

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. This “nomadic-egalitarian model” suffuses the social sciences. It 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 articulate an alternative, the diverse Pleistocene model, to replace it. We review 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 Holocene began some 11,700 years ago? The prevailing understanding can be traced to the 1966 *Man the Hunter* symposium, the first major attempt to synthesize ethnographic research on hunter-gatherers (also known as “foragers” in this article). The findings of the symposium, which helped kick off the field of hunter-gatherer studies, were published in a now-classic monograph (Lee and DeVore 1968a). In the monograph’s opening chapter, organizers Richard Lee and Irven DeVore (1968b:11) synthesized the symposium’s conclusions and wrote, “We make two assumptions about hunters and gatherers: [1] they live in small groups and [2] they move around a lot.” From these features, they derived five characteristics of what they called the *nomadic style*, later referred to as the *generalized forager model* (Isaac 1990; Kelly 2013): Forager societies were said to be (a) egalitarian; (b) small; (c) non-territorial; (d) non-storing; and (e) sufficiently fluid and unattached to any locality that violence was low.

The generalized forager model became a starting point for reconstructing human evolutionary history. Through detailed field studies on mobile foragers and systematic cross-cultural comparisons (Marlowe 2010; Lee 1979b; Hill and Hurtado 1996; Hill et al. 2011; Kelly 2013), evolutionary scientists developed a more sophisticated 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, see work by Fry et al. (2020), Lee (2018), and Boehm (2012)):

For tens of thousands of years before the Holocene, and possibly much earlier,

1. People lived in small bands of up to several dozen individuals. Bands were embedded with ethnolinguistic groups, which comprised hundreds or even a few thousand individuals.
2. Bands were mobile and fluid, and people stored very little, relying 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 coordinated violence.

4. Cooperation was small-scale, occurring mostly among fellow band members. Although bands may have been linked in larger cooperative networks, people did not engage in large-scale collective action.
5. Agriculture, comprising cultivation and the management of animal populations, was absent.

The nomadic-egalitarian model dominates evolutionary analyses, both as researchers consider how behaviors were adaptive in mobile, egalitarian, small-scale settings and as they study those behaviors in contemporary populations to make inferences about the past. It is closely linked to the concept of the “environment of evolutionary adaptedness” (EEA). In their primer to evolutionary psychology, for instance, Tooby and Cosmides (1997) connected the nomadic-egalitarian model to human psychological adaptations (see also Cosmides & Tooby, 2013):

The environment that humans—and therefore, human *minds*—evolved in was very different from our modern environment. Our ancestors spent well over 99% of our species’ evolutionary history living in hunter-gatherer societies. That means that our forebears lived in small, nomadic bands of a few dozen individuals who got all of their food each day by gathering plants or by hunting animals.

Indeed, the nomadic-egalitarian model has become an important lens through which scholars, including us, have studied behaviors as diverse as aggression (Wrangham, 2019), childcare (Hrdy, 2009), cooperation (Apicella et al., 2012), cumulative culture (Hill et al., 2014; Migliano et al., 2020), leadership (von Rueden, 2020), the sexual division of labor (Hawkes & Bird, 2002), social emotion (Hrdy, 2009), storytelling (Smith et al., 2017; Wiessner, 2014), and warfare (Fry, 2013; Wrangham & Glowacki, 2012).

The nomadic-egalitarian model’s popularity transcends the evolutionary human sciences. It suffuses the social sciences, forming “the foundation of all contemporary debate on inequality” (Graeber & Wengrow, 2018). It features in discussions of property (Bowles & Choi, 2013; Hartley, 2019), social structure (Christakis, 2019), and even narrative (Dubourg & Baumard, 2021), and regularly appears in prominent books that take a broad perspective on history, including works on the state (Fukuyama, 2011), inequality (Flannery & Marcus, 2012; Scheidel, 2017), and the differences between past and modern societies (Diamond, 2012).

The continued popularity of the nomadic-egalitarian model conflicts with historic developments in archaeology and hunter-gatherer studies. Since the *Man the Hunter* symposium—and especially since the 1980s—specialists have appreciated the diversity of forager social organizations and the limitations of focusing exclusively on mobile foragers to reconstruct past lifeways (Arnold et al., 2016; Kelly, 2013; Lee & DeVore, 1968b; Lewin, 1988; Moreau, 2020; Murdock, 1968; Price & Brown, 1985; Smith et al., 2010). Yet, for the most part, these scholars’ findings have failed to reach evolutionary social scientists, let alone disciplines outside anthropology—a failure due partly to some specialists’ hesitations in making inferences about Late Pleistocene social organization (e.g., Kelly 2013:xv-xvii).

Here, we synthesize research from hunter-gatherer studies and archaeology with other anthropological findings to propose a new model of pre-Holocene lifeways, referred to as the diverse Pleistocene model. Throughout the Late Pleistocene (c. 129–11.5 ka)—and possibly much earlier—humans lived in societies that varied considerably in 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 managed plants and animals and may have even domesticated species. As a result, human psychology is adapted not just to small, egalitarian bands but to a broader range of social environments. This new model of human psychological evolution helps explain many behaviors difficult to explain under the nomadic-egalitarian model.

We focus on the Late Pleistocene for two reasons. First, key lines of evidence—namely, indications of intensive and systematic coastal resource exploitation—are restricted to the Late Pleistocene or the time-period shortly preceding it (e.g., Marean, 2014). Empirically, we are therefore limited in the claims we can make about eras preceding the Late Pleistocene. Second, the Late Pleistocene is a period both of behavioral modernity and ongoing evolution. Anatomically modern humans emerged before the Late Pleistocene (Bergström et al., 2021), and early Late Pleistocene humans were engaging in many behaviors considered quintessentially modern (McBrearty & Brooks, 2000), permitting us (to some extent) to make inferences about early Late Pleistocene humans using modern analogues. At the same time, the Late Pleistocene was also a time of ongoing human evolution (Cieri et al., 2014; Scerri et al., 2018), suggesting that social organization during that period was relevant for human behavioral evolution.

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 apparently mobile forager groups. We then shift our discussion to low-mobility 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 120 ka. We conclude by reviewing implications for the evolutionary understanding of diverse human behaviors.

Limitations of using recent foragers as models of Late Pleistocene societies

The nomadic-egalitarian model was inspired largely by observations of recent foragers. By “recent” foragers, we mean hunter-gatherer societies observed in the last several hundred years. Such groups, especially those living in Africa such as the Hadza and the Ju/’hoansi (!Kung), appear to mostly live in small, mobile bands with relatively egalitarian relations among individuals of similar age and sex (Ember, 2020). The conviction that these groups represented the typical forager lifestyle (Lee and DeVore 1968b)—and that African hunter-gatherers inhabited an environment similar to the one in which humans spent most of their evolutionary history (Lee 1979a)—motivated the focus on mobile, egalitarian groups. Yet there are major empirical limitations with treating recent foragers such as the !Kung and Hadza as the primary models of Late Pleistocene societies.

Marginal habitats

A common criticism is that many recent foragers have been pushed to ‘marginal’ or poor-quality habitats by agriculturalists (Cunningham et al., 2019; Marlowe, 2005). Regardless of whether foragers admixed with expanding farmer populations (Rivollat et al., 2020) or were demographically replaced by them (Brace et al., 2019), the implication is the same: Recent foragers lived in the subset of environments in which agriculturalists did not settle. Because environments are important factors in shaping forager social organization (Kelly, 2013; Marlowe, 2005), the nomadic-egalitarian model can thus 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 tested this hypothesis using net primary productivity (NPP) as a proxy for habitat quality (Cunningham et al., 2019; Porter & Marlowe, 2007). Both reported no differences in habitat quality between recent hunter-gatherers and agriculturalists. Still, Cunningham et al. (2019:598) point out two critical complications which, they acknowledge, preclude “a more definitive test of the MHH [marginal habitat hypothesis]”:

First, both studies only considered non-industrial societies. They thus overlooked 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 for the hypothesis that modern hunter-gatherers live in less productive habitats than agriculturalists.

Second, NPP is a misleading proxy for habitat quality. Many 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 tissue (Bailey et al., 1989). 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 access (Headland, 1987). Moreover, NPP-based analyses ignore the depletion of wild game in forager habitats, as seems to have occurred in the Hadza-occupied region (Wood et al., 2021).

Future research will better clarify how recent foragers’ habitats compare with those of agriculturalists. What is clear is that recent hunter-gatherers were excluded from highly productive aquatic

environments, such as the Nile and coastal South Africa, and that some popular model populations live in particularly harsh environments.

Sustained interactions with states and agricultural societies

Agriculturalists have shaped forager societies beyond limiting their choice of habitats (Headland & Reid, 1989). These interactions have taken many forms, including trade, political incorporation, and slavery. Marlowe (2010) noted that Hadza access to iron might trace back at least 500 years, that their population experienced pre-20th century declines due to the Masai expansion, and that the ivory trade impacted Hadza lifeways as neighboring groups killed elephants. Other interactions between foragers and agriculturalists, as in the Philippines and Central African rainforests, go back thousands of years (Junker, 2002; Verdu et al., 2009). In fact, the intense economic dependence of some rainforest foragers on neighboring agriculturalists—for instance, an estimated 60% of Mbuti caloric intake came from agricultural exchange (Ichikawa, 1983)—raises the question of whether these groups truly qualify as “hunter-gatherers” (Hames, 2019). Finally, the Ju/’hoansi (!Kung)—the people most often used as stand-ins for the Paleolithic (Flannery and Marcus, 2012; Johnson and Earle, 2000)—interacted extensively with agriculturalists, especially after the 1920s (Solway & Lee, 1990). Although these interactions impact many features of forager social organization (Roscoe, 2016), we focus here on authority, mobility, and corporate group structure as illustrative case studies.

Impacts on leadership and authority

The nomadic-egalitarian model posits that decision-making in ancestral societies was through consensus, with a limited role of leadership and authority (Boehm, 1997). However, this ethnographic pattern may reflect social changes following interactions with agricultural societies which undermine institutions of authority. For example, outside administrators may invade local leaders’ jurisdiction (Singh & Garfield, 2022). Or as crucial services, like coordinating warfare or resolving disputes, decline in importance, the need for and approval of leaders may also diminish (Garfield et al., 2019; Glowacki & von Rueden, 2015).

The !Kung experienced one such decline in leadership following the Bantu incursion in the 1920s (Wiessner, 1994). A number of social changes seem to have contributed to this decline, the most important being the state-backed control of !Kung territory by Tswana headmen and the incorporation of !Kung families into patron-client systems with Tswana and Herero agropastoralists (Lee, 1979b; Solway & Lee, 1990). Just what authority looked like before that time remains unclear, but reports by Fourie (1928) and Marshall (1965) both suggest that leadership positions were hereditary and restricted to men, with the particular norms of heredity varying by area. Although Marshall (1965; 1976) wrote that, in the Nyae Nyae area in the 1950s, leaders lacked coercive authority and resembled mouthpieces of group consent, Fourie (1928, p. 86) 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, Marshall (1965, p. 251) adding that visitors should seek the leader’s permission before taking water.

Mobility

According to the nomadic-egalitarian model, our foraging ancestors were highly mobile, reducing their ability to accrue material wealth and contributing to a decentralized social structure (Lee & DeVore, 1968b). Yet for many contemporary foragers, mobility patterns have been shaped by interactions with large, agricultural societies. Following colonial incorporation and a decreased threat of endemic warfare, large New Guinean fisher-forager communities splintered into smaller groups (Roscoe, 2016). 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” (Hoffman, 1984), yet their mobile, foraging lifestyle seemed an adaptation for collecting products considered valuable to Chinese traders, such as rattan, beeswax, and edible birds’ nests (Hoffman, 1984). Groups might also become mobile to escape political domination. This has been observed among pastoralist groups (Elam, 1979; Irons, 1974), but it likely applies to foragers as well (Rambo, 1988) (see also (Scott, 2009, 2017)).

Corporate groups

Including clans, lineages, and formal age-sets, corporate groups are formal groups that have enduring, selective, and stable membership; confer rights and duties; and, in most human societies, determine

membership on the basis of residence and/or kinship (Glowacki, 2020; Hayden & Cannon, 1982). Popular Late Pleistocene models such as the !Kung and Hadza lack systems of corporate groups, leading some scholars to treat corporate groups as complex innovations that developed recently in sociopolitical evolution (Bellwood, 2005; Flannery & Marcus, 2012). However, the absence of corporate group structure may reflect interactions with large-scale, agricultural societies. States might suppress corporate membership to make a populace easier to govern, such as when the US government unified the clans of the Ifugao (horticulturalists) after taking control of the Philippines (Beyer & Barton, 1911). Or corporate groups, which commonly function to protect life and property (Glowacki, 2020), may become redundant as agricultural states provide the same services. Finally, the demographic and cultural collapse that results from interacting with agricultural societies might also end in the dissolution of corporate social organization, as seems to have happened with various Tupi-Guarani groups (Walker et al., 2012).

Many forager societies seem to have lost corporate group structure in recent historical memory. The Eastern Pomo, Copper Inuit, and Ju/'hoansi are all coded in the Standard Cross-Cultural Sample as lacking kin-based corporate groups, yet each group seems to have lost more elaborate social structure following interactions with states and other agricultural societies. Through comparisons of Eastern Pomo social organization with that of the Southeastern Pomo and the Cupeño, Gifford (1923, p. 84) concluded that the Eastern Pomo had suffered "social disintegration caused by the intrusion of Americans". Condon (1983) posited that the pre-contact Copper Inuit had a system of lineages more similar to that of eastern Inuit groups, or at least that the kinship system studied in the 20th century gave little indication of the social structure two centuries before. And before the incursion of Bantu agropastoralists into their lands, the Ju/'hoansi appeared to have a more complex social structure, involving "a system of exogamous named groups" that held land rights (Wiessner 1994, p. 118).

Mischaracterizations of recent foragers

Even accepting the above limitations, small-scale, mobile, egalitarian foragers exhibit much more variability in social organization than is often appreciated. Insofar as contemporary foragers serve as models for the Pleistocene, their behavior suggests more variation than the nomadic-egalitarian model permits.

Group size and mobility

Several studies suggest that recent mobile hunter-gatherers lived in groups of a few dozen individuals, leading to the conclusion that Late Pleistocene societies were similarly small-scale (Birdsell, 1968; Hamilton et al., 2007; Hill et al., 2011; Marlowe, 2005). In fact, given that so many comparative studies have converged on an estimated group size of about 25 individuals, some researchers refer to it a "magic number" of mobile forager social organization (Birdsell, 1968; Kelly, 2013). Nevertheless, the focus on mean population sizes hides two sources of variation.

First is within-culture variation. Community size varies 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 the so-called "archers" (Efe) and "net-hunters" (Sua Mbuti) (Turnbull, 1965). 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 individuals (Putnam, 1948). Similarly, the 9 !Kung camps recorded by Lee in 1964 ranged in size from 9 to 117 resident !Kung (1984).

Second, the focus on mean population sizes masks temporal variation, manifesting both in seasonal fluctuations and large, periodic aggregations. Seasonal variation was common; many presumably nomadic foragers likely spent just as much time in large, sedentary settlements as in dispersed, mobile groups (Graeber & Wengrow, 2021; Wengrow & Graeber, 2015; White & Peterson, 1969). Various Arctic and Alaskan groups exhibited what Mauss (1950) called "a twofold morphology", transitioning between small, mobile camps in the summer and dense, large, settled villages in the winter. Similarly, peoples of northern Australia, such as the Wik-Mungkan of the Cape York Peninsula, lived in mobile groups during the dry season and permanent settlements during the wet season, when the otherwise arid plains were flooded with brackish water (Thomson, 1939). Archaeological findings provide evidence that Northern Australian foragers engaged in such seasonal transitions for at least 7,000 years (White & Peterson, 1969).

Aside from regular, annual fluctuations, many foragers assembled during serendipitous times and with the purpose of hosting festivities and large-scale ceremonies, reflecting their multilevel social organization (Bird et al., 2019; Layton et al., 2012). The Andaman Islanders sometimes collected into groups of 100 or even 300 people (Man 1932, p. 46). When a dying whale washed up on their coasts, the Selk'nam of Tierra del Fuego collected en masse and feasted for months or even a year, sometimes using the good fortune to host the tribe-wide male initiation, or Hain ceremony (Chapman, 1982; Gusinde, 1971). The Arrernte people of central Australia periodically collected for the Angkwerre (Engwura) festival, which lasted more than four months and comprised initiations and other ceremonies honoring totemic ancestors (Spencer & Gillen, 1927). It's unclear how many people attended, but according to Spencer and Gillen (1927, p. 223), "men and women gather[ed] from all parts of the tribe"—which, at that time, numbered around 2,000 individuals—"and sometimes also from other tribes". In Australia, assemblages of hundreds of individuals, sometimes lasting months, were also observed among the Warlpiri and Pintupi (Meggitt, 1974). Even the Ju/'hoansi assembled into larger groupings. Not only did several camps come together to share water-holes during years of reduced rainfall (Lee, 1972), 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 in (Wiessner 1994, p. 118). Again, it remains unclear how many people collected for chomas, although Lee (1979, p. 365) speculated that an initiation of 20 or more boys could draw together camps together totaling more than 200 individuals. In short, the focus on mean or median group size distracts from the within-culture and temporal variation in group size exhibited by foragers typically often considered small-scale and mobile.

Scale of cooperation

The popularity of the nomadic-egalitarian model has led some researchers to conclude that human cooperation was limited to small groups throughout our evolutionary history (e.g., Tooby and Cosmides 2016). But several lines of research challenge this conclusion. Not only have researchers found that mobile foragers are ensconced in cooperative networks that extend beyond their immediate cooperative group (Bird et al., 2019; Glowacki & Lew-Levy, 2022; Hill et al., 2011; Migliano et al., 2017, 2020), but Boyd and Richerson (2022) recently reviewed numerous examples of large-scale cooperation among mobile foragers in North America, Australia, Europe, and the Arctic. The examples cover many domains, including warfare, communal hunting, and construction of shared facilities, 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 the 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 bison killings c. 400 ka—well before the origins of *Homo sapiens* (Rodríguez-Hidalgo et al., 2017)—and the remains of a large number of reindeer at a Middle Paleolithic (c. 54 ka) in Germany (Gaudzinski & Roebroeks, 2000). A striking example of large-scale cooperation among prehistoric Holocene 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.) (Ortmann & Kidder, 2013).

Non-egalitarianism

Many apparently mobile, small-scale forager societies exhibit deviations from egalitarianism, where "egalitarianism" refers to either a leveling of resources (Woodburn, 1982) or autonomy from political coercion (Boehm, 1993). 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 Warner 1958; Hart and Pilling 1960). Even when considering individuals of similar age and sex, however, mobile or small-scale foragers deviate from egalitarian social arrangements. Using a sample of 59 societies, including 13 foragers, Garfield et al. (2020) found that coercive leadership was present among foragers, although less frequent than in other types of societies. Coercive authority has also been documented among foragers living near the Bering Strait (Nelson, 1900) and among the Khanti of west Siberia, where shamans and elders purportedly "used poor people 'like slaves'" (Bartels and Bartels 1999:164, quoting Khanti linguist N. I. Terioshkin). As indicated both by anecdotal accounts and by Garfield et al.'s (2020) systematic study, shamans and other magico-religious practitioners often leverage perceptions of their supernatural powers to exercise political authority (see also Singh 2018).

Resource management

Considerable ethnographic and archaeological evidence suggests that resource management, such as cultivation and animal management, preceded the Agricultural Revolution. Ethnographically observed foragers engaged in activities including irrigation, arboriculture, the broadcast sowing of annuals, and the creation of clam gardens (Smith 2011; Gerritsen 2008). Holocene foragers managed wild boar populations in Cyprus and Japan before pig domestication (Price and Hongo 2019), while archaeological evidence suggests that Melanesian hunter-gatherers were managing populations of cuscuses as early as 20 ka (Heinsohn, 2010). Archaeologists reported evidence of intensive plant cultivation at the forager camp Ohalo II in Israel 23 ka—at least 11 millennia before the supposed onset of agriculture in the Near East (Snir et al., 2015). Finally, through controlled fires, the Martu of Australia’s Western Desert generated large-scale improvements in habitat quality (Bliege Bird et al., 2008, 2020). Such fire regimes, which have been used to enhance hunting and encourage the growth of plants useful to humans, were likely common elsewhere and seem to have been practiced by Late Pleistocene humans by 72 ka (Thompson et al., 2021). It is no longer clear why we should assume that cultivation, animal management, and other forms of 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, only to have such evolutionary changes disappear with shifting social and ecological conditions (Snir et al., 2015).

The importance of considering low-mobility and non-egalitarian foragers

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-gatherers (Kelly, 2013). These foragers are sometimes equated with “delayed-return” hunter-gatherers, although such a conflation can be misleading, given that many quintessential mobile foragers stored food for very long periods (e.g., !Kung foragers saved dried meat for weeks or even months (Lee, 1965)).

Recent examples of low-mobility foragers include the Chumash (Arnold, 1992), New Guinean fisher-foragers (Roscoe, 2002, 2006), and the peoples of the Pacific Northwest (Ames, 1994). Such peoples tended to exhibit several common features (Kelly, 2013): 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 bestowing status upon individuals who accumulated and redistributed surplus. Some groups kept slaves (Wengrow & Graeber, 2018).

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 Switzerland (Thompson et al., 2018). 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 (Thompson et al., 2018, 2020). Although they appear to have planted some squash and papaya, in addition to managing chili pepper, these seem to have constituted trivial contributions to subsistence (Hutchinson et al., 2016); rather, their wealth and surplus derived from rich aquatic resources (Marquardt, 2014).

Evolutionary scholars tend to ignore such foragers in pre-Holocene reconstructions. When Arnold et al. (2016) 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 the Late Pleistocene (Fry et al., 2020). Boehm (2008; 2012) excluded them from his database of 150 recent ‘Late-Pleistocene-appropriate’ hunter-gatherer societies. Marlowe (2005) wrote that sedentary foragers “may not have been rare” immediately before the Holocene, “but for modeling earlier periods we should exclude them”. Lee (2018) stated that sedentary foragers should be discounted when studying the evolution of violence given that small-scale, egalitarian, mobile foragers best represent our evolutionary past.

Scholars—even those who urge that greater attention be paid to low-mobility foragers (Price and Brown 1985)—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, given archaeological evidence, was believed to develop recently in human history.
3. There is little, if any, archaeological evidence for their existence during the Pleistocene.

Over the last three decades, research has shown these assumptions either to be wrong or to no longer be sufficiently compelling to justify ignoring low-mobility foragers in reconstructions of Late Pleistocene societies. For this reason, we argue that low-mobility foragers are relevant for understanding pre-Holocene lifeways, at least as much as small mobile groups.

Low-mobility foragers are not anomalous and emerge in environments with dense, reliable resources

The longstanding view that low-mobility foragers are exceptional and that “social complexity” emerged with agriculture (reviewed by Arnold et al. 2016) is no longer viable. Researchers have reported evidence of low-mobility and non-egalitarian hunter-gatherers from all over the world, throughout the Holocene, and even in Pleistocene Europe; Table 1 and Figure 1 list examples in 34 world regions.

As anthropologists have long appreciated, low-mobility and non-egalitarian foragers tend to emerge in environments with dense, rich, and predictable resources (Kelly, 2013; Roscoe, 2002; Smith & Codding, 2021). They frequently subsist on aquatic resources (Price & Brown, 1985; Roscoe, 2006; Smith et al., 2010; but see Jeffrey & Lahr, 2020), although as Table 1 illustrates, semi-sedentism and its sociocultural correlates (e.g., large groups, inequality) have also been documented among foragers subsisting on cereals, sheep, gazelles, camelids (guanaco and vicuña), and bowhead whales. Critically, many environments that once supported low-mobility foragers—such as Japan, the Levant, the Nile River Valley, the South China Sea coast, and southern Scandinavia—are now inhabited by agriculturalists. Whether this was because these peoples themselves domesticated local species (Maher et al., 2012), they adopted domesticates from neighbors (Lee, 2001), or they were demographically displaced (Malmström et al., 2009), this pattern further suggests that recent hunter-gatherers are underrepresented in certain environments because of agricultural occupation (Gopalan et al., 2022).

What explains the link between dense, predictable resources, on the one hand, and low mobility and non-egalitarianism, on the other? Low mobility should be favored whenever the benefits of staying in a resource patch or habitat outweigh the costs of moving. As local resources become denser, richer, and more reliable, the benefits of staying increase, although other factors will further favor low mobility, such as significant distances to other patches and large tracts of adjacent, low-quality habitat. Many recently observed foragers varied their mobility patterns as a function of resource availability, including groups that seasonally alternated between small, mobile bands and large, semi-sedentary villages (Mauß, 1950; White & Peterson, 1969).

At least three hypotheses connect dense, predictable resources to non-egalitarianism. According to one, the high population densities of such habitats create the need for social coordination and conflict management, manifesting as sociopolitical hierarchy (Bandy, 2004; Hooper et al., 2010; Johnson, 1982). According to a related second hypothesis, dense and predictable resources give rise to intergroup conflict as coalitions aim to seize and defend resources, creating the need for strong leadership and enabling inequality (Glowacki & von Rueden, 2015; Hooper et al., 2010). These first two hypotheses are supported by observations of authorities emerging in contexts that require social coordination, such as the Plains Indian military societies who enforced order during war raids, buffalo hunts, and tribal aggregations (Llewellyn & Hoebel, 1941; Richardson, 1940).

A third hypothesis points to defensible resources. As factions control rich and defensible resource patches (or stochastically end up with greater stores of resources), they can establish patron-client relations, extracting benefits from subordinates up to but not past the point where subordinates are better off leaving or contesting (Smith & Choi, 2007). Critically, inequality here hinges on individuals' outside options: If resource patches are uniformly high-quality, subordinates will be less willing to accept exploitation. Both a recent analysis of Pacific coast foragers in North America (Smith & Codding, 2021) and the apparent link between food storage, on the one hand, and low mobility and inequality, on the other (Testart, 1982), are consistent with this hypothesis.

Regardless of the mechanism, dense, rich, and predictable resources appear to promote low mobility, non-egalitarianism, and large groups among foragers. As long as Pleistocene hunter-gatherers both exploited such resources and were sufficiently similar to modern humans, we should also expect them to have developed diverse societies.

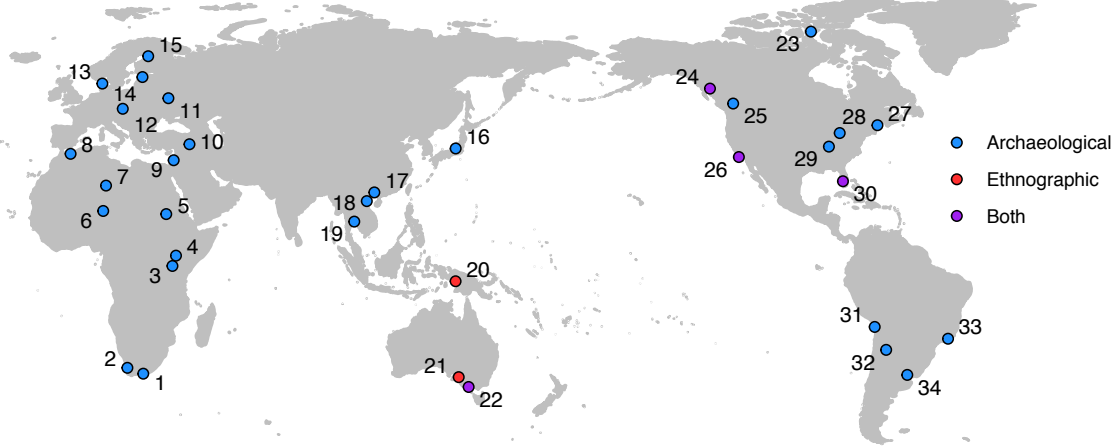


Figure 1. Locations of low-mobility foragers listed in Table 1. All cultures or regions varied considerably in mobility patterns and social organization over time and space; this figure does not imply that every forager group displayed always exhibited low mobility or inequality. The color of each point 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 Supplementary Table 1 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, anthropologists assumed 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 Erlandson 2001). This assumption, which reinforced the view that low mobility foragers emerged only recently (Price & Brown, 1985), no longer holds. Evidence for aquatic resource exploitation goes as far back as 1.95 Ma in northern Kenya (Braun et al., 2010). Humans appear to have been systematically targeting shellfish species by c. 160 ka (Marean et al., 2007), and archaeologists have discovered shell middens—or sites where food remains leave apparently solid deposits of shell (shell supported matrices), potentially indicating a commitment to dense and predictable coastal resources—by c. 130 ka along the southern African coast (Marean, 2014) (Figure 2). The presence of substantial white mussel remains at Pinnacle Point from 110 to 90 ka indicates more skilled and anticipatory foraging, possibly involving cooperation or particular tools (Jerardino & Marean, 2010). There is also evidence that Late Pleistocene humans were exploiting aquatic resources, potentially systematically, along the north African coast and rivers of Central Africa (Marean, 2016) (Figure 2B). They likely inhabited productive lake margins, such as shoreline sites along Lake Victoria rich in shellfish and aquatic and semi-aquatic plants (Tryon et al., 2016). Archaeological evidence indicates that coastal foraging, both of shellfish and marine fish, continued even during the Last Glacial Maximum (Fisher et al., 2020; see also Keller et al., 2019).

Although shellfish are the most common marine organisms discovered in Late Pleistocene sites, humans were clearly consuming other marine resources. In their review of 21 coastal Middle Stone Age sites dated between c. 130 and 40 ka, Will et al. (2016) found that, in addition to consuming mollusks (n = 21 sites), foragers subsisted on marine mammals (n = 8 sites), marine birds (n = 8 sites), and marine fish (n = 5 sites). Between 120 and 55 ka, foragers at Klasies, Blombos Cave, and Die Kelders regularly procured substantial amounts of adult cape fur seal (Will et al., 2016), and although low, fish remains at Klasies and Blombos suggest active marine fishing (van Niekerk, 2011). The discovery of whale barnacle remains at Pinnacle Point indicates that humans have been collecting whale meat since at least 160 ka (Marean et al., 2007). Given the growing recognition of aquatic resource exploitation, some scholars now see aquatic (and particularly coastal) adaptation as central for the origin, evolution, and dispersal of modern humans (Erlandson, 2001; Marean, 2016), although these claims are still debated.

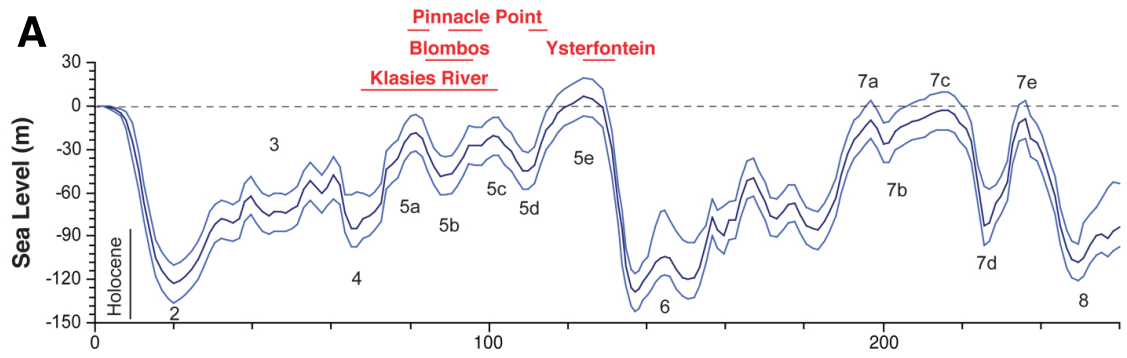


Figure 2. (A) Estimates of sea level fluctuations since 260 ka, bracketed by uncertainty (Waelbroeck et al., 2002). Middle Stone Age sites with *shell middens* (where food remains leave apparently solid deposits of shell, suggesting an adaptation and commitment to dense and predictable coastal resources) 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). Sites are dated to between c. 130 ka and c. 40 ka. Sources: Marean 2014; 2016; Will et al. 2016; Compton 2011; Yellen et al. 2005; McBrearty and Brooks 2000.

The evidence for low-mobility hunter-gatherers during the Pleistocene

Several archaeological sites provide evidence for low-mobility and non-egalitarian hunter-gatherers during the Late Pleistocene, but most are restricted to Europe and the circum-Mediterranean and are more recent than about 35,000 years ago. These sites include elaborate burials, such as in Sungir in Russia, Arene Candide in Italy, Dolní Vestonice in the Czech Republic, Brno 2 in the Czech Republic, and Saint-Germaine-la-Rivière in France (Pettitt, 2010). 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 among ethnographically observed foragers (D’Errico & Vanhaeren, 2015; Vanhaeren & d’Errico, 2005). The discovery of circum-Mediterranean “cemeteries” or “necropolises” provides further evidence of larger groups, intensive exploitation, and greater sedentism (Barton et al., 2019; Formicola et al., 2005). Importantly, however, all of these sites appear at the very end of the Pleistocene and are subject to ongoing debates over their interpretation.

The archaeological record in Late Pleistocene Africa lacks the conclusive finds of Upper Paleolithic Europe, yet there is still evidence of low-mobility population exploiting the kinds of resources that support large groups and inequality. 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 (reviewed in Tryon et al. 2016). Research in the Upper Egyptian Nile Valley shows a large population until about 75 ka (Vermeersch & Van Neer, 2015). The population seems to have declined and then rebounded again about 25 ka, with many sites indicating intensive fishing (Vermeersch & Van Neer, 2015). Figure 2 includes 27 sites where foragers exploited dense, reliable resources during the Middle Stone Age (sites dated to between c. 130 and 40 ka), including 4 sites with shell middens—indications of coastal adaptation (Marean, 2014).

Despite this evidence, there are two reasons the African Late Pleistocene record is biased against signs of social diversity. First, compared to Europe and North America, far fewer archaeologists have worked in Africa. Second, 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 Late Pleistocene Africa comes from elevated caves that were both close to ancient coastlines and protected from surging sea levels (Fisher et al., 2010; Marean et al., 2007).

A new model of Late Pleistocene lifeways

Figure 3 contrasts the nomadic-egalitarian model with what we call the diverse Pleistocene model. Both agree that forager social diversity declined with the spread of agriculture. They differ, however, in what they posit about pre-Holocene social diversity. According to the nomadic-egalitarian model, humans lived predominantly in small-scale, mobile, egalitarian bands, and the social diversity observed among recent foragers vastly exceeds that of Late Pleistocene hunter-gatherers.

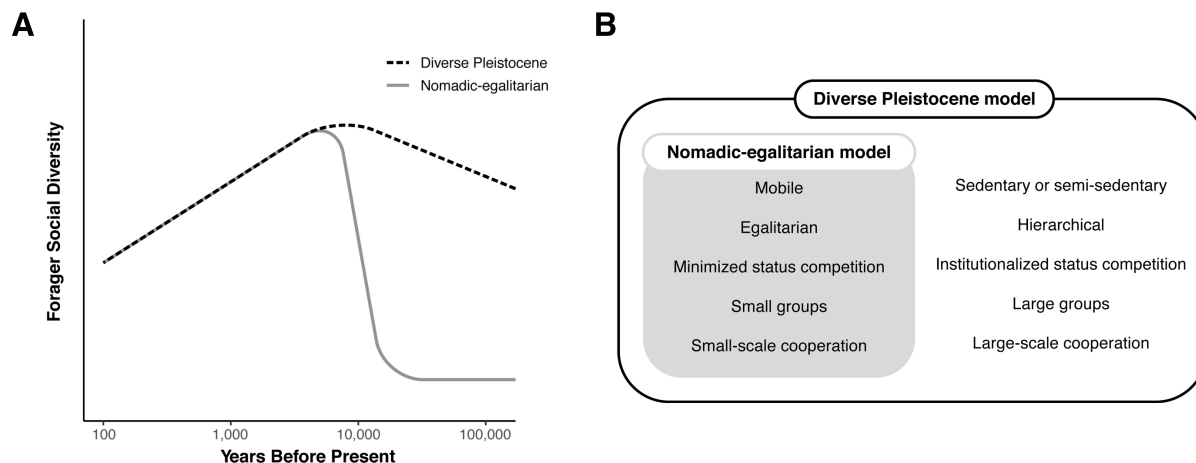


Figure 3. (A) The historical trajectories of social diversity posited by the nomadic-egalitarian and diverse Pleistocene models. According to both models, the diversity of forager societies declined with the spread of agriculture. But whereas the nomadic-egalitarian model posits that pre-Holocene societies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

The diverse Pleistocene model, in contrast, posits a much higher level of pre-Holocene social diversity. Because behaviorally modern humans likely inhabited many habitats during the Late Pleistocene—including productive environments such as coasts, lake margins, or the Nile Valley—we expect social structures to have reflected those diverse ecologies. Just as contemporary foragers living in habitats with dense, predictable resources show a capacity to develop large groups, sedentism, and inequality (Smith and Codding 2021; Kelly 2013; Roscoe 2006), we expect that pre-Holocene foragers could do the same. The diverse Pleistocene model acknowledges that some humans lived in societies similar to recent mobile, egalitarian foragers but posits that these represented one of many social outcomes.

Given the comparably large groups and high densities of foragers living in rich environments, they plausibly represented a considerable proportion of total human population, and thus important environments for psychological adaptation, even if they took up little space in the landscape. Consider a hypothetical habitat with 500 equally sized patches. If 499 are filled with people living at Ju/'hoansi densities (10-16 individuals/100 km²) and only 1 is inhabited by foragers living at the highest densities of New Guinean foragers (2,500 individuals/100 km²), still 1 of every 4 individuals lives in the single dense patch.

The evolution of human behavior in flexible and diverse societies

The nomadic-egalitarian model confronts puzzling inconsistencies. According to it, 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 (Boehm, 2012a; von Rueden, 2020). Status competition was stifled, and domineering behavior invited censure, ostracism, or execution (Boehm, 1993; Wrangham, 2019). Such an environment was purportedly critical in shaping our evolved psychology (Boehm 2012; Lee 2018; Marlowe 2005; Kaplan, Hooper, and Gurven 2009). For instance, many scholars argue that understanding the evolution of the human mind requires considering the egalitarian origins of our species (Boehm, 1999, 2012a; Whiten & Erdal, 2012), 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 (Krasnow et al., 2013; Tooby & Cosmides,

2016). Yet many widespread 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.

Humans seek dominance and other forms of status, even in egalitarian arrangements

Humans reliably exhibit predispositions to seek and recognize dominance (Johnson, Leedom, and Muhtadie 2012; Charafeddine et al. 2015). 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 (Boehm, 1993; Wiessner, 2005). Such behaviors are difficult to explain under the nomadic-egalitarian model, which posits that opportunities for dominance were minimal and met with severe sanctions (Boehm, 2012b). The diverse Pleistocene model, meanwhile, better explains their persistence. 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.

Evolutionary predispositions to identify with very large groups

Humans regularly exhibit ingroup biases evoked through “mere membership” in a group (Dunham, 2018). Even meaningless group assignments, such as on the basis of painting preferences or shirt color, can elicit preferences towards in-group strangers (Dunham, 2018). 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 predispositions to cooperate with strangers based on arbitrary markers seem unnecessary, even costly. Under the diverse Pleistocene 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 (Kelly, 2013; Roscoe, 2006)—and they cooperated at times with hundreds of individuals (Boyd & Richerson, 2022), then prosocial predispositions towards in-group strangers make more evolutionary sense, especially if groups developed markers of group membership.

Predispositions for war and peace reflect a flexible intergroup psychology

Using the nomadic-egalitarian model, researchers have advanced opposing arguments about the role of war in human evolution. Some conclude that war was a regular feature of ancestral societies and a major selective force in shaping psychology (Wrangham & Glowacki, 2012). Others conclude that war was absent during human evolution, appearing only with sedentary and non-egalitarian societies c. 10 ka (Fry et al., 2020). Both approaches have difficulty accounting for observed variation: Many peoples never participate in war (Fry, 2007), and groups which formerly engaged in it quickly abandon warfare when social conditions change (Roscoe, 2016). If, however, humans evolved in a diversity of social environments, 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 (Glowacki, 2022).

The role of gene-culture coevolution in shaping human social psychology

The diverse Pleistocene model suggests 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 other dimensions of social identity (Smaldino, 2019). The ease with which we live in contemporary societies dramatically different from small, mobile bands may reflect psychological adaptations designed for similar social ecologies.

Evaluating social diversity during the Late Pleistocene

Our argument partly rests on the assumption that environments with dense, rich, reliable resources are more likely to support foragers that are semi-sedentary, live in large groups, and exhibit some inequality. This assumption can be tested in many ways. Researchers can test whether prehistoric populations living in environments with rich, dense, and predictable resources are more likely to have reduced mobility, measured, for instance, with paleopathology (Pate, 2006), variability in isotope data from bones and teeth (Sealy, 2006; Stojanowski & Knudson, 2011), and even, potentially, familiarity with obesity (Trinkaus, 2005). Researchers can also test whether rich environments are more likely to produce inequality, measured with bone morphology or grave goods (Schulting et al., 2022; Vanhaeren & d'Errico, 2005). Finally, they can assess whether such environments give rise to denser or larger populations, assessed from archaeological settlement patterns (Hayden et al., 1985; Hayden & Ryder, 1991). These patterns can be investigated in Holocene foragers, although given that our argument uses observed socioecological relationships to make inferences about Late Pleistocene social organization, ideal tests would use Late Pleistocene samples.

Several areas of study will prove valuable for evaluating Late Pleistocene social diversity. First is archaeological work in promising locations. Rising sea levels submerged coastal sites likely to host societies that violate the nomadic-egalitarian model. Yet this does not preclude useful investigations. Sea level history is complex and heterogeneous. For instance, on the North American Pacific coast, ice sheets created a raised bulge offshore, meaning that, at the Last Glacial Maximum, sea levels were hundreds of meters lower, rather than higher, in some places (Shugar et al., 2014). Research on sites in Africa that have similarly escaped fluctuating sea levels will likely prove fruitful (Fisher et al., 2010, 2020). Indeed, archaeological investigations of coastal sites protected from rising sea levels on the South African coast have yielded indications of behavioral sophistication during the Late Pleistocene (Marean et al., 2007). Similarly, as techniques of submerged landscape archaeology improve, our understanding of previously coastal regions—and, as a result, of Late Pleistocene lifeways—will likely advance.

Another potentially promising 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 (Sikora et al., 2017). Existing research suggests that hunter-gatherer populations today are smaller and more isolated than their Pleistocene predecessors (Bergström et al., 2020). Future research with Pleistocene samples will provide more precise characterizations of prehistoric social organization, allowing us to better evaluate the extent to which our model describes Late Pleistocene human social organization.

Summary

For over 50 years, the human evolutionary sciences have taken as a starting point the nomadic-egalitarian model, according to which humans lived in small, mobile, relatively egalitarian bands until some 12,000 years ago. We have shown that the empirical foundations of this model are weak and have proposed an alternative, the diverse Pleistocene model, to replace it. Given (a) the diversity of Late Pleistocene habitats, (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. Deep diversity during human evolution 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 is correct, our reconstructions of Late Pleistocene lifeways require reconsideration.

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