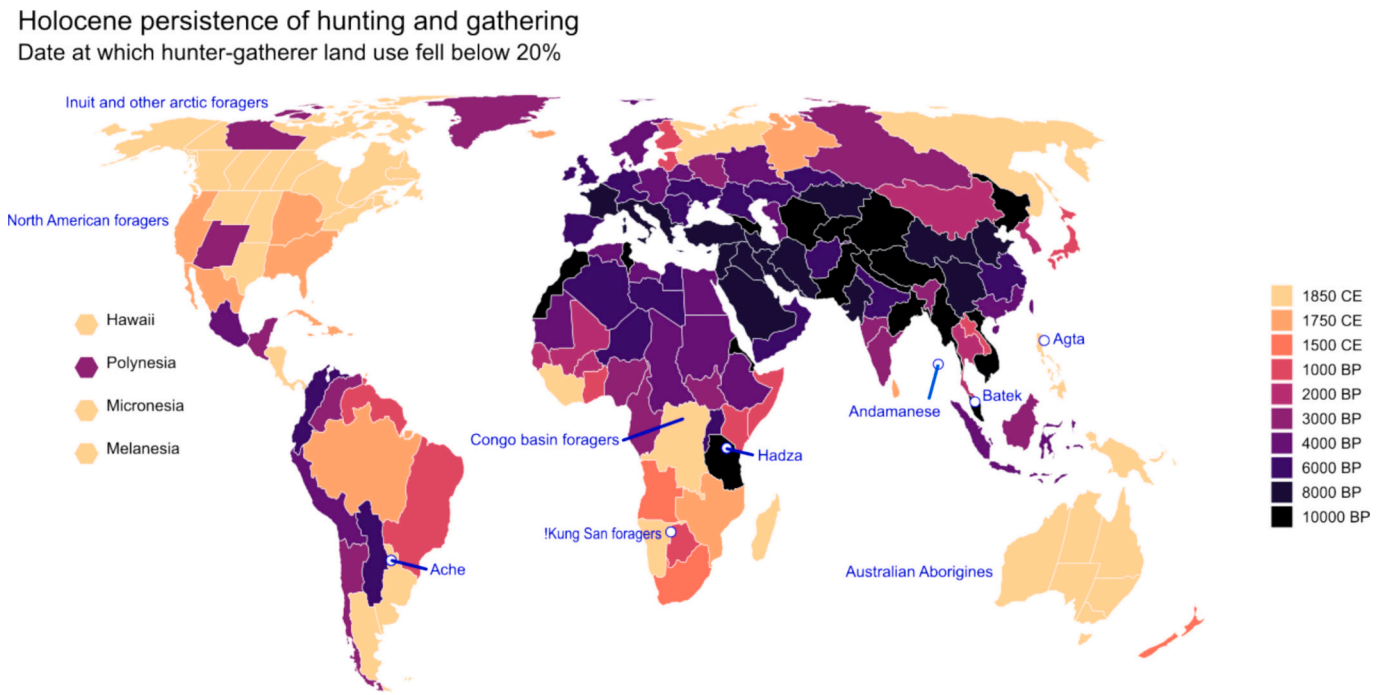


**Fig. 7.** Land use by hunter-gatherers during the Holocene (hunting, gathering, fishing). Data are from Stephens et al. (2019), who coded hunter gatherer land use at each date as "Widespread (>20%)", "Common (1-20%)", "Minimal (<1%)", or "None". Colors represent the oldest date at which land use by hunter-gatherers transitioned from "Widespread (>20%)", to "Common (1-20%)" (if coded as "Widespread" for all dates then the date was set to 1850 CE). Morocco, Pakistan, and Northwestern China were coded as "Minimal" or "None" for all time periods, so we coded their transition date as 10,000 BP. Ethnographically studied foraging populations are labeled in blue (see also Table 1).

sizes (Bowles, 2009; Boyd & Richerson, 2022; Tomasello & Vaish, 2013; Gavrilets, 2015; Syme & Balliet, 2025); whether encephalization was driven primarily by social (Alexander, 1989; Dunbar, 2024; Flinn et al., 2005) or ecological selection pressures (González-Forero & Gardner, 2018; Kaplan et al., 2000); whether human cognition primarily involves relatively few universal evolved individual and social learning mechanisms supporting cumulative culture (Henrich, 2016; Richerson & Boyd, 2008), or whether it instead comprises a much richer evolved psychology (Baumard & André, 2025; Cosmides & Tooby, 1994); why and how language evolved (Fedorenko, Piantadosi, & Gibson, 2024; Fitch, 2017; and references therein); whether human overkill (Svenning et al., 2024) or climate change (Meltzer, 2020) was primarily responsible for the extinction of most megafauna by the end of the Pleistocene (Stewart et al., 2025); and the extent to which Neanderthals and Denisovans possessed modern human cognitive abilities, and why these sister species went extinct (Nowell, 2023).

By far the most contentious issue, however, is the importance of violence and warfare in human evolution (Ember, 1978). In brief, there is now widespread agreement that warfare had an important impact on social organization and demography in a broad range of small-scale societies in both ethnographically studied populations (Glowacki, 2025), and in similar archaeological populations throughout the Holocene (Meijer, 2024), including some hunter-gatherer societies. There is also widespread agreement that chimpanzees exhibit lethal war-like behaviors but that, to date, these have not been observed in bonobos (Samuni & Surbeck, 2023; but see Pashchevskaya et al., 2025, for a lethal intragroup coalitional attack in bonobos). Finally, there is widespread agreement that there is currently no concrete evidence for warfare in hominins since our divergence from chimpanzees in the late Miocene until the terminal Pleistocene. Thus, the case for the importance of warfare in human evolution depends largely on the behaviors of populations in the Holocene, scattered bioarchaeological evidence of interpersonal violence in the Pleistocene, comparative evidence from the few nonhuman species that also have lethal intergroup conflicts, and theoretical arguments (for recent reviews, see Ferguson, 2021; Gat, 2015; Glowacki, 2024; Gómez, Verdú, González-Megías, & Méndez, 2016; Halstead & Thomson, 2022, 2025; Kissel & Kim, 2019; Wilson et al., 2014; Hames, 2019).

### 5.2. Contemporary foragers

The diverse lifeways of contemporary foragers, documented by contributors to MTH, their students and collaborators, and many others (see Table 1), are comprehensively situated in an HBE framework by Kelly (2013), who emphasizes cost-benefit analyses (for supporting evidence of claims in this section, see Kelly, 2013, and references therein). Kelly reviews optimal foraging studies showing that forager diets cannot be stereotyped yet are related in a fairly straightforward fashion to gross environmental characteristics such as effective temperature and primary productivity, with meat comprising a greater proportion of the diet with increasing distance from the equator (Lee, 1968). Mobility is a defining feature of many hunter-gatherer societies that has a major impact on other dimensions of life, and the often substantial costs of moving must be outweighed by the benefits. The use of simple or complex technology seems to be determined by the tradeoffs of investing time and energy into its manufacture and transport vs. the benefits gained from it, rather than intrinsic limits of a hunting and gathering lifestyle. An ethic of sharing is fundamental in many hunter-gatherers, where again, they balance the costs and benefits of sharing resources when making decisions to share food or to admit outsiders into their territory. Much research has focused on demography, such as optimal group sizes, population growth rates, carrying capacity, mortality (including from violence and warfare), fertility, infanticide, birth spacing, maternal condition, and more. There is dramatic variation in social complexity among hunter-gatherer societies, as well as variation in egalitarianism, postmarital residence, descent, marriage, and the division of labor. Women do hunt. But the real division of labor is not hunting vs. gathering but risky vs. non-risky foraging. Kelly (2013, p. 272) concludes

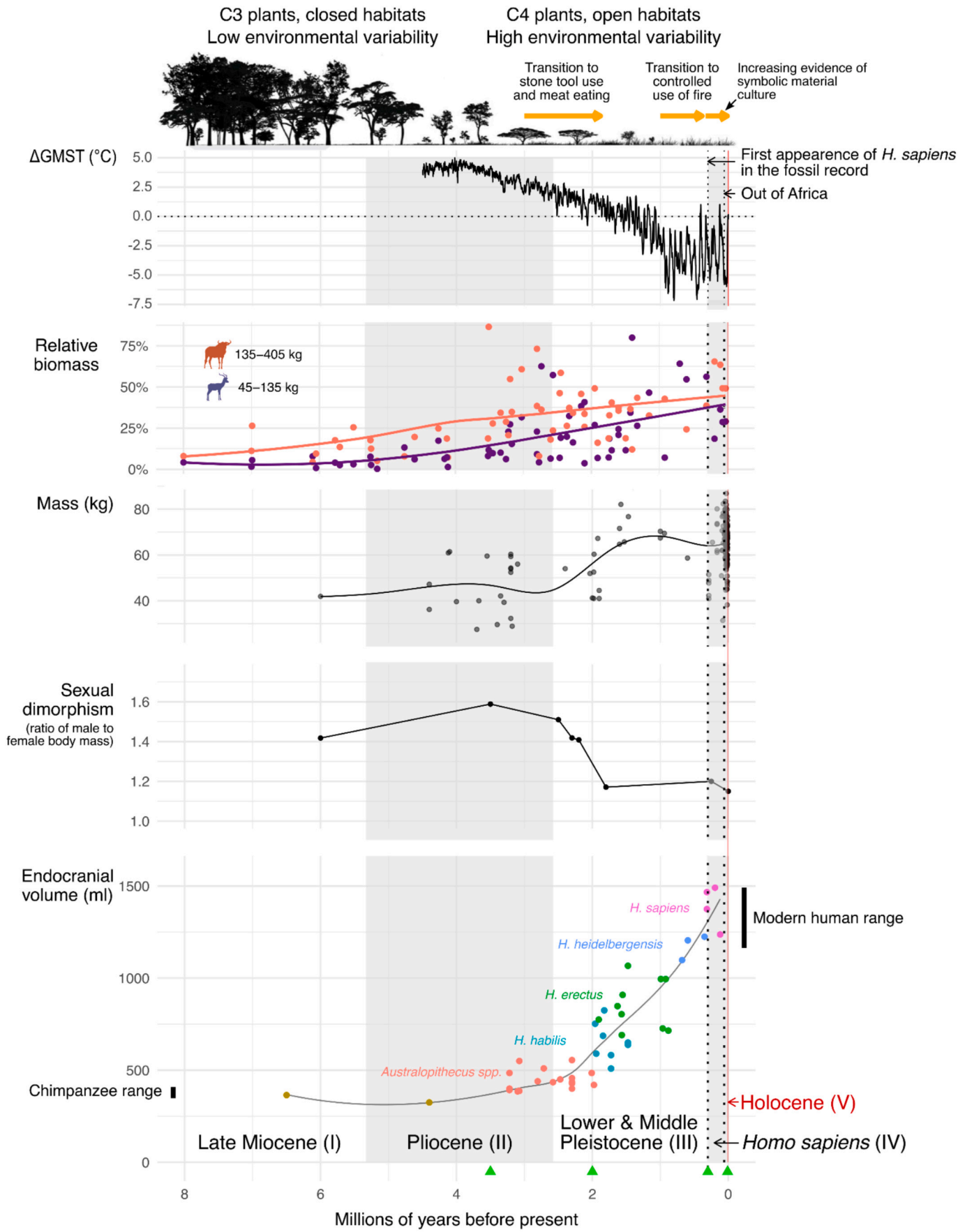


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**Fig. 8.** Changes in habitat and morphology during Phases I-V of human evolution (see text). Top panel: Diagram of the hominin transition from closed woodland habitats dominated by C3 plant foods, to more open habitats dominated by C4 plant foods. Illustration from Peppe et al. (2023). Second panel: Global Mean Surface Temperature (ΔGMST) relative to late Holocene preindustrial value. Data from Clark, Shakun, Rosenthal, Köhler, and Bartlein (2024). Third panel: Relative biomass of medium-sized herbivores. Not depicted: Relative biomass of small herbivores (15-45 kg) also increased across this time period, whereas that of megaherbivores (>405 kg) decreased. Data and code from Bibi and Cantalapiedra (2023). Fourth panel: Estimated hominin body masses (excluding *Paranthropus* spp., *A. africanus*, and Eurasian hominin species prior to 100 kya that presumably did not belong to the human lineage). Each dot is a fossil specimen. Data from Ruff and Wood (2023). Fifth panel: Estimated hominin sexual body dimorphism (the ratio of male to female body mass). Each dot represents a different hominin clade (except the two rightmost dots, which are both *H. sapiens*). Data from Grabowski, Hatala, Jungers, and Richmond (2015) and Ruff and Wood (2023). Note that despite low body size dimorphism, modern humans exhibit substantial sexual dimorphism in body compostition (Lassek & Gaulin, 2022). Sixth panel: Estimated endocranial volumes of species thought to belong to the human lineage. Each dot is a fossil specimen. Data from Du et al. (2018) and Neubauer, Hublin, and Gunz (2018). Green markers at the bottom indicate proposed dates for the emergence of a sexual division of labor.

that the "misuse of modern hunter-gatherer research provides spurious support for the idea of a single primitive human society, a uniform hunter-gatherer stage."

## 6. Connections between Dart/Ardrey, MTH, and the contemporary science of human evolution

In the previous sections, we outlined several distinct framings of MTH, focusing on the popularized framing (Section 3), the MTH conference and volume (Section 4), and the contemporary science of human evolution it inspired (Section 5). We now ask: to what extent was the popularized framing connected to MTH and the emerging science of human evolution? The historical evidence suggests the answer is very little.

Robert Ardrey was a strategic popularizer, cultivating a network of connections with leading popular scientists of the day, including the paleoanthropologist Louis B. Leakey, with whom he once shared the stage for a dialogue at Caltech (Weidman, 2011). Hart and Sussman (2008) argue that Leakey promoted Ardrey's ideas, catalyzing their acceptance across the Western world, but we have uncovered little evidence for this claim. At the Caltech dialogue, Leakey vehemently disagreed with Ardrey on the idea that predator instincts are basal to humanity (Leakey & Ardrey, 1971). Nevertheless, Ardrey was instrumental in creating a novel contact point between zoology and paleoanthropology (Weidman, 2011).

Ardrey's public campaign to promote Dart's ideas rarely involved contemporary ethnographic data. In general, Ardrey (1961, 1966, 1970, 1976) and Morris (1967) hardly cited anthropologists[10], instead focusing on homologies between humans and other primates through an ethological lens, prioritizing the work of Konrad Lorenz and Niko Tinbergen, and highlighting ethological studies of birds, lions, and wolves. Ardrey and Morris did not incorporate new theoretical insights that would later give rise to human behavioral ecology, cultural evolution, and evolutionary psychology.

Ardrey and Morris eschewed ethnographic studies because they were more concerned with the 'pre-cultural' phases of human evolution. In fact, Ardrey displayed outright hostility toward ethnographic approaches to reconstructing the past. In *The Hunting Hypothesis*, Ardrey wrote: "The 'living fossil' fallacy is accepted by observers who take as their model contemporary hunting peoples to inform us as to our way in ancient times" (Ardrey, 1976, p. 75). In *The Social Contract*, he described modern foragers as "human evolution's losers" (Ardrey, 1970, p. 238). Ardrey criticized the MTH conference for neglecting the importance of long-distance weaponry, which he viewed as instrumental in human origins (Ardrey, 1970, p. 271). Ardrey outlined three shortcomings of ethnographic analogy: first, contemporary foragers have fire, cooking utensils, and relatively recent weaponry, making them poor models for past foragers. Second, citing Lee's work on the !Kung, Ardrey saw the life of contemporary foragers as too easy, with people living into their sixties and beyond, whereas lives would have been far shorter in the past due to hardship. Third, contemporary foragers relied too much on vegetable foods, again complicating inferences about the past. Even after reviewing Lee's (1968) data on forager consumption of plant foods in some detail, Ardrey rejected them without presenting any credible counter-evidence: "Our remaining primitive hunting peoples depend more on the hunt than is generally accepted." (Ardrey, 1970, p. 239).

At the same time, anthropologists virtually ignored Ardrey and Morris. There is only one mention of Ardrey in the MTH volume, in which Julian Steward critiques Ardrey for his 'sensational' and 'genetically determined' view of human territoriality (Steward, 1968). There is no mention of Dart. Contrary to Sussman (1999), who conflated Ardrey's, Dart's, and Washburn's ideas, Washburn thought little of Ardrey's work, calling him a "popularizer of data he does not understand." (Time, 1970). The edited volume *Omnivorous Primates* (Harding & Teleki, 1981), which, as the title indicates, drew attention to dietary diversity in primate and human evolution, was conceived as a corrective to Dart and Ardrey's narrative. British anthropologist Edmund Leach said that Ardrey's series of books was "best left alone altogether" (Time, 1970). As summarized by MTH attendee Marshall Sahlins (1962, p. 172), "Ardrey presents us with a view of human nature that does not make relevant the accumulated anthropological evidence of man's behavior."

Numerous scholars of the human evolutionary sciences who attended graduate school in the 1970s and 1980s stated that Robert Ardrey's thinking played no role in their training or thinking and was largely dismissed as irrelevant (*pers comm*, R. Wrangham, K. Hill, R. Kelly). Thus, there is little evidence that Ardrey was an intellectual influence on developing scholarship within academia in the 1970s. We uncovered two minor exceptions. One is paleoanthropologist Rick Potts, Curator of Biological Anthropology at the Smithsonian's National Museum of Natural History, who, as a ninth grader, was inspired by Morris's and Ardrey's books (Selig, 1999). The second is Leda Cosmides, a prominent founder of evolutionary psychology, who, as an undergraduate at Harvard, was influenced in her thinking about human behavior by Ardrey's *The Territorial Imperative* (Wolpert, 2003), which motivated her to meet with E.O. Wilson, and eventually to connect with DeVore and his group.

It was not only the content of Ardrey's works that drew consternation from anthropologists. It was also his method. In his teaching, DeVore presented Ardrey's selective evidence in *African Genesis* as a way to not do research, as contrasted with Ernst Mayr's *Animal Species and Evolution*. As described by Mel Konner, "Ardrey stated his thesis and spent hundreds of pages presenting evidence that supported it; Mayr stated his and spent even more pages trying to deal with evidence inconsistent with it. There was no doubt about how Irv wanted us to proceed" (Fleagle et al., 2015. p. 87). DeVore was well aware of the cultural

[10] One exception: Morris acknowledges Nick Blurton Jones in *The Naked Ape*.

implications of Ardrey's theory[11].

Taken together, the historical evidence suggests that popularized versions of MTH, shaped in large part by Ardrey, had little basis in or relationship with an adaptive approach to human behavior, as employed at the MTH conference, and later by human behavioral ecologists.

## 7. Washburn's outsized influence

Our paper offers a conceptual advance in distinguishing three framings of MTH, while also emphasizing historical contingencies and power imbalances that shaped subsequent thought. In particular, Sherwood Washburn played a powerful role in the genesis and execution of the *Man the Hunter* conference. Washburn's choice of title for the 1966 conference and 1968 volume has contributed to substantial scholarly and popular confusion. Moreover, many of the critiques levied at the volume do apply to particular conference papers, especially Washburn and Lancaster's (1968) version of the HH, in which "…hunting and butchering large animals put a maximum premium on cooperation among males" (Washburn & Lancaster, 1968, p. 296). While gathering and food processing are not entirely ignored ("man gathers a wide range of items that he cannot digest without soaking, boiling, grinding, or other special preparation.") (p. 295), there is no mention that in contemporary foraging societies, this is typically work performed by women and provides a vital contribution of labor and calories (but see Abraini, 2025, for an argument that by frequently referring to hunting *and* gathering, and by identifying the development of container technology for the plant foods gathered by women as "one of the most fundamental advances in human evolution," Washburn and Lancaster did explicitly include women in their scenario). Despite evidence available at the time about women's cooperation, including from the MTH conference itself (e.g., women's hunting among the Ainu, Watanabe, 1968), Washburn and Lancaster (1968) missed an opportunity for discussion of female cooperation as an evolutionary force. At the same time, this area of work was also relatively neglected by scholars in the behavioral ecological tradition until relatively recently (Fox, Scelza, Silk, & Kramer, 2023; Kramer, 2023).

Additionally, alloparenting and other forms of cooperation are a major focus of today's evolutionary anthropologists, but cooperation was a relatively neglected topic at *Man the Hunter*, mostly limited to the domains of male hunting behavior, marriage alliances, and food sharing within families. Washburn resisted the revisionist views of Lee and others who saw hunter-gatherers in the context of an overarching socioecological system in which cooperation across multiple domains, such as foraging, food sharing, child rearing, and predator defense, drove human adaptation (Venkataraman & Lee, 2025). Instead, Washburn appeared to endorse a narrow version of the HH in which males hunted cooperatively and then shared meat within their nuclear families (Washburn & Lancaster, 1968; Washburn & Ranieri, 1981).

Nevertheless, through his training of female students, Washburn helped to lay the foundation for the feminist critique that would come to augment his vision of the HH (Marks, 2000).

## 8. Discussion

*[T]he "woman the gatherer" model by Tanner, Zihlman, and others…has offered a healthy corrective on key issues in hominid evolution.*[12]
- Tooby & DeVore, 1987

*All models are wrong, but some are useful.*
- Aphorism attributed to statistician George Box.

The Nativism-Empiricism debate, also known as the Nature-Nurture debate, has endured for millenia (Samet, 2024). Empiricism gained the upper hand in the 17th and 18th centuries with the influential works of Locke, Hume, and Berkeley, and maintained it through the mid 20th century with the influential works of behaviorists like Pavlov, Watson, and Skinner (Graham, 2023; Samet, 2024). Nativist views of the mind made a comeback in the post WWII period, however, led by Chomsky's work on language cognition (Chomsky, 1959, 1965; Griffiths & Linquist, 2024). Chomsky's work coincided with two other developments to set the stage for clashes over MTH. First, a genuine science of human evolution was materializing with spectacular fossil discoveries in Africa, systematic studies of primates, increasingly detailed investigations of contemporary foragers, and breakthroughs in unravelling the genomes of humans and other species. Second, there were major advances in evolutionary theories of behavior (e.g., Alexander, 1974; Hamilton, 1964; Maynard Smith & Price, 1973). Washburn and DeVore both recognized that integrating research on cognition, behavior, and human evolution had immense scientific potential (Tooby & DeVore, 1987; Washburn, 1972). This synthesis, which we have termed HBE, and which has deep ramifications for both Nativism and Empiricism, emerged alongside the atomic weapons arms race, movements to secure civil rights, gender equality, and independence from European colonialism, the onset of the Cold War, increasing human impacts on the environment, and in the long dark shadow of the Holocaust. Controversy over the implications of HBE, and of Nativism and Empiricism more generally, for progress on each of these pressing social and political challenges was inevitable (Tam & Lange, 2024).[13]

Lacy & Ocobock (2023, p. 2) open their article *Woman the Hunter: The archaeological evidence* by conjuring an image from Mel Brooks's film, *History of the World, Part 1*, that depicts "a caveman hitting a woman over the head and dragging her back into the cave as property", and claim "The term 'Man the Hunter' *and its modern connotations* [our emphasis] were coined at a conference and then promoted in an edited volume of the same name…." Fuentes (2017, p. 51) characterized the thesis of the MTH volume as "Early man (and they meant only males, not females) made a place for himself and his group in the world by banding together and using sharp sticks and edged stones to hunt down animals, kill them, and consume them."

In this paper, we have challenged these reductive and inaccurate portrayals. We have distinguished popular and scientifically unsound framings of MTH from more nuanced framings within anthropology and the field of hunter-gatherer studies. The above portrayals, while rhetorically effective with popular audiences, bear more similarity to Raymond Dart's Killer Ape Theory (Dart, 1953), popularized in the writings of Robert Ardrey and Desmond Morris, and mischaracterize the MTH conference and volume. In fact, Brooks's scene is an explicit parody of *2001: A Space Odyssey*'s "Dawn of Man" scene.

We argue that distinguishing between the three frames of MTH is critical for future productive dialogue regarding this controversial

[11] Lee (2018) presented the following anecdote: "I vividly remember the late Irven DeVore coming into my office at Harvard University. "I just got off the phone with Senator William Fulbright calling from Washington," DeVore said. "He asked me 'Professor DeVore, if Konrad Lorenz is right, how are we ever to negotiate a nuclear arms reduction treaty with the Soviet Union?'" DeVore reassured Fulbright that Lorenz's views were far from universally accepted among anthropologists, that violence in human history was a variable not a constant, and that its causes and expressions were far more complex than could be explained simply by pure animal instinct. DeVore's disclaimers appeared to calm Senator Fulbright's nerves, and in fact the United States and the Union of Soviet Socialist Republics (USSR) went on to successfully negotiate a series of nuclear arms reduction treaties over the years."

[12] Tooby and DeVore (1987) credit the "woman the gatherer" model for emphasizing the equal importance of both sexes in human evolution but critique elements of it in favor of their version of the hunting hypothesis.

[13] The so-called "cognitive revolution" was sparked by Chomsky's nativist account of language and various computational theories of mind (Rescolra, 2025). See Núñez et al. (2019) on the failure of the cognitive revolution to coalesce into a unified cognitive science.

concept. Research in the human behavioral sciences is frequently co-opted and misinterpreted to serve different popular narratives (Milam, 2019; Weidman, 2021, p. 14). Simplified and unnuanced treatments of MTH exacerbate this problem of science communication and may cause simplifying or misleading claims to propagate through the literature (Banobi, Branch, & Hilborn, 2011), as indeed they already have (Alex, 2023; Anderson et al., 2023).

To move beyond these simplistic characterizations, the critical question is: how should we talk about Man the Hunter? Our aim is not to prevent or discourage scientific critiques of MTH or models of human evolution, but instead to improve them. To advance this goal, we offer three suggestions.

First, we suggest that researchers avoid referring to a general Man the Hunter paradigm, which does not exist in any unified sense. Some anthropologists critique behavioral ecological approaches to hunter-gatherer behavior when they mean to target the long-discredited Dart and Ardrey version of MTH (Anderson et al., 2023; Fuentes, 2021; Haas et al., 2020; Lacy & Ocobock, 2023; Ocobock & Lacy, 2023). These critiques often equate violence with hunting, evoking the ideas of Dart and Washburn & Lancaster (1968). Even Cartmill's (1996) excellent analysis of the cultural history of hunting conflates hunting and violence (or murder and warfare). But, contrary to Dart, Ardrey, Washburn & Lancaster, and Cartmill, hunting is a dietary adaptation, whereas violence against other humans or groups is a sociopolitical strategy. Moreover, hunter-gatherer societies typically conceptualize their prey species and other natural elements of their world as respected and powerful beings with whom they must maintain trusting relationships (Bird-David, 1992; Bodenhorn, 1990; Ingold, 2002; Sharp & Sharp, 2015). A similar mistake of conflating behavioral ecological approaches with popular accounts occurred in debates over the chimpanzee violence hypothesis (CVH)[14]. We are concerned that these framings, rather than serving to dispel long-discredited versions of the hunting hypothesis, instead serve to perpetuate it.

With this in mind, we suggest that critiques of MTH should specify the particular model(s) they are focusing on. Rather than referencing the MTH volume in its totality, for instance, it would be more useful to highlight particular chapters and specific claims. Being more precise will avoid conflating coarse depictions of human evolution - shaped by Dart, Ardrey, and Morris - with the scientific legacy of primate and hunter-gatherer studies that the MTH conference and its participants helped initiate, which now provide several interrelated and plausible scenarios for human evolution. Washburn's MTH model (Washburn, 1960; Washburn & Lancaster, 1968) was wrong, but it was a useful starting point and played a key role in motivating the research that eventually replaced it. The MTH conference — in spite of its name (Venkataraman & Lee, 2025) — revealed the important role of women in foraging societies (Lee, 1968) and showed that hunter-gatherer existence was not a constant struggle for survival (Sahlins, 1972). It emphasized cultural diversity and quantitative research among foragers (Table 1), and its legacy continues to influence contemporary forager research and inform theories of human evolution and the nature of hunter-gatherer social life. The HBE research tradition, which provides a promising resolution to the Nativism-Empiricism debate (Boyd & Richerson, 2009; Smith, Borgerhoff Mulder, & Hill, 2001; Tooby & Cosmides, 1992), can trace its lineage to the MTH conference and volume, but it bears little connection to Dart, Ardrey, and Morris (Fig. 2).

Second, when discussing subsistence strategies based on foraging wild animals and plants, as well as gendered divisions of labor in the present and past, we recommend that scholars look beyond stereotypic dichotomies of 'Man the Hunter, Woman the Gatherer' (Panter-Brick, 2002) and strive to accurately characterize the nuanced position that most scholars take on these issues. In the optimal foraging framework adopted by HBE, maximizing energetic returns, whether from animal or plant foods, and buffering risk in specific ecological conditions are key considerations, which demand significant flexibility in gender roles while also recognizing cross-cultural regularities in foraging specialization do exist (Noss and Hewlett 2001; Bird & Codding, 2015; Venkataraman et al., 2024). Emic perspectives of individuals from forager populations themselves should be carefully considered in such critiques, to avoid projecting our own social norms onto their societies, and inadvertently over-valuing hunting, which is only one important behavior among many. For instance, Martin, Mora, Valeggia, & Veile, 2024, p. 1) observed that the critique of Ocobock and Lacy (2023) is "rooted in assumptions that hunting is a superior, more-desirable activity", a view that is "not shared…by many women in foraging societies themselves." In the cosmology of marriage among one Arctic foraging society, for instance, husbands depend on their wives' generosity in distributing hunted meat and their skill in sewing to attract prey animals, respected beings in their own right (Bodenhorn, 1990).

Third, and most importantly, the term "hunter-gatherers" emphasizes the importance of these modes of extracting energy from the environment. Yet what was already apparent at the MTH conference, and has since been revealed in much greater detail, is that obtaining these forms of energy from variable environments was but one step in achieving the ultimate evolutionary "goal" of increasing fitness (survival and reproduction), which also requires sophisticated forms of cooperation and information transmission by both women and men, and by both children and adults (Jang & Redhead, 2025), who live in interconnected multilevel societies (e.g., communal drive hunting; Boyd & Richerson, 2022; Morin et al., 2024). Researchers should consider which elements of these complex dynamic systems are most relevant to their work.

The deeper issue underlying our three suggestions, as well as the larger controversies we are addressing, is what many authors refer to as the "is-ought" distinction or the "naturalistic fallacy" (e.g., Hume, 1739; Moore, 1903): scholars should recognize that there are no simple or easy inferences from theories of human evolution to how we ought to organize modern societies (Gould, 2011). Following our three suggestions, and avoiding naturalistic fallacies, will certainly improve the quality of scholarship, and it might also help inform the public what almost six decades of research has revealed about foraging lifeways today and in the past.

## Credit authorship contribution statement

**Vivek V. Venkataraman:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Conceptualization. **Edward H. Hagen:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Conceptualization. **Duncan Stibbard-Hawkes:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Raymond Hames:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Sheina Lew-Levy:** Writing – review & editing, Conceptualization. **Haneul Jang:** Writing – review & editing, Conceptualization. **Luke Glowacki:** Writing – review & editing, Writing – original draft, Conceptualization. **Jordie Hoffman:** Writing – review & editing, Visualization. **Karen Kramer:** Writing – review & editing, Conceptualization. **Helen Elizabeth Davis:** Writing – review & editing, Conceptualization. **Kathrine Starkweather:** Writing – review & editing, Conceptualization. **Barry Hewlett:** Writing – review & editing, Conceptualization. **Zachary H. Garfield:** Writing – review & editing, Conceptualization. **Robert L.**

[14] The CVH which proposes deep roots for human violence, grounded in shared ancestry with chimpanzees (Wrangham, 1999). This idea derives from the behavioral ecology tradition, but it has been synonymized with the Killer Ape Hypothesis (Sussman, 1999). Yet, as Wrangham (1999, p. 02) clarified, these are not the same thing: "Like the killer ape hypothesis, the CVH proposes that human warfare is built on pre-human tendencies. In contrast to the killer ape hypothesis, however, the CVH does not posit a prior history of hunting, nor an aggressive instinct. These and other differences make the killer ape hypothesis irrelevant to the CVH."

**Kelly:** Writing – review & editing, Conceptualization.

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