

Human social organization during the Late Pleistocene: Beyond the nomadic-egalitarian model

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Abstract

Many researchers assume that until 10-12,000 years ago, humans lived in small, mobile, relatively egalitarian bands composed mostly of kin. This “nomadic-egalitarian model” informs evolutionary explanations of behavior and our understanding of how contemporary societies differ from those of our evolutionary past. Here, we synthesize research challenging this model and propose an alternative, the diverse histories model, to replace it. We outline the limitations of using recent foragers as models of Late Pleistocene societies and the considerable social variation among foragers commonly considered small-scale, mobile, and egalitarian. We review ethnographic and archaeological findings covering 34 world regions showing that non-agricultural peoples often live in groups that are more sedentary, unequal, large, politically stratified, and capable of large-scale cooperation and resource management than is normally assumed. These characteristics are not restricted to extant Holocene hunter-gatherers but, as suggested by archaeological findings from 27 Middle Stone Age sites, likely characterized societies throughout the Late Pleistocene (until c. 130 ka), if not earlier. These findings have implications for how we understand human psychological adaptations and the broad trajectory of human history.

What did human societies look like before the Neolithic Revolution some 10-12,000 years ago? Through detailed field studies of mobile hunter-gatherers such as the Ju/'hoansi, Ache, and Hadza¹⁻⁴ and systematic comparisons of (mostly mobile) hunter-gatherers⁵⁻⁸, evolutionary anthropologists have developed a model of pre-Holocene lifeways—a model that represents the conditions under which our species evolved and from which modern societies developed. We refer to this as the *nomadic-egalitarian model* and characterize it as follows (for recent formulations by anthropologists, see work by Fry^{9,10}, Lee¹¹, and Boehm¹²):

- For tens of thousands of years before the Holocene, and possibly much earlier (e.g., ≥ 200 ka),
1. People lived in small bands of up to several dozen individuals. Any focal individual was likely related to most fellow band members, either through blood or marriage. Bands were embedded with ethnolinguistic groups, which comprised hundreds or, in rare cases, a couple thousand individuals.
 2. Bands were mobile and fluid, and people stored very little, relying instead on sharing to insure against risk. As a result, people had few material possessions, and notions of property were weak.
 3. Social relationships were egalitarian, at least among individuals of similar age and sex. Egalitarianism was maintained both by minimal differences in wealth and by leveling mechanisms such as gossip, teasing, and the threat of coordinated violence.
 4. Cooperation was small-scale, occurring mostly among fellow band members.
 5. Agriculture, comprising cultivation and the management of animal populations, was absent.

This model dominates evolutionary analyses of behavior, both as researchers consider how particular behaviors may have been adaptive in mobile, egalitarian, small-scale settings and as they study those behaviors in contemporary populations to make inferences about the past. Indeed, the nomadic, egalitarian model has become an important lens through which scholars, including us, have studied

behaviors as diverse as aggression^{13,14}, childcare¹⁵, cooperation^{16,17}, cumulative culture^{18–20}, leadership^{21,22}, morality¹², religion²³, the sexual division of labor²⁴, social emotion¹⁵, storytelling^{25,26}, violence^{11,27}, and warfare^{28,29}.

Because it posits that “historically nomadic foragers (HNF), small in scale, mobile, and egalitarian, reflect most closely the characteristics of ancient foragers”¹¹, the nomadic-egalitarian model casts many features of contemporary societies as historically novel and in need of explanation. If humans evolved in contexts where they cooperated with, at most, dozens of individuals, then large-scale cooperation becomes a puzzle^{30,31}. If humans evolved in contexts where status-seeking or domineering behavior was constantly suppressed^{16,32}, then the emergence of stratification and inherited inequality becomes a puzzle^{33,34}. If, during 95% of our species’ history, we lacked property^{35–37} or cultivation^{38,39} or large-scale political consolidation and decision-making⁴⁰, then the emergence and ubiquity of those phenomena demands explanation. Depending on how one interprets ethnographic reports of mobile foragers, either the modern capacity for peace²⁸ or the predilection for war^{10,29} are also historically peculiar and, as a result, demand special explanation.

Although the nomadic-egalitarian model has long attracted skepticism⁴¹, researchers in recent years have expressed a growing dissatisfaction with features of the model^{42–46}. Here, we synthesize this and other literature and propose a new model of pre-Holocene lifeways, referred to here as the *diverse histories model*. As early as the penultimate interglacial (c. 130 ka)—and possibly much earlier—humans lived in societies that varied considerably in their social organization. Some humans lived in large, sedentary, dense communities. Some lived in stratified societies with inherited status. Some engaged in cooperative projects with hundreds, even thousands, of people. Some cultivated plants and managed animal populations and may have even domesticated species. As a result, human psychology is adapted not just to dwell in small, relatively egalitarian bands, but to flexibly traverse a broader range of social environments. This new model of human psychological evolution helps explain many reliably developing behaviors that are otherwise difficult to explain if most of our recent evolution was spent in small, mobile, egalitarian bands.

The rest of the paper is structured as follows: We first outline weaknesses of the empirical foundation of the nomadic-egalitarian model. We review limitations of using extant foragers as the primary models of Late Pleistocene and highlight the variation exhibited among mobile forager societies, focusing especially on evidence for large groups, inequality, large-scale cooperation, and cultivation. We then discuss sedentary and non-egalitarian foragers. We show that such forager societies are far from anomalous, reliably emerging in environments with dense, rich, and predictable resources. Given that humans have occupied and intensively exploited these environments throughout the Late Pleistocene, there is little reason to suspect that they did not correspondingly build societies that were large, hierarchical, and/or (semi-)sedentary by at least 130 ka. We conclude by reviewing implications for the evolutionary understanding of diverse human behaviors.

Limitations of using extant foragers as models of Late Pleistocene societies

The nomadic-egalitarian model was inspired largely by observations of recent foragers^{11,12,47,48}. Such groups, especially those living in Africa such as the Hadza and the Ju’/hoansi (a !Kung-speaking people and one of the “San” or “Bushman” peoples of southern Africa), appear to mostly live in small, mobile bands with relatively egalitarian relations among individuals of similar age and sex⁴⁹. The conviction that these groups represented the typical forager lifestyle⁴⁷, and that African hunter-gatherers in particular inhabited an environment similar to the one in which humans spent most of their evolutionary history, motivated the focus on mobile, egalitarian groups. Yet there are major empirical limitations with treating mobile foragers such as the Ju’/hoansi as the primary models of Late Pleistocene societies.

Marginal habitats

The most common criticism of using recent mobile foragers for modeling pre-Holocene societies is that many modern foragers have been pushed to ‘marginal’ or poor-quality habitats by agriculturalists^{47,48}. Because environments appear to be major determinants of forager social organization⁷, the nomadic-egalitarian model can be criticized as reflecting lifeways in a narrow range of harsh environments. Given that Late Pleistocene humans likely lived in both poor- and high-quality habitats, researchers argue,

recent forager societies are not representative of the total social diversity that likely characterized the Late Pleistocene.

Two studies have now tested this hypothesis with the Standard Cross-Cultural Sample using net primary productivity as a proxy for habitat quality^{50,51}. Contrary to a widespread expectation, both studies reported no differences in habitat quality between recent hunter-gatherers and agricultural populations. Still, Cunningham et al.⁵¹ point out two critical complications:

First, the Standard Cross-Cultural Sample only includes non-industrial societies. It thus underrepresents highly productive aquatic environments such as the Amazon, Ganges, Mississippi, Nile, and Yangtze River valleys and deltas, which have long hosted industrial agricultural societies and were likely appealing to foragers in the past. The published comparisons are thus not between recent foragers and agriculturalists but between recent foragers and the subset of agriculturalists that do not live in industrial societies. Were industrial societies to be included, the analysis would likely provide support to the hypothesis that modern hunter-gatherers live in less productive habitats than agriculturalists.

Second, net primary productivity is a limited, and possibly misleading, proxy for habitat quality. Many of the foragers reported as inhabiting the most productive environments lived in equatorial rainforests, such as the Amazon (Sirionó) and the Congo (Mbuti). While these environments are productive, much of the productivity is stored in non-edible forms, such as woody tissue⁵². Resources that are edible, meanwhile, are often poisonous or involve high foraging costs, either because they are dispersed, expensive to process, or too high in the canopy to easily access⁵³. Some anthropologists have even argued that, without the help of cultivated foods, a foraging lifestyle would be impossible in tropical rainforests^{52,54}.

Future research will better clarify how the habitats of recent foragers compare with those of agriculturalists. What is clear, however, is that recent hunter-gatherers were excluded from highly productive aquatic environments, such as the Nile and South Africa's Cape Floral Region, and that popular model populations live in particularly harsh environments.

Other interactions with states and agricultural societies

Agriculturalists have shaped forager social organization in ways beyond just limiting their choice of habitats, further challenging the assumption that modern mobile, egalitarian foragers are models for the past^{55,56}. These interactions have taken many forms, including state incorporation, long-term trade, and slavery. For instance, Marlowe⁵⁷ noted that Hadza access to iron might back at least 500 years, that their population experienced pre-20th century declines due to the Masai expansion, and that "they were definitely affected by the ivory trade as neighboring groups came to Hadzaland to kill elephants." Some interactions between foragers and agriculturalists, as in the Philippines and Central African rainforests, go back thousands of years^{58,59}.

The Ju/'hoansi (!Kung)—the people most often used as stand-ins for the Paleolithic^{31,33}—interacted extensively with agriculturalists. Although researchers debate the magnitude and antiquity of the relationships, several points seem less disputed^{60,61}: The Ju/'hoansi began trading with Bantu agriculturalists by at least 500 to 1,500 years ago⁶⁰. In the 1920s, Bantu agropastoralists entered the Dobe area so that, by the time the Kalahari Research Project was established there in 1962, the Ju/'hoansi were already ensconced in a "larger regional pastoral, tributary, and mercantile economy"⁶⁰. In 1964, the Dobe Ju/'hoansi numbered 466 individuals across 9 camps⁶². That same area held 340 Bantu pastoralists and thousands of livestock. In 8 of the 9 camps, Bantu pastoralists and Ju/'hoansi lived together. At any given time, about 20 percent of Ju/'hoansi young men were working with cattle⁶³. Lee recorded little cultivation during his first fieldtrip (1963-1964), although this seems the result of a drought. On his return (1967-1969), he recorded 51% of Ju/'hoansi men planting fields¹.

Recent and contemporary foragers are intimately connected with agricultural societies. These relationships impact important features of forager social organization, such as authority, mobility, and corporate group structure, further demonstrating the limitations of relying on mobile and egalitarian foragers as models of pre-Holocene lifeways.

Leadership and authority

The nomadic-egalitarian model implies that decision-making in ancestral societies was through consensus, with a limited role of leadership and authority⁶⁴. However, this ethnographic pattern may

reflect social changes following interactions with agricultural societies which undermine institutions of authority. For example, as foragers become incorporated into larger political entities, outside administrators may monopolize leadership. Or as crucial services, like coordinating warfare or resolving disputes, decline in importance, the need for and approval of leaders may also diminish^{65,66}.

The !Kung experienced one such decline in leadership following the Bantu incursion in the 1920s⁶⁷. Just what leadership and authority looked like before that time remains unclear, but reports by Fourie⁶⁸ and Marshall⁶⁹ both suggest that some positions were hereditary and restricted to men, with the particular norms of heredity varying by area. Although Marshall^{69,70} was careful to specify that, in the Nyae Nyae area in the 1950s, leaders lacked coercive authority and were more akin to mouthpieces of group consent, Fourie⁶⁸ wrote that the leader “in fact does exercise considerable influence in the life of the community”. Both wrote that leaders were said to be the true owners of the waterhole, Marshall⁶⁹ adding that visitors should seek the leader’s permission before taking water.

Mobility

According to the nomadic-egalitarian model, our foraging ancestors had a high degree of mobility, reducing their ability to accrue material wealth and contributing to an egalitarian, decentralized social structure⁴⁷. Yet many contemporary forager mobility and settlement patterns have been shaped through interactions with large, agricultural societies. Following colonial incorporation and a decreased threat of endemic warfare, large New Guinean fisher-forager communities splintered into smaller groups⁷¹. Meanwhile, some peoples lived in small, mobile groups to specialize in the collection and trading of forest products. The Penan of Borneo were long considered “an inordinately primitive hunting and gathering people”⁷², yet their mobile, foraging lifestyle seemed an adaptation for collecting products considered valuable to Chinese traders, such as rattan, beeswax, and edible birds’ nests⁷².

Groups might also become mobile to escape political domination. This has been observed among many pastoralist groups, including the Hima of Ankole⁷³, the Yakut Turkmen⁷⁴, and some pastoral Fulani⁷⁵, but it likely applies to foragers as well⁷⁶. In his analyses of upland Southeast Asia and the earliest states in the Levant, Scott^{77,78} argued that many traits normally considered prototypical of foragers—including not only their mobility and dispersed communities but also non-hereditary social ranking—represent cultural adaptations for escaping state control.

Corporate groups

Several mobile hunter-gatherers, especially popular Paleolithic models such as the !Kung and Hadza, lack systems of corporate groups, such as clans, lineages, and moieties. As a result, some scholars treat corporate groups as complex innovations that developed recently in sociopolitical evolution³³. However, the absence of corporate group structure may too reflect interactions with large-scale, agricultural societies. Powerful states might suppress corporate membership to make a populace easier or more productive to govern, such as when the US government unified the clans of the Ifugao people (horticulturalists) after taking control of the Philippines⁷⁹. Or corporate groups, which commonly function to protect life and property⁸⁰, may become redundant. By providing the same services, agricultural states may reduce the need for corporate group membership, leading the groups to dissolve with disuse. Finally, the demographic and cultural collapse that results from interacting with agricultural societies, such as through slavery, disease, or rapid acculturation, might also end in the dissolution of corporate social organization⁸¹, as seems to have happened with various Tupi-Guarani groups⁸². Such changes likely occurred among many foragers. The Eastern Pomo, Copper Inuit, and Ju/’hoansi are all coded in the Standard Cross-Cultural Sample as lacking kin-based corporate groups, yet anthropologists studying each of these groups posited that they lost more elaborate social structure following recent interactions with agriculturalist societies^{67,83,84}.

Mischaracterizations of recent foragers

Although many recent and extant foraging groups are assumed to be small-scale, mobile, and egalitarian, such conclusions are often misguided. Instead, recent foragers exhibit considerable variability in group size, mobility, and other features. Insofar as contemporary foragers serve as models for the Pleistocene, their behavior suggests much more variation than the nomadic-egalitarian model permits.

Group size and mobility

Various lines of research suggest that recent mobile hunter-gatherers lived in groups of a few dozen individuals, leading to the conclusion that Paleolithic peoples were similarly small-scale. In a survey of 294 forager societies, Marlowe⁴⁸ found that the median local group size was 29.5 individuals. Hill et al.⁵ analyzed field data on a sample of 32 forager societies, including 58 precontact Ache bands and six Ju/'hoansi bands, and reported a weighted mean band size of 28.2 individuals (see also ref. ⁶). In fact, given that so many comparative studies have converged on an estimated group size of about 25 individuals, Kelly⁷ has referred to it a “magic number”. Critically, these bands appear to be fluid in composition and nested within larger networks^{5,18,42}.

The focus on mean population sizes hides two important sources of variation. First is within-culture variation. Communities size can vary considerably within a given forager culture, sometimes by as much as an order of magnitude. According to Turnbull's survey of the Mbuti, group sizes differed dramatically between two Mbuti sub-groups, referred to as the archers (Efe) and net-hunters (Sua Mbuti)⁸⁵. The archers lived in groups of between 2 and 12 huts, averaging about 6 huts, or 36 individuals, per camp. Net-hunters, meanwhile, lived in groups of between 20 and 40 huts with an average of 25 huts, or 150 individuals, and a maximum of 50 huts, or 250 individuals⁸⁶. Similarly, Lee recorded the size of 9 !Kung camps in 1964⁶². Excluding visitors and Bantu pastoralists staying in those camps, camp sizes ranged from 9 people at !Kangwa Matse to 117 at /Xai /xai.

The focus on mean population sizes also masks temporal variation. Nomadic foragers in Alaska and northern Australia were both observed to seasonally shift between large, sedentary settlements and dispersed mobile groups^{43,87,88}. Meanwhile, many foragers assembled during serendipitous times and with the purpose of hosting festivities and large-scale ceremonies⁶. These assemblies commonly numbered in the hundreds, if not low thousands, of individuals and could go on for months, such as occurred among the Warlpiri of Australia⁸⁹. Even the Ju/'hoansi assembled into larger groups. Not only did several camps share water-holes during years of reduced rainfall⁹⁰, but people also traditionally held the choma, a 6-week-long male initiation which “drew in young men within a radius of 100 km or more” and was gradually phased out at the time Bantu pastoralists moved in⁶⁷. It remains unclear how many people collected for chomas, although Lee¹ speculated that an initiation of 20 or more boys could draw together camps together totaling more than 200 individuals.

Scale of cooperation

The popularity of the nomadic-egalitarian model has led many researchers to conclude that human cooperation was limited to small groups throughout our evolutionary history (e.g., ref. ⁹¹). But several lines of research suggest this wasn't necessarily the case. Boyd and Richerson⁴⁶ recently reviewed numerous examples of large-scale cooperation among mobile foragers in North America, Australia, Europe, and the Arctic, drawn from archaeological data, historical accounts, and ethnographic descriptions. The examples cover many domains, including communal hunting, construction of shared facilities, and warfare, with cooperative projects often involving hundreds of people, sometimes from neighboring groups. Examples of large-scale cooperation among apparently small-scale foragers appear earlier in the Holocene and even in Pleistocene. Especially striking is evidence of large-scale communal foraging in Middle and Late Pleistocene Europe, including indications of at least two instances of mass buffalo killings c. 400 ka—well before the origins of *Homo sapiens*⁹²—and the remains of a large number of reindeer at a Middle Paleolithic (c. 54 ka) in Germany⁹³. Another striking example of large-scale cooperation among prehistoric foragers comes from Poverty Point, where an estimated 2,000 laborers and 1,000 supporters cooperated to build Mound A in less than three months (c. 3260 cal. B.P.)⁹⁴.

Non-egalitarianism

Many apparently mobile, small-scale forager society exhibit coercive authority. Most common is inequality on the basis of age and sex, with a coalition of older men (“elders”) exercising ritual or political authority over other group members (for notable Australian examples, see refs. ^{95,96}). Even when considering individuals of similar age and sex, however, mobile or small-scale foragers exhibit deviations from egalitarianism. Using a sample of 59 societies (including 13 foragers), Garfield et al.⁹⁷ found that coercive leadership was present among foragers, although less frequent than in other types of societies. Among

the Toba of South America's Gran Chaco, for instance, war chiefs had more wives, were richer, had to be obeyed during war, were stylistically distinguished by "a peculiar arrangement of the hair", and, with their children, enjoyed "greater esteem than other members of the society"⁹⁸. Coercive authority has also been documented among peoples living near the Bering Strait⁹⁹ and among the Khanti of west Siberia, where shamans and elders' peoples purportedly "used poor people 'like slaves'"¹⁰⁰. The Warao of northern South America had a "social hierarchy based on political and magico-religious authority"¹⁰¹. Particular individuals were regarded as leaders: They had dominion over the supernatural, imparted orders, and were excluded from hard work, and a leader's son was said to enjoy "easy access to political leadership". As these examples demonstrate, shamans and other magico-religious practitioners are especially likely to leverage their supposed supernatural powers to exercise political authority⁹⁷ (see also refs. ^{102,103}).

Resource management

Researchers have accumulated considerable ethnographic and archaeological evidence suggesting that resource management, such as cultivation and animal management, preceded the Neolithic Revolution. Recent foragers engaged in activities including irrigation, arboriculture, the enhancement of salmon streams, the broadcast sowing of annuals, and the creation of clam gardens¹⁰⁴. Holocene foragers managed wild boar populations in Cyprus and Japan before pig domestication¹⁰⁵, while archaeological evidence suggests that Melanesian hunter-gatherers were managing populations of cuscuses as early as 20,000 years ago¹⁰⁶. Archaeologists reported evidence of intensive plant cultivation at the forager camp Ohalo II in Israel 23,000 years ago—at least 11 millennia before the supposed onset of agriculture in the Near East¹⁰⁷. Finally, through controlled fires, the Martu of Australia's Western Desert generated large-scale improvements in habitat quality^{108,109}. Such fire regimes were likely common among foragers elsewhere, including Middle Stone Age hunter-gatherers¹¹⁰. It is no longer clear why we should assume that cultivation, animal management, and other forms of delayed-return resource management developed at the beginning of the Holocene. In fact, indications of domestic-type evolutionary change in wheat and barley at Ohalo II suggest that Late Pleistocene humans may have even incipiently domesticated species, possibly often, well before the Holocene, only to have such evolutionary changes disappear after social and ecological conditions changed¹⁰⁷.

The importance of considering sedentary and non-egalitarian foragers

Up to this point, we have focused on populations understood to be mobile and relatively egalitarian. But a large subset of non-agricultural populations clearly violates the nomadic, egalitarian model—those referred to variously as sedentary, hierarchical, or complex hunter-gatherers⁷.

Evolutionary scholars tend to ignore sedentary or non-egalitarian hunter-gatherers. When Arnold et al.⁴⁴ examined biological anthropology textbooks published between 2006 and 2014, they found that none mentioned them. Others acknowledge their existence yet reject them as relevant for understanding life in the Late Pleistocene⁹. Boehm^{12,111} deliberately excluded them from his database of 150 recent or extant 'Late-Pleistocene-appropriate' hunter-gatherer societies. Marlowe⁴⁸ wrote that sedentary foragers "may not have been rare" immediately before the Holocene, "but for modeling earlier periods we should exclude them". Lee¹¹ pointed out that sedentary foragers should be discounted when studying the evolution of violence given that small-scale, egalitarian, mobile foragers best represent our evolutionary past.

In contrast, we argue that sedentary hunter-gatherers are relevant for understanding pre-Holocene lifeways, at least as much as small mobile groups.

Recent examples of sedentary foragers include the Chumash¹¹², New Guinean fisher-foragers^{113,114}, and the peoples of the Pacific Northwest¹¹⁵. Such peoples tended to exhibit several common features⁷: They tended to exploit coastal resources. They sustained very high population densities. Although not necessarily completely sedentary, they exhibited less mobility than classically "nomadic" foragers. They had much larger group sizes, with some villages exceeding 1,000 individuals. They permitted and often institutionalized hierarchy by ceremonially bestowing status upon individuals who accumulated and redistributed surplus. Some groups kept slaves.

Sedentary foragers have demonstrated a profound capacity for building large, politically stratified societies with large-scale cooperation. The Calusa of southern Florida lived in a state or large chiefdom

when the Spanish documented them in the mid-1500s. They comprised 50-60 politically consolidated villages along Florida's southwest coast, although their domain extended from Tampa to Cape Canaveral and down to the Florida Keys, an area larger than modern-day Switzerland¹¹⁶. They collected tribute, centralized power in a hereditary sovereign who ruled for life, supported full-time religious and military specialists, and built large infrastructure projects^{116,117}. Although they appear to have planted some squash and papaya, in addition to managing chile pepper, these constituted trivial contributions to subsistence¹¹⁸; rather, their wealth and surplus derived from rich aquatic resources¹¹⁹.

Scholars—even those who urge that greater attention be paid to sedentary foragers¹²⁰—have presented at least three reasons why such societies were absent before the Holocene (or the millennia immediately preceding it):

1. They seem anomalous.
2. They seem to rely on aquatic resources—a capacity that, on the basis of archaeological evidence, was believed to develop recently in human history.
3. There is little, if any, archaeological evidence for their existence during the Pleistocene.

These assumptions either have been shown to be wrong or are no longer sufficiently compelling to justify ignoring sedentary foragers in reconstructions of Late Pleistocene human societies.

Sedentary foragers are not anomalous

A longstanding assumption is that sedentary foragers are rare or exceptional, contributing to the conviction that many features of social complexity emerged with agriculture (recently reviewed in ref. ⁴⁴). Yet this view is no longer viable. Over the past four decades, archival and archaeological research has revealed evidence of sedentary and non-egalitarian hunter-gatherers from all over the world, throughout the Holocene, and even in Pleistocene Europe; see Table 1 and Figure 1 for 34 examples of world regions. As these examples illustrate, many environments that once supported sedentary foragers—such as Japan, the Levant, the Nile River Valley, southern Scandinavia, and the South China Coast—are now inhabited by agriculturalists. Whether this was because these peoples themselves domesticated local species¹²¹, they adopted domesticates from neighbors¹²², or they were demographically displaced, this pattern further suggests that recent hunter-gatherers are underrepresented among particular environments because of agricultural occupation.

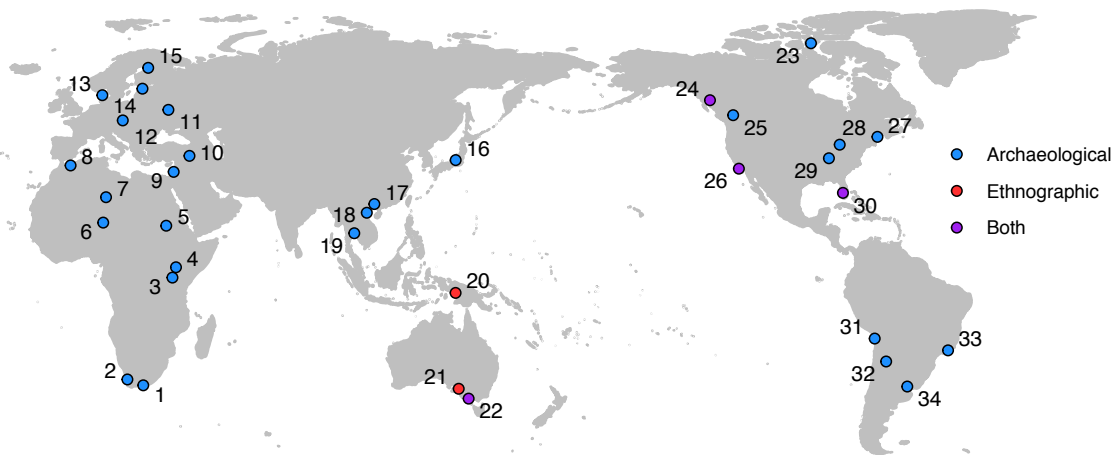


Figure 1. Locations of sedentary or semi-sedentary foragers listed in Table 1. All cultures or regions varied considerably in mobility patterns and social organization over time and space; this figure does not imply that every forager group displayed always exhibited low mobility or inequality. The color of each point signifies the source of evidence (archaeological, ethnographic, or both). Numbers refer to the IDs in Table 1.

Table 1. Examples of sedentary or semi-sedentary foragers

ID	Region	Culture/Sub-region	Time	Subsistence	Environment	Reduced mobility	Large groups	Inequality ¹	Resource mgmt.
1	Africa	Southern South Africa Coast (Plettenberg Bay & Cape St. Francis)	4,500–2,000 BP	Marine resources, including high-trophic-level animals (e.g., seals)	Coastal	X	.	X	.
2	Africa	Western South Africa Coast (Eland's Bay & Lambert's Bay)	3,000–2,000 BP	Marine resources, especially shellfish	Coastal	X	.	.	.
3	Africa	Kansyore (Lake Victoria)	8,000–4,500 cal. BP	Terrestrial and aquatic resources, especially fish	Lacustrine and riverine	X	.	.	.
4	Africa	Lothagam (Lake Turkana)	10,000–7,000 BP	Primarily aquatic resources (e.g., Nile perch); terrestrial hunting	Lacustrine	X	.	.	.
5	Africa	Early Khartoum	10,000–8,000 cal. BP	Primarily aquatic (riverine) resources	Riparian with floodplains, grasslands, woodlands	X	.	.	.
6	Africa	Gobero Lake	9,500–8,200 cal. BP	Terrestrial and lacustrine resources	Lacustrine	X	.	.	.
7	Africa	Late Acacus	8,800–8,000 BP	Wild cereals, cattails, barbary sheep	Arid mountains	X	.	.	X
8	Africa	Taforalt	13,000–11,000 BP	Diverse terrestrial fauna, esp. land snails, Barbary sheep, and nuts	Arid semi-desert	X	.	.	.
9	Middle East	Early Natufian	12,800–11,000 BP	Cereals, legumes, gazelles, cattle, deer	Coastal plain	X	X	X	X
10	Middle East	Körtik Tepe	12,300–11,200 cal. BP	Riverine and terrestrial resources (e.g., fish, mammals, plants)	Riverine and open woodland	X	.	.	X
11	Eurasia	Russian Plain	18,000–12,000 BP	Terrestrial game, especially large gregarious herbivores (mammoths, bison, horse)	Periglacial steppe; valleys in which megafauna seasonally migrated	X	.	X	.
12	Eurasia	Pavlovian	29,000–22,500 BP	Mammoths and other terrestrial resources	Shifting landscape (steppe, shrub, forested)	X	X	.	.
13	Eurasia	Ertebølle	6,400–5,900 cal. BP	Marine resources, especially fish	Coastal	X	X	.	.
14	Eurasia	Bothnian Bay Eastern Coast	6,500–4,000 cal. BP	Anadromous fish, sea mammals (seals)	Coastal	X	X	X	.
15	Eurasia	Narva	7,200–5,900 cal. BP	Diverse aquatic and terrestrial resources, esp. fish	Coastal	X	.	.	.
16	Eurasia	Jomon (Early period to Final period)	7,000–2,400 cal. BP	Diverse resources, incl. intensive exploitation of nuts, tubers, and marine resources	Coastal	X	X	X	X

ID	Region	Culture/Sub-region	Time	Subsistence	Environment	Reduced mobility	Large groups	Inequality ¹	Resource mgmt.
17	Eurasia	Dingsishan	9,000–5,000 BP	Diverse terrestrial and aquatic resources (e.g., fish, shellfish, deer)	Riparian	X	.	.	.
18	Eurasia	Da But	6,000–5,500 BP	Fish; mollusks and mammals in swamp and lake environments	Coastal	X	.	.	.
19	Eurasia	Khok Phanom Di	4,000–3,500 BP	Estuarine resources (esp. fish, crab, shellfish, turtles)	Coastal	X	.	X	.
20	Oceania	New Guinean fisher-foragers (e.g., Asmat)	1960 AD	Sago, aquatic resources	Coastal	X	X	X	.
21	Oceania	Murray River, Australia (e.g., Yaraldi)	1860 AD	Broad-spectrum (freshwater, marine, and terrestrial resources)	Riparian and lacustrine	X	X	X	X
22	Oceania	Southwest Victoria, Australia	2,000 BP–1850 AD	Aquatic wetland resources (esp. eel) & terrestrial plants (e.g., tubers, ferns)	Coastal plain	X	X	X	X
23	North America	Thule	1100–1500 AD	Bowhead whale, as well as caribou, fish, seals, and bears	Coastal (warm period)	X	X	X	.
24	North America	Pacific Northwest Indians (e.g., Tlingit, Haida)	3,500 BP–1900 AD	Terrestrial and aquatic resources, especially anadromous fish	Coastal	X	X	X	X
25	North America	Interior Plateau, British Columbia	2,000–1,000 BP	Terrestrial and aquatic resources, especially anadromous fish	Canyon/river drainage	X	X	X	.
26	North America	Chumash & ancestors	6,500 BP–1770 AD	Marine resources, trade with mainland	Coastal islands	X	X	X	X
27	North America	St. George River Drainage, Maine	5,000 BP–1650 AD	Shellfish, fish (e.g., cod, swordfish), deer, birds	Coastal	X	.	.	.
28	North America	Libben	800–1100 AD	Riparian resources (incl. fish, small mammals, migratory birds) ²	Riparian	X	.	.	.
29	North America	Indian Knoll	6,100–4,500 BP	Aquatic and terrestrial resources (e.g., shellfish, deer)	Riparian	X	.	.	.
30	North America	Calusa	800–1550 AD	Marine resources and C ₃ plants (e.g., tree fruits, tubers) ¹	Coastal	X	X	X	X
31	South America	Chinchorro	7,000–4,000 BP	Marine resources (e.g., fish, sea lions, shellfish); some plants and terrestrial meat	Coastal	X	X	X	.
32	South America	Puna (high altitude Andean grasslands)	6,200–3,500 BP	Camelids	Arid high plateau	X	.	X	X
33	South America	Southeastern coastal Brazil	4,000–2,000 BP	Marine and some terrestrial resources (e.g., fish, shellfish, tapir, whale, dolphin)	Coastal	X	X	X	.
34	South America	Plata-Purana Wetlands	1,700 BP–1500 AD	Wetlands resources (e.g., fish, large rodents, deer, palm)	Coastal wetlands	X	.	.	.

All cultures or regions varied considerably in social organization. No example listed here exclusively exhibited the noted traits. See Table S1 for details and references. ¹Inequality refers to substantial differences in material wealth, institutionalized status hierarchies, and/or coercive political authority.

Humans have exploited aquatic resources deep into the Pleistocene

For most of the twentieth century, a common assumption among anthropologists was that humans did not exploit aquatic resources until recently in human history, such as the outset of the Holocene or even later (for a review, see ref. ¹²³). This was based partly on the apparent rarity of evidence of aquatic resource exploitation in the archaeological record¹²⁴. This assumption no longer holds. Evidence for aquatic resource exploitation goes as far back as 1.95 Ma in northern Kenya¹²⁵. Archaeologists have discovered shell middens, indicating a commitment to dense and predictable coastal resources, by at least c. 130 ka along the southern African coast¹²⁶ (Figure 2). There is also evidence that Late Pleistocene humans were systematically exploiting aquatic resources along the north African coast and rivers of Central Africa¹²⁷ (Figure 2B), and they likely inhabited productive lake margins, such as shoreline sites along Lake Victoria rich in shellfish and aquatic and semi-aquatic plants¹²⁸. In fact, some scholars now see aquatic (and particularly coastal) adaptation as central for the origin, evolution, and dispersal of modern humans^{123,127,129}.

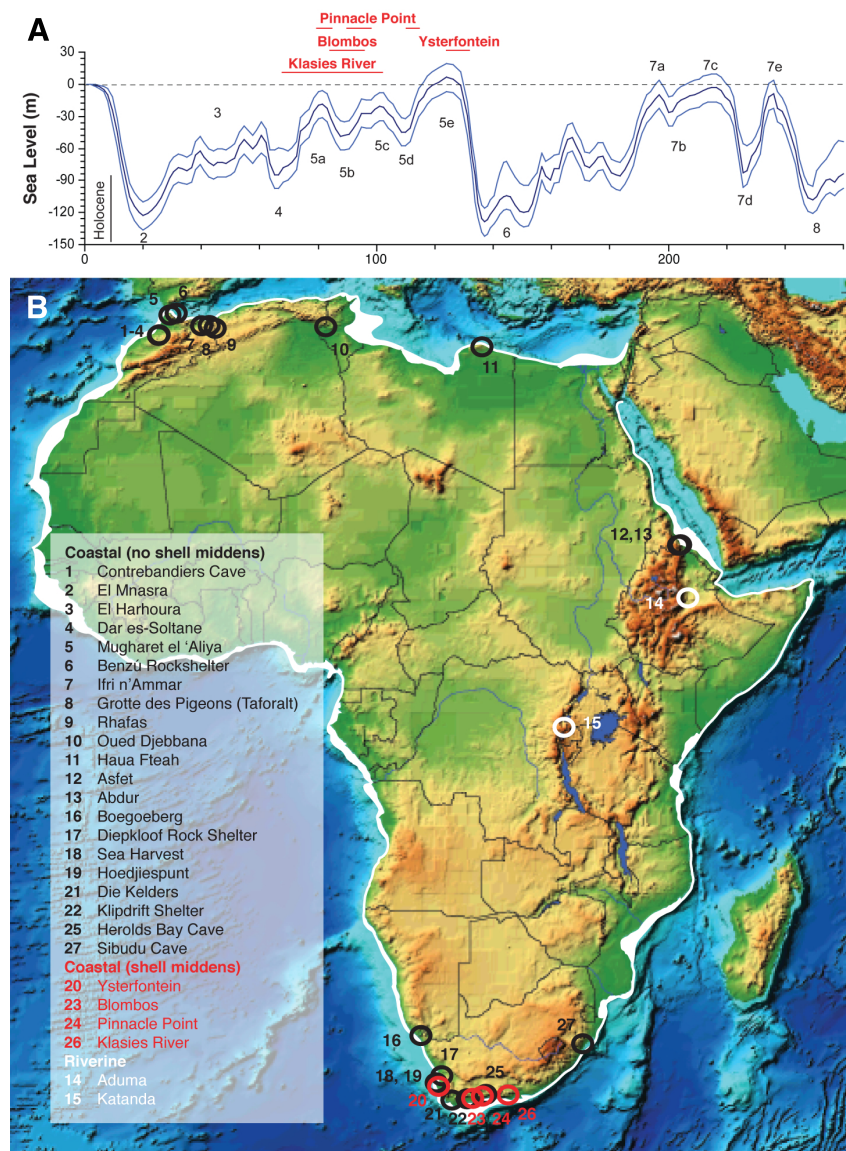


Figure 2. (A) Estimates of sea level fluctuations since 260 ka, bracketed by uncertainty¹³⁰. Middle Stone Age sites with shell middens, indicating an adaptation and commitment to dense and predictable coastal

resources, are shown with date ranges in red. (B) The African continent and shelf area (in white) exposed during glacial maxima. The circles indicate Middle Stone Age coastal sites with and without strong evidence of middens (in red and black, respectively), as well as sites in which humans systematically exploited riverine resources (in white). Sources: Refs. ^{126,127,131–134}

Even accepting the antiquity of aquatic resource exploitation, it is important to realize that sedentary and non-egalitarian hunter-gatherers do not require aquatic resources. Rather, they seem to emerge in environments with dense, rich, and predictable resources^{7,135} (although see ref. ¹³⁶). As Table 1 demonstrates, semi-sedentism and its sociocultural correlates have been documented among foragers subsisting on cereals and sheep, cereals and gazelles, camelids (guanaco and vicuña), mammoths and other large terrestrial herbivores, and bowhead whales.

The evidence for sedentary hunter-gatherers during the Pleistocene

Several archaeological sites provide evidence of sedentary and non-egalitarian hunter-gatherers during the Pleistocene. The most striking are in Upper and Epipaleolithic Europe and include elaborate burials in Sungir (Russia), Arene Candide (Italy), Dolní Věstonice (Czech Republic), Brno 2 (Czech Republic), and Saint-Germaine-la-Rivière (France)¹³⁷. These burials, many of which are of juveniles, were accompanied by lavish grave goods, such as perforated deer canines and objects made of mammoth ivory. Such goods were often rare or exotic and appeared to require time and mastery to produce—indications of wealth and inequality^{138,139}. Some scholars have gone so far as to argue that the elaborate burial of children in particular suggests inherited status or wealth (e.g., ref. ¹⁴⁰). The discovery of circum-Mediterranean sites in which many individuals were buried—known variously as “cemeteries” or “necropolises”—provides further evidence of larger groups, intensive exploitation, and greater sedentism^{141,142}. Again, however, all of these appear at the very end of the Pleistocene.

The archaeological record in Late Pleistocene Africa lacks the conclusive finds of Upper Paleolithic Europe, yet there is still evidence for low-mobility population exploiting the kinds of resources that support large groups, hierarchy, and political complexity. Findings from Late Pleistocene Equatorial Africa, such as 60-70 ka deposits near Lake Edward in the Democratic Republic of the Congo, indicate that populations exploiting dense, predictable aquatic resources lived in communities with low residential mobility (e.g., multi-seasonal occupation with patchily dense artifact accumulations) (reviewed in ref. ¹²⁸). Archaeologists have uncovered evidence of aquatic resource exploitation in many African Middle Stone Age sites, with indications of systematic marine foraging in South Africa by 160 ka^{127,134} (Figure 2). Marean¹⁴³ interprets Middle Stone Age settlements at PP13B (south coast of South Africa) to be residential sites of large social groups that exploited marine resources throughout the year and which exhibited stable and relatively long-term occupations. As Table 1 illustrates, there is strong evidence of semi-sedentary fisher-foragers soon after the Pleistocene-Holocene transition in Africa, such as in the Nile (10 ka), Gobero Lake (9.5 ka), and Lake Turkana (10 ka). There is little reason to presume that such groups would have been rare or non-existent before.

Although large cemeteries, settlements of pit-houses, and elaborate burials with marked social differentiation are absent in the Middle Stone Age record, there are at least three reasons the record is biased against such indications of prehistoric social diversity. First, compared to Europe and North America, far fewer archaeologists have worked in Africa, limiting the opportunity to discover such sites. Second, Africa has fewer caves than Europe and, thus, fewer high-quality preservational environments. Third, and critically, promising sites have likely been submerged or damaged with fluctuating sea levels. Sea-levels today are 120 m higher than at the last glacial maximum, and there were few times in the last 200,000 years when the sea was at or above the present level (Figure 2A). Recognizing these biases, it is of little surprise that some of the best evidence coastal adaptation in Middle Stone Age Africa comes from elevated caves that were both close to ancient coastlines and protected from surging sea levels¹⁴⁴. We expect that, with the development of submerged landscape archaeology¹⁴⁵, the African archaeological record will yield new discoveries that alter our understanding of social diversity in the Pleistocene.

A new model of Late Pleistocene lifeways

Figure 3 contrasts the nomadic-egalitarian model with what we call the *diverse histories model*. Both models agree that forager social diversity has declined recently with the spread of agriculture. The models differ, however, in what they posit about social diversity before the Holocene. According to the nomadic-egalitarian model, humans lived predominantly in small-scale, mobile, egalitarian bands before the Holocene. There was minimal diversity across forager societies. In fact, the social diversity observed among recent sedentary and mobile foragers exceeds that of Late Pleistocene hunter-gatherers.

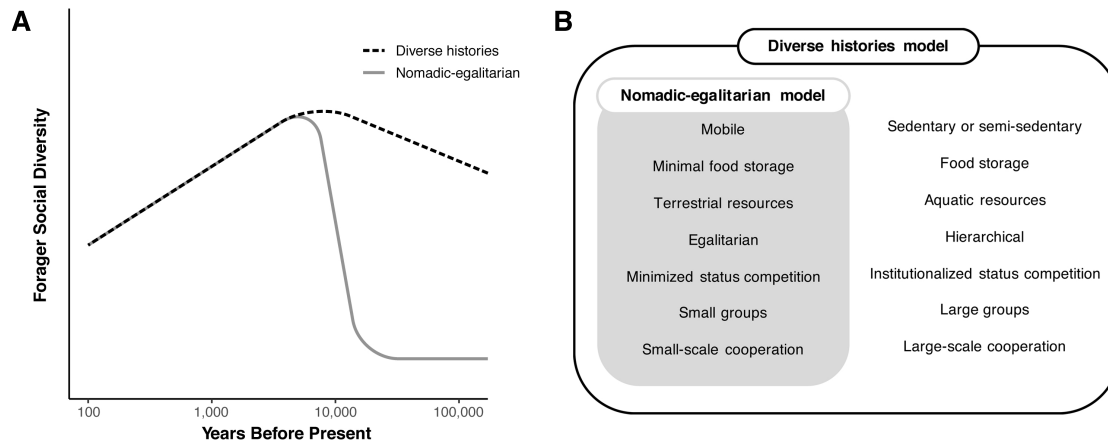


Figure 3. (A) The historical trajectories of social diversity posited by the nomadic-egalitarian and diverse histories models. According to both models, the diversity of forager societies declined with the recent spread of agriculture. But whereas the nomadic-egalitarian model posits that pre-Holocene societies exhibited little variation in features of social organization, the diverse histories model posits that, throughout the Pleistocene, social diversity approached or even exceeded recent forager social diversity. (B) Features of pre-Holocene societies, according to the nomadic-egalitarian and diverse histories models. The diverse histories model contains the nomadic-egalitarian model: It posits that some Late Pleistocene societies were small-scale, mobile, and relatively egalitarian, but sees these as a subset of much broader social diversity.

The diverse histories model, in contrast, posits a much higher degree of social diversity throughout the Late Pleistocene. Because behaviorally modern humans likely inhabited many habitats over the last hundred thousand or more years—including not only dry areas like the Kalahari but also consistently productive habitats, such as lake margins, the Nile Valley, or South Africa’s Cape Floral Region—we expect social structures to reflect those diverse ecologies. Just as contemporary foragers living in habitats with dense, predictable resources show a capacity to develop large groups, sedentism, hierarchy, institutionalized authority, and large-scale political consolidation, we expect that pre-Holocene foragers could do the same.

The diverse histories model acknowledges that some humans may have lived in societies similar to contemporary mobile, egalitarian foragers, but posits that these represented one of many common social outcomes. Some foragers would have lived at densities comparable to the Ju/’hoansi (10-16 individuals/100 km²), but others would have lived at densities approaching those of recent coastal foragers like the Chumash (900 individuals/100 km²) or even certain New Guinean groups (2,500 individuals/100 km²)⁷. Some would have lived in small mobile bands while others would have dwelled in chiefdoms like those in the Pacific Northwest or even, potentially, small tributary states, as with the Calusa of Florida.

These diverse social environments would have represented important habitats for human psychological adaptation. Given the comparably large groups and high densities of foragers living in rich environments, they represent a large proportion of the total human population, even if they take up very little space in a landscape. Imagine, for instance, an expanse with 500 equally sized patches. If 499 were filled with people living at Ju/’hoansi densities and only 1 was inhabited by foragers living at highest

densities of coastal New Guinean foragers, still 1 of every 4 individuals would live in the single dense patch.

Implications for the evolution of human behavior

The nomadic-egalitarian model confronts puzzling inconsistencies. On the one hand, our ancestors are said to have spent an appreciable duration of prehistory—anywhere from the last 40,000 to several million years—living in small, egalitarian, mobile bands^{12,146}. Status competition was stifled, and domineering behavior invited censure, ostracism, or execution^{13,32}. This social environment was purportedly critical in shaping the biological foundations of our psychology^{11,12,48,147}. Many scholars argue that understanding the evolution of the human mind requires considering the egalitarian origins of our species^{12,16,147,148}, while others, especially evolutionary psychologists, posit that the cooperation humans exhibit in contemporary large-scale societies reflects adaptations for interacting in small groups of non-strangers^{91,149,150}.

Yet, as we will show, many reliably developing human behaviors are difficult to explain if the primary or exclusive social environment shaping human psychology was the small-scale, mobile, egalitarian band. Rather, such behaviors become much easier to understand when considered as the products of an evolutionary history involving diverse social environments.

Dominance and other status-seeking behaviors

According to the nomadic-egalitarian model, humans lived in small, egalitarian social groups with little dominance or opportunities for dominance. Moreover, attempts to domineer were presumably met with sanctions such as ostracism or even execution, selecting against such predispositions^{13,32}. Yet, humans everywhere exhibit predispositions to seek and recognize dominance^{151–153}. Even in the egalitarian societies of contemporary foragers, individuals are motivated to domineer each other, creating the demand for the strict sanctions and norms against bullying^{32,154}. The diverse histories model helps explain the persistence of dominance seeking. Humans would have inhabited many environments, including those in which it was possible to accrue resources and wield them for coercive ends. As long as such environments were common enough during our evolutionary history, selection would have favored flexible psychological mechanisms underlying the pursuit and recognition of dominance. A similar argument applies to other status-seeking behaviors, such as the pursuit of prestige (although evolutionary anthropologists have begun to acknowledge the role of prestige competition during our evolutionary past¹⁴⁶).

Group identity and minimal group affiliation

From early in development, humans exhibit ingroup biases that are evoked through “mere membership” in a group^{155,156}. Even meaningless or random group assignments—such as on the basis of painting preferences, a coin toss, or shirt color—are sufficient to elicit preferences towards in-group strangers^{155,157}. This is puzzling by the standards of the nomadic-egalitarian model. If, until the last 10,000 years, group sizes were in the dozens and individuals cooperated on a small-scale and rarely with strangers, then it seems unnecessary, even costly, to have psychological predispositions to cooperate with strangers on the basis of arbitrary markers. Under the diverse histories model, however, such psychological predispositions become more understandable. If humans lived in villages of more than a thousand individuals—not uncommon among recent fisher-foragers^{7,158}—and they cooperated at times with hundreds of individuals⁴⁶, then such prosocial predispositions towards in-group strangers make more evolutionary sense, especially if ancestral groups developed cultural indicators of group membership¹⁵⁹.

Intergroup relationships

Using the nomadic-egalitarian model, researchers have advanced opposing arguments about the role of war in human evolution. On the basis of ethnographic descriptions of recent mobile foragers, some conclude that war was a regular feature of human evolution and a major selective force in shaping human psychology²⁸. Others conclude that war was absent during human evolution, appearing only with sedentary and non-egalitarian societies around 10,000 years ago⁹. Both approaches have difficulty accounting for the flexible range of behaviors seen in contemporary societies: While war continues to be

common, many peoples never participate in it¹⁶⁰, and groups which formerly engaged in regular warfare quickly abandoned it when social conditions change⁷¹. If, however, humans evolved in a variety of social environments—including sedentary settlements, hierarchical societies, and mobile, egalitarian groups—then the frequency and importance of war would have likely varied throughout our evolutionary history. Rather than humans exhibiting a psychology specialized for either peace or war, our diverse evolutionary histories may have endowed us with a flexible behavioral repertoire for interacting with outgroups. Our capacity both to wage war with ease and to abandon it quickly is consistent with humans evolving in diverse social settings involving a range of out-group interactions.

Gene-culture coevolution and human social psychology

An implication of the diverse histories model is a potentially expanded role of gene-culture coevolution in shaping human social psychology. Insofar as (1) cultural evolution allowed humans to build a diversity of societies, and (2) humans either reliably assembled similar societies in similar ecologies or remained in particular societies on temporal scales relevant for genetic evolution, then we would expect culturally evolved features of societies to have been important selection pressures for shaping human psychology. If, for instance, humans regularly developed mechanisms for incentivizing cooperation among large groups of strangers, then our ability to cooperate in modern, large-scale societies may result from adaptations designed for similar institutional settings. If, as we just argued, humans could reliably develop societies on the scale of Californian, Floridian, or New Guinean coastal foragers, then such environments may have selected for predispositions to interact with strangers on the basis of shared group membership rather than individual familiarity. And similarly, if humans lived in societies with substantial social differentiation, such as with economic specialization or defined social classes, then humans may have evolved psychological adaptations for signaling and interpreting those dimensions of class-based identity¹⁶¹. The ease with which we live in contemporary societies dramatically different from small, mobile bands may reflect psychological adaptations designed for similar social ecologies.

Conclusion

We have shown that the empirical foundations of the nomadic-egalitarian model are weak and have a proposed an alternative, the diverse histories model, to replace it. Given (a) the likely diversity of Late Pleistocene environments, (b) the capacity for recent foragers to flexibly build different societies contingent on their ecologies, and (c) the variation in social organization exhibited even among apparently small-scale, mobile foragers, we expect Late Pleistocene social organization to have been much more variable than the nomadic-egalitarian model permits. The diverse histories model helps explain many human behaviors that are puzzling under the prevailing model, including dominance-seeking, minimal group affiliation, and flexible intergroup interactions. Whether or not our alternative model is correct, scholarly reconstructions of Late Pleistocene lifeways require reconsideration.

At two least areas of research will prove valuable for evaluating the diverse histories model. The first is underwater archaeology. Rising sea levels at the end of the Pleistocene submerged the sites most likely to host societies that violate the nomadic-egalitarian model. As techniques of submerged landscape archaeology improve, these previously coastal regions will become critical in determining whether pre-Holocene societies were non-egalitarian, sedentary, large-scale, and capable of cultivation. Recent discoveries gesture at just how paradigm-shifting these underwater findings may prove to be. Ohalo II in Israel, for instance, was submerged until 1989, when a drop in water levels in the Sea of Galilee exposed it for 10 years. The site has since provided evidence of a 23,000-year-old fisher-forager camp, along with the oldest evidence of plant cultivation and the discovery of hut structures suggesting repeated and prolonged occupations^{107,162}.

The second critical area of study is ancient genetics. As the quality and historical depth of genetic samples increases, our ability to make inferences about ancient demographics will improve. Existing research suggests that hunter-gatherer populations today are smaller and more isolated than their Pleistocene predecessors¹⁶³. Future research with Pleistocene samples will provide more precise characterizations of prehistoric social organization, allowing us to better evaluate the extent to which the diverse histories model describes Late Pleistocene human social organization.

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