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Large-scale cooperation in small-scale foraging societies

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Abstract

We present evidence that people in small-scale mobile hunter-gatherer societies cooperated in large numbers to produce collective goods. Foragers engaged in large-scale communal hunts and constructed shared capital facilities; they made shared investments in improving the local environment; and they participated in warfare, formed enduring alliances, and established trading networks. Large-scale collective action often played a crucial role in subsistence. The provision of public goods involved the cooperation of many individuals, so each person made only a small contribution. This evidence suggests that large-scale cooperation occurred in the Pleistocene societies that encompass most of human evolutionary history, and therefore it is unlikely that large-scale cooperation in Holocene food producing societies results from an evolved psychology shaped only in small-group interactions. Instead, large-scale human cooperation needs to be explained as an adaptation, likely rooted in distinctive features of human biology, grammatical language, increased cognitive ability, and cumulative cultural adaptation.

KEYWORDS

collective action, communal foraging, cooperation, foragers, hunter-gatherers, mismatch hypothesis, public goods

1 | INTRODUCTION

In complex societies, large groups of unrelated people cooperate to produce collective goods. They construct shared capital facilities like roads, fortifications, and irrigation works, and they risk their lives in large-scale warfare. Such behavior is unknown among other vertebrate species. Some taxa, including communally nesting birds and chimpanzees, cooperate with small groups of distantly related individuals, but very few species cooperate in larger groups, and those that do, like African mole rats, live in groups of close kin.[1]

Many authors believe that until 10,000 years ago people mainly lived in small, mobile, face-to-face bands, with little social hierarchy. Based on ethnographic studies of contemporary foragers, they believe that these groups were intensely cooperative. They shared food, provided mutual aid, and participated in other forms of small-scale cooperation. However, such cooperation was largely limited to band-sized groups of 20 or 30 people,[2–10] and only rarely extended to larger groups.[5] As people began to domesticate plants and animals about 10,000 years ago, groups became larger and more sedentary, and people began to cooperate on a larger scale.

People have other-regarding preferences that lead to cooperation in anonymous settings.[11] People also readily learn and internalize moral norms that enforce cooperative behavior.[12] A number of authors[3,4,9,10] have suggested these psychological systems evolved in band-sized groups in which they were adaptive, and that contemporary behavior represents a maladaptation resulting from the increase in group sizes caused by agricultural subsistence systems in the Holocene. This kind of explanation is often called a "mismatch hypothesis" because modern human cooperation results from a mismatch between current social environments and those in which our psychology evolved.

Over the last decade or so this picture of Pleistocene foragers has come under fire. Systematic studies of contemporary foragers indicate that members of residential bands are not closely related,[13] and mechanisms other than reciprocity seem to be important.[14] Band membership is highly fluid and people form close social ties with a

much larger network of people within a regional (or "maximal") band numbering between 500 and 2000 people.[15,16] A recent review[17] argues that Pleistocene foragers often lived in rich environments and formed larger, and more sedentary societies with considerable social stratification.

Here we review empirical evidence that people in Holocene hunter-gatherer societies regularly cooperated in large groups to produce collective goods, a fact that further weakens the mismatch hypothesis. Foragers worked together with hundreds of others in communal hunts and the construction of shared capital facilities like drivelines, hunting nets and fish weirs. They made shared investments in improving the local environment through burning, irrigation and other habitat modifications, and they participated in warfare, peace-making and trade on tribal scales. In many foraging societies, such large-scale collective action played a crucial role in subsistence. The provision of public goods involved the cooperation of hundreds of individuals, so relatedness was very low, and the incremental effect of each person on the outcome was small. We also review archaeological evidence that suggests that Pleistocene foragers cooperated in sizable groups as early as 400 ka.

The evidence comes from historical accounts and archaeological data—mainly from North America, Australia and Pleistocene Europe—and from ethnographic descriptions of foragers in Western North America, the Arctic and Australia where hunting and gathering persisted until recent times. Most of the data comes from foragers living at relatively low population densities. This is important because many authors believe that late Pleistocene foragers lived at low population densities, and some authors infer from this that only data from low-density Holocene foragers should be used to make inferences about Pleistocene behavior.[3] We use two standards of comparison to support the claim that our data come from foragers living at relatively low population density. First, we will compare population densities of groups where there is evidence of collective action to the cumulative distribution of population densities in contemporary foraging groups. Kelly[18] (Table 1, his tab. 7.3) lists densities for 201 historical and contemporary foraging groups, including many of the groups that we discuss here. The median population density in the sample is 13 persons per 100 km^2. A second database[19] reports a median of 11 persons per 100 km^2. Table 1 lists the groups and population densities. Second, we compare population densities to three groups that have been the focus of much detailed ethnographic research, the Dobe Ju/'hoansi (13 persons per 100 km^2), the Hadza (19.5 persons per 100 km^2), and the Aché (24 persons per 100 km^2), and so have influenced our thinking about the behavior of Pleistocene foragers. We mainly avoid data from sedentary hunter-gathers with extensive social hierarchy because some authors[2,3] believe that such societies do not provide a useful model for ancestral human environments, but we do include such data in a couple of cases, and note that other authors believe that Upper Paleolithic societies frequently were socially complex.[20]

We describe the evidence in some detail. Much of the historical and archaeological data that we rely on is incomplete, and any single example is suspect. We freely acknowledge that this is not a random sample of the literature. We do not discuss sources that do not provide evidence of large-scale cooperation because the absence of evidence is difficult to interpret. Large-scale cooperation might not have existed in these cases, or it might have existed but left no trace in the archaeological or historical records. This kind of research is like fossil hunting. Paleontologists don't usually search the world at random; they look where they think they are most likely to find informative specimens. We have done the same. Moreover, the question is not what the average group did, but what humans living in small-scale societies could do under favorable ecological circumstances.

On the basis of this evidence, we conclude that (1) the economics of foraging in nomadic, low-density populations did not preclude large-scale cooperation among Holocene foragers, and (2) there is suggestive evidence that Pleistocene foragers cooperated in large groups, perhaps for several hundred thousand years. These data cast further doubt on the foundational premise of the mismatch hypothesis, namely that cooperation in low-density foragers is limited to small groups. Given that cooperation in large unrelated groups is unknown among other vertebrates, this evidence suggests that the evolutionary mechanisms that gave rise to human cooperation likely depend on peculiarities of human biology like our exceptional cognitive ability, combinatorial language, and cumulative cultural evolution.

2 | WHY SCALE IS CRUCIAL

This paper focuses on the production of collective goods. Take, for example, the construction of shared hunting facilities like blinds and drivelines. A small group of men build a blind. Each makes a substantial contribution to the construction, so that if one man free-rides the effect on the collective good is large—the blind doesn't get built, it is too small, or the walls are too low. This means that free riding may not pay, and if not, each individual is motivated to participate by their private benefit. Here participation is mutualistic.[21] Now suppose the group is much larger. To facilitate communal hunting, Inuit and Athabascans built drivelines, fences of wood or stone, to concentrate caribou in locations where they could most easily be killed. Some drivelines were 50 km long. Once built, everyone in the group could benefit even if they did not contribute to the construction. Constructing drivelines is a lot of work, so unless groups are very small, the effect of free riding on the construction is small, and the benefit to the free-rider is substantial. Selection would favor individuals who avoid participating. Participation is no longer mutualistic.[21] So, something has to be added to motivate people to participate.

Reciprocity seems to be a possibility, but theory strongly suggests that reciprocity, meaning "I'll pitch in if other people do the same" does not work well for collective goods. The problem is that reciprocators have to cease cooperating if even a few others slack off—otherwise slackers will prosper and achieve higher payoffs than reciprocators. As a result, reciprocation is very

TABLE 1 Groups and population densities mentioned in the text of the paper. Population densities are in persons per 100 km^2

Region	Group	Population/100 km^2	Time period
Caribou Hunters			
	Polar Inuit	0.5	Late 19th century
	Tagiugmiut (Barrow)	4	1850
	Mackenzie River delta	3.5	Early 19th century
	Quebec Inuit	0.8	Early 19th century
	Copper Inuit	1.2	Early 20th century
	Igluglingiut	0.5	1670
	Netsilik	0.5	Late 19th century
	Nunamiut	2	Late 19th century
	Laborador Inuit	2.8	1600
	Caribou Inuit	0.2	1670
	Koetezbue sound Inupiaq	6.8	19th century
	Naskapi (Innu)	0.25	18th century,
	Chipewyan	0.4	1960s
	Tutchone	0.6	"Aboriginal population density"
	Ahtna	0.8	1818
	Kaska	1	1670
	Tanaina (Dena'ina)	5	"Aboriginal population density"
	Attawapiskat Cree	1.4	1670
	Kutchin	1.1	"Precontact," early 19th century
	Dogrib	0.6	"Early 19th century"
	Hare	0.3	19th century
	Kolchan (related to Tanana)	0.5	"Aboriginal times"
	Slave (Dene Tha', Gr Slave Lake)	1.4	1670
	Han (E. Yukon River)	1.6	"At the time of contact"
	Nabesna (upper Tanana R.)	0.6	Late 19th century
	Yellowknife	0.2	1670
	Median	0.8	
Equestrian Bison Hunters			
	Blackfoot	4.3	1780
	Plains Cree	1.9	1670
	Assiniboin	5.8	1780
	Crow	2.6	1780
	Arapaho	3	1780
	Cheyenne	3	1780
	Kiowa-Apache	1.4	1780
	Comanche	5	1690
	Median	3	

(Continues)

TABLE 1 (Continued)

Region	Group	Population/100 km^2	Time period
Great Basin			
	Sampits Ute	6	Late 19th century
	Wind River Shoshone	1	Late 19th century
	Wadadika (Ruby Valley)	13.4	Early 20th century
	Agaiduka (Lemhi)	2.8	Early 20th century
	Gosiute	1.5	Early 20th century
	Timpanogots (Utah L.)	10.3	Late 19th century
	Reese R. Shoshone	10	Early 20th century
	Tosawihi (White Knife)	15	Early 20th century
	Kawich Shoshone	1.9	Early 20th century
	Kuyuidokado (Pyramid Lake)	18	Early 20th century
	Pahvant Ute	10.3	Late 19th century
	Kaibab (Paiute)	3.5	Late 19th century
	Owens Valley Paiute	19	Early 20th century
	S. Paiute	1.3	Early 20th century
	Panamint	2.1	Early 20th century
	Kidutoado	1.1	Early 20th century
	Median	4.75	
California	Yurok	180	1670
Congo Basin	Mbuti	17	20th century
Tierra del Fuego	Selk'nam	4	Late 19th century
Queensland			
	Mamu	55	Circa 1800
	Madjandji-Wanjuru	49	Circa 1800
	Idindji	38	Circa 1800
	Tjapukai-Buluwai	19	Circa 1800
	Kongkandji	200	Circa 1800
	Djirbal	26	Circa 1800
	Ngatjan	149	Circa 1800
	Djiru	125	Circa 1800
	Wikmunkan	18.7	Precontact
	Yor Yoront	16	Early 2th century, still nomadic
	Median	43.5	
SE Australia			
	Keramai	29	Circa 1800
	Wongaibon	19	19th century
	Median	24	

TABLE 1 (Continued)

Region	Group	Population/100 km^2	Time period
Arnhemland			
	Murgin	5	Circa 1920
	Murinbata	8	Early 20th century
	Anbarra	43	"At time of first European Contact"
	Median	8	

Note: Data from Kelly except in the case of Selk'nam where data is from the source cited in the paper.

sensitive to errors. Somebody gets lost and doesn't make it to contribute, reciprocators notice and they all stop cooperating. It also means that cooperation among intolerant reciprocators is very difficult to get going, and if it does, it will soon collapse[7,22,23]

Direct sanctions work much better. Suppose people impose sanctions on individual cheaters. They can ostracize the offenders, or deny them the privileges that are sustained by various forms of reciprocity. The next time slackers are ill or injured, nobody feeds them; when they come home empty-empty handed from a hunt, no one gives them meat. Or, they can be physically punished. These sorts of sanctions can motivate people to contribute to building the drive line[3,5,8,24] and other forms of collective action such as communal whaling.[25]

The problem is, why should anybody impose sanctions on slackers? Many authors seem to believe that imposing sanctions is just retaliation for harm imposed by the defector's failure to contribute to the collective good.[3,5,8,26] But whether this makes evolutionary sense depends crucially on the size of the cooperating groups. In small groups, collective benefits created by sanctioning can be enough to compensate the individual imposing the sanctions[3,8,26] and as a result people will seek to motivate behavior that benefits the group. Singh et al.[8] call this the "self-interested enforcement" hypothesis. As groups get larger, the incremental effect of a defector on any other individual in the group becomes smaller, and at some point, it no longer pays individuals to punish. Some additional motive besides increased benefits of cooperation has to be added to motivate the imposition of sanctions.

There have been a number of proposals. Punishment may be normative just like contributing to the collective good, and nonpunishers are sanctioned just like noncooperators.[11,27,28] This is the basis of self-sustaining institutions that are essential in large-scale, complex societies.[7,29] Participating in sanctioning may signal an otherwise hard to observe individual characteristic that is desirable in social partners, so that those who impose sanctions are benefited.[30,31] Participants may agree to allocate a big enough share of the benefits to a leader so that it is in the leader's interest to impose sanctions.[32] Or, noncooperators can be deprived of the protections that are normally due to members of the society, who are then victimized by others for selfish reasons.[33,34] In all these cases, cooperation has direct fitness benefits, but they are not usually thought to be mutualistic because they do not arise from the immediate benefits associated with participation.[21]

This is why scale is crucial. All of these mechanisms depend on singular aspects of human biology—language, exceptional cognitive ability, and cumulative cultural evolution. Small-scale cooperation can be sustained by the same mechanisms that give rise to cooperation among nonrelatives in other animals—reciprocity and self-interested sanctions. Large-scale cooperation requires something more. If there were no large-scale cooperation in the Pleistocene, it would be possible to believe that human psychology was shaped in a world of small-scale cooperation, and this psychology misfires to give rise to modern large-scale, inclusive fitness reducing cooperation. If foragers did cooperate on large-scales during the Pleistocene, additional, human-specific, mechanisms were necessary, and this leads to quite different proposals about the psychology of contemporary human cooperation.[35]

Exactly how large is large depends on how group size affects the returns from cooperation. If returns are additive, then the contribution of each individual is 1/(group size). So, if 50 people construct the drive line, a defector increases the total workload for the rest by 2%, and the workload of each individual by less than a tenth of a percent. If the defector learns a lesson, and so cooperates over many interactions, this will increase the return to punishment. However, to be significant, there would need to be many interactions. Increasing returns with group size will increase the effect of defection; decreasing returns will decrease it. Cooperation becomes large-scale when the incremental effect of a defector on the benefits of collective action is not large enough to make sanctions pay the individual imposing them. Zefferman and Mathew[1] set the limit at three dozen for warfare, and we will label as large-scale any collective action in excess of this threshold, keeping in mind that it depends on the costs and benefits of collective action.

3 | COMMUNAL HUNTING

There is considerable evidence that hundreds of individuals regularly cooperated in communal hunts in hunter-gatherer societies. Structures like drivelines, jumps, and corrals once dotted much of North America. In less-developed regions, ancient structures have survived and archaeologists can estimate the number of people involved in communal hunts. Moreover, historical accounts and early ethnography help us understand how Native Americans hunted communally. There is also historical and archaeological evidence for communal hunting in South America, Australia, and Africa, and archaeological evidence for communal hunting in Middle and Upper Paleolithic Europe and Middle Stone Age Africa.

3.1 | High latitude caribou hunting

Inuit and Athabascan speakers hunted caribou (*Rangifer tarandus*, called reindeer in Eurasia) communally throughout the North American Arctic. Caribou played an important role in the subsistence economy. The meat was an important food source, and caribou hides were essential for winter clothing and bedding.[36] An Inuit household required 30 hides every year, all harvested in the early fall.[37] The median population density for Inuit and northern Athabascan groups tabulated in Kelly[18] is 0.8 persons per 100 km^2, lower than the density of 89% of the groups listed there (see Table 1 for list of groups included).

Communal hunts mainly used one of two methods. The simplest was to mobilize enough people to surround a portion of a herd and drive the caribou into a lake or river where hunters waiting in kayaks or canoes could easily lance the swimming animals. Historical accounts indicate that such drives could employ hundreds of people.[38] Both Inuit and Athabaskans also built concentrating structures like drivelines and corrals. The tundra-living Inuit typically constructed drivelines made of rock cairns (called *inukshuk*) supplemented with organic materials like willow branches, turf, and hides. In the boreal forest, Athabaskans built substantial wood and brush fences often anchored to living trees.[38]

Historical accounts make it clear that Inuit and Indian groups built drivelines all across high latitude North America (Table 2). These structures varied from a few hundred meters to up to 50 km in length. Substantial investments of time and labor were required to build and maintain such drivelines, especially north of tree line where wood and stone often had to be carried long distances.[38] During hunts, large numbers of people were needed to drive herds along the drive lines. For example, in 1771, Thomas Hearne observed between 350 and 600 people operating a driveline near the Coppermine River.[38]

Only communal hunting could satisfy subsistence requirements before rifles were available.[39:41] Blehr[37] presents ethnographic evidence that solitary, non-communal hunts using bows had a low success rate. Communal hunts were not commonly observed by 20th century ethnographers probably because firearms made small-scale non-communal hunting more effective.

Communal caribou hunting has been going on for a long time in North America. Archaeologists have studied a number of drivelines on Victoria Island[40] some built by the Dorset people who lived there more than 800 years ago. A series of structures closely resembling drivelines used to hunt caribou in the Canadian Arctic have been found under Lake Huron. These would have been on a narrow isthmus crossing the lake from 7500 to 10,000 years ago.[41] Communal hunting at water crossings is also ancient. In the Canadian Barrenlands, water crossings have been used continuously for communal hunts for the last 6000 years. Some sites have more than 2 m of uninterrupted strata with tools and caribou bones.[38:279]

3.2 | Great Plains bison hunts

Until the middle of the 19th century, immense herds of bison (*Bison bison*) ranged over the plains and woodlands of much of North America. The densest populations were in the Great Plains, extending from northern Alberta to northern Mexico. These animals, colloquially called buffalo, are large—males weigh 544–907 kg and females 318–545 kg.[42]

Before the arrival of horses, Great Plains foragers used a variety of communal methods to drive bison into a confined space where they could be killed. The population densities for pedestrian foragers on the Great Plains is not known, but a sample of equestrian Plains people had a median density of 3 persons per 100 km^2, lower than 70% of the foraging groups listed in Kelly.[18] Bison were driven into arroyos which narrowed and steepened leading to ravines where hunters waited on the banks above, and they were also driven into deep snowdrifts and sand dunes where they were unable to escape. Where there was sufficient relief, bison were driven over cliffs; in places without relief, they were driven into corrals.[26:62–121, 27:215–288]

Communal hunts often involved hundreds of people. The number of animals butchered provides an estimate of the number of people involved in a hunt. For example, the Olsen Chubbuck site in eastern Colorado preserves the remains of a single event 8500 years ago in which about 200 *Bison occidentalis* (an extinct species that was 25% larger than *B. bison*) were driven into a ravine and killed. Wheat et al.[43] estimate that about 26,000 kg of flesh were harvested producing an estimate of 150 participants. There are many carefully excavated sites where the evidence indicates that more than 100 people were involved in communal hunts.[44] Historical accounts do not provide much detail about numbers but sometimes suggest that large numbers of people were engaged in hunts.[45]

Bison jumps also involved large numbers of people. For a jump to be successful, hunters had to stampede a large group of bison over a cliff edge.[46] Despite their great mass, bison are agile and can turn rapidly even when running at full speed.[47] This means that bison will plunge over a cliff only if propelled by a mass of bison stampeding behind them. Jack Brink's[46] beautifully detailed description of the site of Head-Smashed-In in southern Alberta provides a good example of

TABLE 2 A summary of historical accounts of communal caribou hunting in the North American Arctic taken from Gordon[38]

Location	Group	Method
Pt. Barrow	Tikkerarmiut	16 km willow drivelines
Anaktuvuk	Iñupiaq	8 km stone and willow driveline sending into water crossing
Kobuk	Noatagmiut	Drive into water crossing, driveline
NE Alaska	Nunamiut	300 people built log and post drivelines 8 km long
Mackenzie River	Mackenzie River Inuit	Encircled herd, drove into water
Central Arctic	Copper Inuit	Drove herd between *inukshuk*
Central Arctic	Netsilik	Drove herd into water using 3–5 km *inukshuk* drivelines
W. of Hudson Bay	Caribou Inuit	Drove herds into river using *inukshuk* drivelines "many kilometers long"
Southhampton Island	Sadlermiut	Drove herd into water using *inukshuk* driveline
Saputit Fjord	W, Greenland Inuit	Used 600 m drive fence to drive herd into water
Aasivissuit	W. Greenland Inuit	4 km long stone driveline channeled herd to hidden hunters
E. Alaska, Yukon	Chandalar, Peel Kutchin	2 km wide log corral with drivelines
Old Crow Flats	Vanta Kuchin	70–100 people, drivelines and water drives
Tanana & Yukon Rivers	Alaskan Tanana	48 km fence between Tanana and Yukon Rivers converging on corral. "Large investment in time and labor"
Upper Koyukuk River	Koyukon	30 km willow and post driveline with snares
Cook Inlet	Tanaina	16 km drives up to 6.4 km apart took 2 years to build
Eastern Yukon River	Han	Corrals and human surround requiring 200 people
S. of Artillery lakes	Yellowknife	Brush corrals up to 2 km diameter with 3–5 km drivelines
Fort Prince of Wales to Bloody Falls	Chipewyan Indians	350-600 people at 1.6 km brush corrals in July, 400 people 3-5 km brush fences in fall and winter
Thelon River	Chipewyan Indians	32 blinds and 3.3 km of drivelines operated by 200 people
S. of Thelon River	Chipewyan Indians	2 km wide pole and brush corral kept animals that fed 300–400 people for most of the winter
Slaughter & Faithful Isles Newfoundland	Beothuk	Wood fences up to 50 km long

how this worked. A system of long drivelines extended many kilometers behind the cliff. Small piles of stones marked the paths of the lines, and these were augmented with willow branches, hide, and other temporary additions, and backed by large numbers of men and women. The bison were persuaded to enter the converging drivelines, and proceed slowly toward the jump. Finally, when the herd was a few hundred meters from the jump, a mass of people converged behind the animals causing them to stampede over the cliff. This yielded tens of thousands of kilograms of meat and large amounts of fat and hides. It took many people to process this bounty fast enough to prevent spoilage. Hundreds of 500 kg animals had to be dragged down from the cliff face, rapidly skinned, defleshed and disarticulated to reduce the temperature of the carcass, and butchered into thin strips for drying.[46] Bones were broken into small pieces and boiled to extract bone grease, an important component of pemmican (a mixture of dried meat, fat, bone grease and berries that could be stored for months).[48] This was done in hide-lined pits heated by thousands of quartzite boiling stones carried from a riverbed 6 km away. (The nearby sandstone was too friable to be used in this way.) Brink[46] suggests that these tasks were organized assembly-line style with cooperative division of labor.

People have acquired bison using communal methods for as long as they have been in North America. Hundreds of sites have been identified.[44,49] The earliest date to the Clovis period, shortly after the arrival of people on the Great Plains.[25:217–219,27] Larger sites with the remains of more than 100 animals become common in the Folsom and Paleoindian periods about 12 ka, and very large communal hunts utilizing cliff jumps became common about 6000 years ago.[47:79] For example, people used the Head-Smashed-In jump from 5700 to about 700BP. Driver[48] argues that the invention of pemmican for storage and the arrival of the bow 2000 years ago made large-scale hunts more profitable. Communal hunting declined in the Southern Plains as people became semi-sedentary villagers who mixed farming and foraging.[42]

Many archaeologists believe that annual communal hunts played a crucial role in the yearly subsistence round.[42,44,46] Most large

TABLE 3 Ethnographic reports giving number of participants in five communal pronghorn hunts (cited in Jensen[55:75])

Ethnographic account	Numerical estimate	Basis of estimate
Saline Valley, A few families	12–24	Average family size
All Little Smoky Valley people	96	Census data
Antelope Valley, 40–50 men and women	40–50	Verbatim
All villages in Promontory Point area	47–50	Number families per village, size
Surprise Valley, 15-20 camps, maybe 100 men	90–120	Verbatim, average family size

communal hunts occurred in the northern plains where winters are long and severe. Frison and colleagues[50:284] argue that communal hunts occurred in the fall, and meat and fat were preserved as pemmican for use during the winter. Historical accounts suggest that communal fall harvests were common in the region, and archeological analyses of a number of sites are generally consistent with this model.[49:138] However, there is also evidence for communal hunts during the late winter and spring when bison were very lean, possibly because thinner hides were useful for making tipi covers.[46]

All of the evidence presented for Great Plains communal bison hunts precedes the arrival of horses and likely precedes the advent of agriculture. Horses appeared in the southern Great Plains about 1600. It is somewhat harder to date the beginning of agriculture in this region. Maize seems to have reached the NE plains about 500CE,[51] but it is possible that less productive cultivars were used earlier. Much of the evidence of communal hunting comes from sites that are dated to earlier than 500CE and from locations in the western Great Plains where low rainfall may have inhibited farming.

3.3 | Communal pronghorn hunts

Pronghorns (*Antilocarpa americana*) are small (50 kg) antelope-like herbivores that were common throughout the Great Plains and Great Basin until the late 19th century. They are extremely fast, able to reach speeds of 100 km per hour in short bursts, have excellent eyesight, and are accomplished broad-jumpers, but very poor at jumping vertically over obstacles. They form large herds in the winter and smaller groups in the spring.[52]

Native Americans hunted pronghorns throughout western North America, but they were most important in the Great Basin and Southwest.[53:34–36] Pronghorns were hunted individually by stalking, from behind blinds, and using disguises,[53:71–75] but the pronghorn's speed and wariness made this difficult,[54:34] and communal drives were common.[53:54, 55:28] Archaeological data indicate that some drives utilized large corrals and drift fences or drivelines.[56] The Whisky Flat pronghorn trap in western Nevada provides a well-studied example.[57] A fence 2.3 km long channeled the pronghorn into a large circular corral where they were shot by hunters armed with bows. The fence and corral were built from about 5000 juniper posts spaced about 50 cm apart and braced with stones. At other sites, corrals and fences were built using stone.[46,58] For example, the Fort Sage drift fences were built with dry stone masonry. When the fences were new, they were about 1 m high, 1 m thick, and 1.1 km long.[58]

TABLE 4 Ethnographic reports giving length of corrals and estimates of the number of participants in a number of communal pronghorn hunts (Jensen[55:75])

Area	Corral (m)	Material	Labor (h)	Participants
Deep Creek NV	207	Timber	69	6
Varede Valley NM	550	Timber	183	16
Yerington NV	864	Timber	288	24
Humbolt Sink NV	864	Sagebrush	288	24
Pyramid Lake NV	1413	Sagebrush	471	40
Morey NV	2513	Sagebrush	838	70
Surprise Valley #1 NV	2529	Sagebrush	843	70
Honey Lake NV	3141	Sagebrush	1047	88
Powder & Snake Rivers OR	3141	Sagebrush	1047	88
Surprise Valley #2 NV	3219	Brush	1073	89
Reese River NV	5026	Sagebrush	1674	140
Ruby Valley NV	5026	Sagebrush-pole	3351	280

Several lines of evidence suggest that communal pronghorn hunts involved sizable numbers of people. Five ethnographic sources report group sizes ranging from 18 to more than 100[55:77] (Table 3). A larger number of ethnographic sources (Table 4) and archaeological data (Figure 1) provides estimates of the size corrals used in communal hunts. The sizes of juniper traps in the ethnographic and archaeological samples roughly match.[55:116] Jensen[59:74] used the archaeological and ethnographic data to estimate the number of people involved in the construction of corrals, assuming that corrals

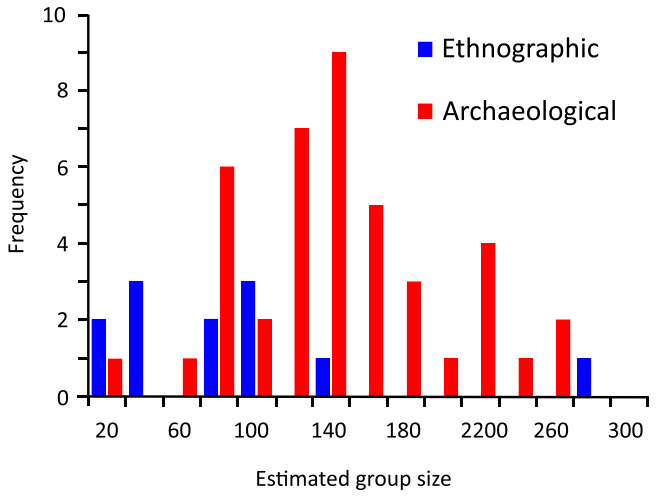


FIGURE 1 The distribution of group sizes estimated from the length of corrals, drift fences, and wings recorded ethnographically and measured in the archaeological record. Ethnographical data include both brush and post corrals while the archaeological data include only post corrals which require more labor to construct. Depopulation due to European contact may have also affected corral size. Group size estimates from Jensen[55:75,60]

were built in one 12-h day and that it took between 1 and 2 h per person to build each 1.5 m of fence. These corrals ranged in length from 66 to 1600 m, yielding estimates of group size that range from 6 to almost 300 individuals, with an average of about 78. Measured lengths for 43 archaeologically known corrals in northeastern Nevada range from 600 to 4475 m (data from Jensen[55:124] and McCabe et al[53:66]). According to Jensen's method, this corresponds to a mean group size of 143 people. These estimates do not include labor required to construct the wings. Stone corrals were more labor intensive. Hockett et al.[58] experimentally constructed a replica of the stone Fort Sage drift fence, and found that they could build 0.66 m of wall per person per hour, between two and six times slower than rate for juniper fences.

The Shoshone and Paiute peoples in the Great Basin were mobile foragers. The median population density of 15 groups listed in Kelly is of 4.75 persons per 100 km^2, about 40% of the median value of Kelly's[18] sample. The location of communal hunts and estimates of local population densities suggest the frequency of communal hunts was not affected by local population density.[61:34] People sometimes had to travel as far as 90 km to participate.[61:430] These communal hunts usually occurred in the fall,[53:54] and often lasted more than 2 weeks.

Pronghorns were an important component of the foraging economy in the Great Basin for many thousands of years. It seems likely that communal hunting dates as far back as 12,000 years ago.[50:291] The oldest dense bone beds that are consistent with mass kills associated with communal hunting, at Trapper's Point, Wyoming, date to the Archaic period (10–12 ka). However, the oldest evidence for a trap is at the Laidlaw site in Alberta which dates to about 3000 years ago.[47:140] It is uncertain how often these sites were utilized. Steward[54:33] argued that the large kills reduced herds so much that drives could only be held once a decade. However, Steward's observations were made during the early 20th century when herds had been depleted, and some authors think that when pronghorn densities were higher, drives were held annually.[55,62:26]

3.4 | Rocky Mountain alpine drivelines

Native Americans built stone drivelines to intercept big horn sheep and elk herds as they migrated eastward through passes over the Front Range of the Rocky Mountains.[63] Archaeologists have discovered 70 sites at elevations above 3000 m in Colorado that have stone blinds or walls that were used to aid hunting. The oldest sites date to 8000 years ago, and they became more common about 3000 years ago.[64] Some of these sites are very large. For example, an 8-km stone wall blocked Rollins Pass. Given the size and location of the site, LaBelle and Pelton[63] argue that hunters from multiple bands gathered to wait for sheep herds to arrive, encouraged the sheep to enter the drivelines, and then killed them. It is not certain sheep were the prey because there is little faunal material due to rapid weathering.

There is little doubt that mountain sheep were hunted communally at sites in Wyoming and Montana that date to the 18th century.[47:155–161, 50:306–307] These sites have the remains of substantial fences made of logs that average 30 cm in diameter and extend for hundreds of meters. The fences leaned inwards so that the agile sheep could not clamber over them.[50:305–306] George Frison[47:156] argues that "The effort needed to move, even over short distances, timbers the size of those used in constructing the traps soon convinces one that they were not constructed for the procurement of small numbers of animals." We don't know how far this practice extends back in time because these structures were constructed from perishable materials.

3.5 | Large-scale communal hunting outside of North America

3.5.1 | Southwest Asia

There is much archaeological evidence for drivelines in desert environments in southwestern Asia. These structures, called *kites*, typically consist of pairs of stone walls that converge on a fenced corral, much like the pronghorn traps used in the Great Basin. Hundreds of these structures have been detected using satellite imagery[65] in the Levant, Arabian Peninsula, Armenia, and central Asia. These very large stone structures were used in communal hunts of gazelle. A few of them have been dated to about 4000 BCE,[66,67] and may have been constructed by people living in farming and herding societies. However, they may also have been built and used by foragers. Until the first part of the 20th century, a foraging group called the Solubba lived throughout much of the Arabian Peninsula.[68]

They built kites up to 3 km in length, and used them to harvest gazelle, their main source of subsistence, in large communal hunts.[69]

3.5.2 | South America

There is evidence for communal hunting in Tierra del Fuego. The explorer-ethnographer Charles Furlong spent 2 years in Tierra del Fuego and Patagonia living with indigenous groups[70] including the Selk'nam (also called the Ona) a hunting and gathering group that specialized on hunting guanaco (*Lama guanicoe*) and lived at an estimated population density[71] of 4 persons per 100 km^2. These medium sized camelids aggregate in sizable groups in the fall and winter, and disperse into territorial one-male groups and bachelor herds in the spring and summer. The Selk'nam stalked guanacos individually, ambushed them using blinds, and hunted them communally. Furlong[72] describes two large-scale drives (Figure 2) in which the Selk'nam used natural features to concentrate and harvest substantial numbers of guanacos. This ethnographic account is supported by archaeological work in eastern Tierra del Fuego, the region occupied by the Selk'nam. Archaeologists excavated a site on a peninsula between two small lakes where they found the remains of a large number of mainly male guanacos.[73,74] The characteristics of the assemblage suggests it is the result of a single event consistent with the kind of communal hunt described by Furlong.

There are also two unpublished ethnographic reports of large-scale communal hunts in South America. Kim Hill (personal communication) observed more than 80 Ache foragers in Paraguay engaged in communal fishing, and among the Hiwi of Venezuela, Hill witnessed a communal hunt of semi-aquatic capybara that involved more than a dozen canoes, each carrying several men.

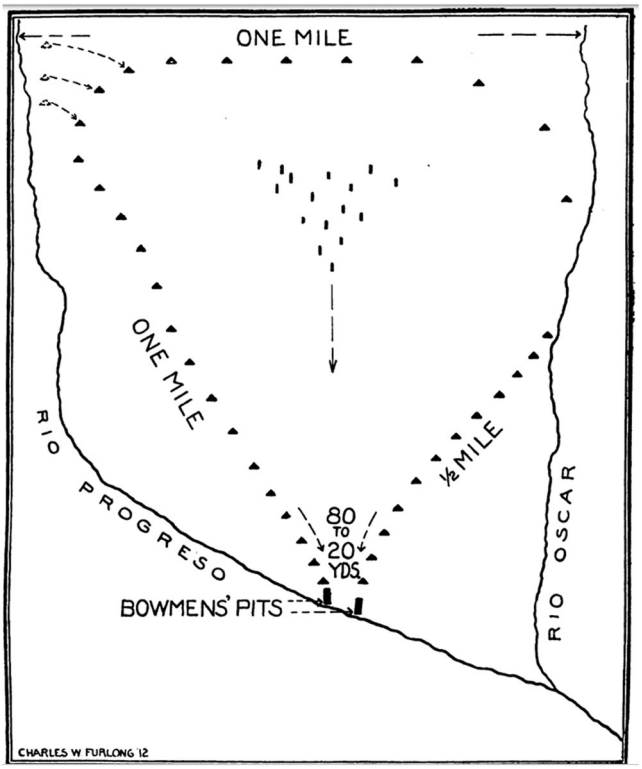


FIGURE 2 A diagram portraying communal guanaco hunting by the Selk'nam.[72] The vertical marks represent the guanaco, and the triangles Selk'nam foragers. There are 38 individuals pictured, but it is not clear whether this was meant to be numerically accurate as it would mean that the spacing between drivers was approximately 100 m

3.5.3 | Africa

Recently, a number of V-shaped stone walls, similar to those used to hunt pronghorns in the Great Basin have been discovered in the Nama Karoo region of South Africa.[75] These structures are difficult to date, but the presence of pottery and the absence of metal in the associated material, suggests that they were built in the last 2000 years, after the arrival of Koekhoe herders in the area, but before the arrival of Bantu speakers. In addition, the stonework resembles structures made in the region before the Bantu arrived. Lombard and Badenhorst [75] argue that these structures were used by /Xam San foragers to hunt springbok, a small antelope. Large herds of springbok migrated seasonally in response to changing availability of water. Ethnohistorical research in the early 20th century indicates that springbok played a crucial role in the /Xam San foraging economy and that the /Xam San had a deep knowledge of springbok behavior. Lombard and Badenhorst[75] suggest that during seasonal migrations several bands of /Xam San camped and worked the drive lines together. The largest of these structures is about 300 m in length so these groups need not have been extremely large. Rock art also suggests that southern African foragers may have used nets in communal hunts.[76]

Congo basin foragers also engage in communal net hunting.[77] Individually owned nets are combined to form a large circular or semi-circular barrier, and animals, principally duiker, are driven into the nets. Both men and women own nets and participate in these hunts; net owners own the game caught in their nets. The largest groups involved more than 60 participants, but many were smaller and in all cases, hunters were drawn from a single residential band. Kelly's estimate of the population density for one Congo basin group, the Mbuti,[18] is 17 persons per 100 km^2.

3.5.4 | Australia

Aboriginal foragers in Australia hunted a number of species communally, including kangaroos, wallabies, emus and waterfowl. There are some reports of the use of V-shaped wood and brush drivelines to hunt wallabies. In one case, the wings were 0.4 km long.[78:117] Aboriginal foragers also used various kinds of nets as concentrating devices in communal hunts. For large terrestrial prey, like kangaroos and emus, a number of loosely woven linear nets with a combined length of about 1 km were arranged to form a large

semi-circle. One group of hunters held the nets, while the rest, often including men, women and children would drive the animals toward them. Resulting yields could be very large.[79,80]

Much time and effort went into production of the large nets used in communal drives. For example, one early account[80] reports that a 7.2 × 4.6 m kangaroo net took a local camp 3 weeks to make. This is consistent with modern experiments. A 52 × 0.8 m emu net in the South Australian Museum contains 350 m of 5 mm cordage and would have taken 4 weeks to construct.[79] These estimates do not include the time and effort needed to acquire and process the fiber and spin it into cordage. Nets could be curated, and so each hunt didn't require a whole new construction.

Communal hunts in Australia were often associated with large seasonal gatherings that brought together people from many different residential groups. Historical accounts speak of "whole tribes" gathering. Sometimes people gathered to hunt, but other times people gathered for ceremonial reasons or to harvest seasonally available plant resources. For example, groups of 3000 people gathered to harvest bunya fruits in Queensland.[79] Communal hunts were important for large gatherings because they were capable of producing sizable amounts of meat to prolong the time large numbers could aggregate.

3.6 | Communal hunting in the Pleistocene

So far, we have presented examples of communal hunting that occurred during the Holocene among societies where food production was rare or absent. They show that large-scale communal foraging occurs among mobile foragers living at low population densities, and augment the picture of foraging life provided by ethnographic work on Holocene foragers. However, it is clearly of great interest to know whether Pleistocene foragers also participated in large-scale communal hunts. Two lines of evidence suggest that this is the case.

First, archaeological studies suggest that communal foraging dates back to the lower Paleolithic (400 ka) and that large-scale drives occurred in Europe and Africa beginning about 124 ka. The oldest evidence for communal foraging comes from Gran Dolina cave in the Sierra de Atapuerca, Spain.[81] A dense accumulation of bison bones with butchery marks along with stone tools indicates that hominins killed and processed the animals in quantity. The age profile of the bison and tooth wear patterns indicate that these bones were the result of least two mass kills. This site dates to about 400 ka and so the hunters were likely *Homo heidelbergensis* or Neanderthals. Rodriguez-Hidalgo et al conclude, "… our data on mortality, seasonality, skeletal profiles, taxonomic diversity and taphonomy support at least two overlapping mass predation events in which a large number of people had to participate."[81] It is difficult to know how large this number might have been. The minimum number of individuals (MNI) found at the site is 60, which, using the same the method used for Olsen-Chubbuck yields an estimate of 25 hunters. The MNI is known to underestimate the actual number of individuals, sometimes quite substantially. It is also possible that there were more than two mass killing events.

At a number of younger sites there is stronger evidence for large-scale communal hunting.[82] The Middle Paleolithic site of Salzgitter Lebensted in Germany provides a good example. This site dates to about 54 ka and preserves the remains of a large number of reindeer, probably killed in a single hunt.[83] Adult male bones predominate and this reflects reindeer herd composition before the fall rut. The bones of larger males were intensively processed while those of smaller animals were skinned, but not processed for marrow. Intensive processing is consistent with the fact that reindeer males are in best condition during the fall. The site is located in a narrow valley close to where it opens up onto a wider flood plain suggesting that Neanderthals drove the reindeer into the narrowing valley and then killed them, much like arroyo hunts of bison in North America.[82,83] White and Schreve[83] suggest that the width of the flood plain would have required "every member of the society" to participate in the drive. The MNI for reindeer at this site is 196. Reindeer are about 20% of the weight of bison yielding a lower bound estimate of roughly 35 hunters. Communal hunts are also thought to have taken place at a number of MIS 5 (120–80 ka) sites where the remains of only a single species are found, including Les Pradelles and Facies 2[84] (reindeer), Mauran[83,84] (bison), Soultré,[85] and Zwoleń[83] (horses).

There is also suggestive evidence for communal foraging in East Africa during the Middle Stone Age (MSA). There are many archaeological sites in East Africa with MSA tools, but only a handful have faunal assemblages large enough to allow inferences about foraging behavior.[59] Two MSA sites in Kenya, Lukenya Hill[86] (GvJm-22 and GvJm-46) and Bovid Hill at Rusinga Island,[59] provide evidence for communal hunting. The Bovid Hill site is a dense assemblage of bones of an extinct antelope (*Rusingoryx atopocranion*) closely related to contemporary wildebeest and tools that date to 35–100 ka. Based on the age profile of the bones, the presence of stone tool marks on the bones, and the geology of the site, Jenkins and her coauthors conclude that the site results from a single, large-scale collective hunt in which the antelope were driven into a seasonal stream and killed.[59] However, they acknowledge that a long-term accumulation cannot be excluded with certainty. Similarly, the assemblage at Lukenya Hill is consistent with communal hunting, but other explanations are possible.[86]

A second line of evidence comes from cave paintings at Lascaux and Altamira. Thomas Kehoe,[87] an authority on Great Plains bison hunts, has argued that these images contain elements that picture drivelines and communal hunts. At Lascaux, one of the famous "Chinese" horses stands below a fence-like structure, and on either side of the horse are feathery leaves like those used to augment drivelines in North America (Figure 3). Other images contain lines of dots that may represent lines of stone cairns used in drivelines. For example, on the Axial Wall at Lascaux, a horse and a reindeer run parallel to lines of dots, and one of these ends in a square box perhaps indicating a corral. Many other images contain features that could represent drivelines.

FIGURE 3 One of the "Chinese" horses at Lascaux showing a fence that Kehoe[87] argues represents a corral, and feathers or leaves like those used to lie drivelines in North America

4 | FISH TRAPS AND WEIRS

Coastal and riparian foragers in Australia constructed fish traps. Most of these were stone walls that enclosed an area adjacent to the shore. The tops of these walls were underwater at high tide, but above the water line at low tide. Fish swam in when the tide was in, and were then trapped when the tide receded. These kinds of traps were very common in some regions. For example, there were more than 39 traps on Sweers and Betnick Islands in the Gulf of Carpentaria, or about one trap for every 0.4 km of coastline. A survey of fish traps in Queensland and the Gulf of Carpentaria[88] lists 124 structures. Lengths can be estimated for 24 of these structures, and they varied from less than 10 m to more than 700 m in length with a mean length of about 150 m. The oldest traps in this area date to about 7500 years BP.

Substantial labor was required to construct these coastal traps. Many traps were constructed from rock carried from the bush. Rowland and Ulm[88] estimate that each meter of wall required about 500 kg of stone. Since the traps averaged about 150 meters in length, 75,000 kg of stone had to be carried from the bush to the coast, on average, for each trap. They assume that one person could carry 35 kg of stone per trip. This means that the construction of a trap required about 2150 trips. The population densities in this part of Australia were relatively high with a median of 52 persons[18] per 100 km^2.

Weirs were used to harvest silver eels throughout southeastern Australia.[89:39–41] During the eel migration, 800–1000 people gathered at the most productive sites.[90] The oldest of these traps date to 6600 BP.[91] Aboriginal people constructed two large facilities to aid in harvesting eels. Near Mount William, a weir redirected the river into a large maze of trenches that covered about 6 hectares and involved thousands of meters of trenches.[90] At Toolondo, Aboriginal people built a 2.5 km long canal, 2.5 m wide and 1 m deep, which linked two natural swamps. The canal increased eel habitat because it linked one of the swamps to the ocean where the eels breed.[90] Kelly[18] list densities for two groups in this area with a median population density of 24 persons per 100 km^2.

5 | INVESTMENTS IN HABITAT IMPROVEMENT

People in many foraging societies undertake activities that increase the productivity of the local habitat.[60] For example, Native American groups along the Mississippi and the Colorado Rivers sowed the seeds of wild grasses on mudflats exposed after seasonal floods. Other groups transplanted tubers and fruit trees. The Aché of Paraguay cut down trees and returned months later to harvest beetle larvae from the dead tree trunks.[92] Any member of the Aché who happened by could have benefited. The Owens Valley Paiute in California built diversion dams and canals to irrigate land and increase the growth of water-loving plants with edible roots. The largest of these irrigation areas covered about 10 km^2 and was fed by canals that were several kilometers long.[93] The Aché and the Owens Valley Paiute lived at about 19 persons[18] per 100 km^2.

In many places, people use fire to create more productive plant communities. Fire shifts nutrients from old inedible plants and plant parts to fresh growth that herbivores can utilize. For example, the Mardu, an Aboriginal group living in Australia's Western Desert, set fires in grasslands during the winter season that increased foraging returns for small game like monitor lizards.[94] The environmental changes induced by burning may be public goods because the people who manage the burning experience costs, and the benefits of their efforts are shared by everyone in the community. Burning differs from building weirs, drive lines, and canals because it is relatively easy to set and manage a fire. Thus, it is possible that the individuals who set the fires and manage the burning gain enough benefits themselves to offset their costs.[94]

6 | WARFARE

There has been much debate about whether warfare occurs among hunter-gatherers.[1:95–97] Comparative data[95] make it clear that lethal violence was common among foragers, and much of the debate is about what constitutes warfare. Here we focus on whether foragers engaged in intergroup conflict in groups large enough to create a collective action problem, very roughly three dozen warriors on a side.[1] Twentieth century studies of foraging groups support the view that large-scale conflict is rare among hunter-gatherers. However, there are good reasons to suspect that these societies are not representative of our evolutionary past because during the 20th century many foraging groups are surrounded by more powerful farmers or herders and are often embedded in states that suppress warfare.[96]

We present data on warfare among foragers who lived among foragers and were not subject to control by a state. We believe that these historical accounts support three claims about forager warfare. First, conflict occurred on all scales ranging from small-scale raids to battles involving hundreds of warriors on each side. Second, large-scale conflict caused many casualties and much mortality. Third, larger scale conflict was more common between members of

different ethnolinguistic groups than within such groups. Ethnolinguistic groups typically numbered from 500 to a few thousand, indicating the scale of cooperation was larger than the size of war parties.

The data is mainly ethnohistorical. There is ample data from bioarcheology indicating that violence was common among foragers, but not reliable quantitative estimates of how many people were involved on each side. Most military weapons can also be used for hunting, and shields and armor were made from perishable materials. Mobile groups, including mobile foragers, rarely construct masonry fortifications.[97] Rare fortifications and rock art provide some evidence, but for the most part we have to rely on the accounts of travelers and the memories of informants. The best data come from Australia, a continent of foragers until the arrival of Europeans at the beginning of the nineteenth century, but there are also useful data from western and arctic North America, places where foragers predominated until the middle of the 19th century.

6.1 | Australia

Until the beginning of the 19th century, Australia was occupied only by hunter-gatherers, and there is considerable evidence that they sometimes fought large-scale battles. William Buckley, a young man transported to Australia in 1803, escaped and lived with an Aboriginal group for most of the next 35 years. His account is saturated with interpersonal violence on all scales, including murder, small-scale raids, and large battles in which whole tribes were mobilized. In one conflict, 300 men from an enemy tribe, attacked his group leading to a bloody fight.[98:1011] After 2 h, the fighting ended, and during the night, the other tribe withdrew from the area. Buckley's tribe followed them, and made a surprise attack on their camp. They fled, leaving three dead.[98:1011–1024] Buckley describes several other large-scale intertribal conflicts with substantial mortality. When he was younger, Buckley fought with the British army, and was seriously injured in battle. He found the hand-to-hand combat he witnessed among Aborigines "much more frightful" than European warfare.

More scholarly accounts confirm Buckley's picture—intergroup conflict was common, war parties were sometimes large, and death rates were substantial throughout Aboriginal Australia.[99] Some of the larger scale conflicts were prearranged ritualized battles, but others were raids or pitched battles in which many people were wounded or killed.[100–102] According to Basedow,[103:183] whole tribes frequently engaged in warfare in central Australia, ambushing their foes with the goal of massacring them. Strehlow[104] describes a conflict in which a war chief assembled a large party from the Matunara area to ambush another group with the goal of killing everyone so that there would be no witnesses. An evening ambush was successful and men, women, and children were slaughtered. W. L. Warner[105:457] begins a paper devoted to Murngin warfare as follows: "Warfare is one of the most important social activities of the Murngin people and the surrounding tribes." The Murngin recognize three types of large-scale conflict: *maringo*, a night raid in which an entire camp is surrounded; *milwerangel*, an open, formalized fight between at least two groups; and *gaingar* a large-scale regional conflict in which several tribes are involved. Maringo and gaingar conflicts led to large numbers of casualties.[105:458] Note that Murngin behavior may have been affected by contact with Indonesians and conflict with British settlers starting in the late 19th century. Murngin population density was 5 persons[18] per 100 km^2. Accounts of battles with large number of casualties also provide evidence for large-scale conflict. Gat[99] describes an attack on the Finke River in 1875 in which 80 to 100 men, women, and children were killed. Similarly, Meggit[106:42] describes a conflict in the Western Desert over access to wells. In a pitched battle more than 20 warriors on each side died. Population density in the latter group was one person[18] per 100 km^2. Unless casualty rates were extremely high in these battles, sizable numbers of warriors must have been involved.

Rock art suggests that large-scale conflict is at least 6000 years old in Arnhemland. During the "Simple Figures" period (>6000 BP) there are many rock art sites at which groups of thin, stick-like human figures are shown opposing each other. In many, boomerangs and spears fly overhead, and some figures appear to drop their weapons.[107] In one spectacular case, there are 68 figures in two opposing groups.

6.2 | North America

6.2.1 | Pre-horse, pre-gun Plains Indians warfare

There is ethnohistorical evidence that Great Plains and Great Basin groups engaged in large-scale infantry conflict before the arrival of horses. During the equestrian period, Great Plains groups had a median density of 3 persons 100 km^2, and Great Basin foragers had a median population density of four persons[18] per 100 km^2. At the time of first contact with Europeans, various Numic speaking groups on the eastern periphery of the Great Basin were engaged in persistent military conflict with non-Numic groups, and these conflicts drove the Numic expansion.[108] The preferred military tactic was to assemble a large war party, sneak up on an enemy encampment during the night, and attack at dawn. Camps had 10–30 families, and attacking war parties would need to be large enough to achieve overwhelming force.[109,110:1–2] In one battle between the Shoshone and the Blackfoot that occurred in 1726, the Blackfoot faction numbered 350 warriors.[111:34–35,112:431]

6.2.2 | Modoc warfare

The Modoc lived in the plateau country of northeastern California and southern Oregon. They were semi-sedentary hunter-gathers. Horses were used for transport, but not for hunting and didn't play the central role that they did in Great Plains groups.[113:181–200] Modoc society was more sedentary than the nomadic foragers of the Great

Basin, but lacked the hierarchy and tribal institutions seen in many other groups in California and the Northwest Coast.

The Modoc frequently fought with their neighbors over territorial incursions, retaliation for past attacks, and to capture slaves. Men with reputations as formidable warriors organized raiding parties of 10–100 warriors. Participation was voluntary. Raiders typically traveled about 50 km with the goal of launching a surprise attack on an enemy village. Battles were short and bloody. Horses seem to have played little role in these raids.[113:134–145] The Modoc mainly raided Pit River tribes, and never raided other Modoc villages.

6.2.3 | Fortifications in the Interior Northwest

Defensive fortifications are a classic example of a public good that provides a benefit to anyone who takes shelter, regardless of whether they contributed to their construction. An absence of fortifications in the archaeological record is not evidence for the absence of warfare because construction of fortifications often does not pay even where warfare is common. However, the presence of large fortifications does provide evidence for warfare.

In the plateau region of eastern Washington and Oregon there is ethnohistorical and archaeological evidence for large fortifications.[114] For example, a Numic speaking group (probably Northern Paiute) living on the Crooked River in eastern Oregon created a fortification that could contain 60 or 70 fighters.[114] Farther north, Teit and Boas[115:117–118] describe the fortifications built by Cour d'Alene and Thompson peoples. Stockades were circular structures built from vertical wooden poles about 9 m high with loopholes that allowed archers to shoot arrows out. Bunkers were rectangular structures built from horizontally laid logs banked with earth to create walls about 2 m high. Like the Modoc, these peoples were semi-sedentary foragers who lived at low population density largely subsisting on aquatic resources and deer. Archaeological data suggest that fortifications predate the arrival of Europeans and horses.[114]

6.2.4 | Iñupiaq in northwestern Alaska

During the first half of the 19th century, Iñupiaq groups in western Alaska conducted regular large-scale warfare against members of other Iñupiaq groups, Athabaskan speakers to the east, and Chukchi people on the Asian side of the Bering Strait. Our knowledge of these events comes from Iñupiaq ethnohistory collected by the anthropologist Ernest "Tiger" Burch[116] who interviewed Iñupiaq elders about 19th century Iñupiaq life, conflicts, and alliances. By collecting and collating many accounts of the same events, he was able to create a picture of Iñupiaq life before extensive contact with Europeans and North Americans.

The Iñupiaq economy was based on fishing and hunting large game, mainly caribou and marine mammals. They lived in villages during the fall and winter, and then moved to fishing and hunting camps in the spring and summer. According to Burch, population densities were about 5.5 persons per 100 km^2, at the low end of the forager range documented by Kelly.[18] Villages were mainly quite small. In the NANA region around Kotzebue Sound that was the focus of Burch's research, they ranged in size from 8 to 160 people, but 80% had less than 32 people.[116:70] Some villages outside of this region were larger. People were collected into territorial groups that Burch refers to as nations. In the NANA region there were 10 nations with an average population size of 470 people and average territory size of 8600 km^2.[116:7]

Burch[116:140] compiled accounts of 77 raids and battles that occurred in the first half of the 19th century. Like other foraging groups, attackers preferred surprise nighttime raids. These occurred mainly in the fall because low temperatures kept people inside at night, frozen rivers made travel easier, and the lack of snow made it difficult to track retreating raiders. Raiding parties armed with bows, lances, and knives traveled long distances, sometimes as much as 300 km each way, and never less than 80 km.[116:80] Villages were centered around a community hall or *qargi* where men spent much of their evenings. Attackers hoped to surprise all the men in the *qargi* and kill them as they exited. If the raid was successful, attackers killed everyone in the village. Sometimes young women were taken as slaves, but usually they were raped, tortured, and killed[116:104]

The threat of raids prompted people to take defensive action. Some villages had defensive stockades, and others were surrounded by fields of sharpened caribou bones driven into the ground, much like the punji sticks used by Viet Cong fighters. They also built escape tunnels in the *qargi*. Raiders were sometimes detected and ambushed themselves.[116:71–72] Small villages could be attacked by raiding parties numbering 10 or 20 warriors. However, Iñupiaq sometimes attacked larger villages, and this required much larger raiding parties. Although it was more difficult to feed a large war party during travel and larger villages were harder to approach undetected, raids on large villages did occur.[116:102]

Burch[116:103] gives detailed accounts of several large raids. For example, a party of 350–400 men attacked a village of about 600 people at Point Hope, just outside the NANA region. The attackers wore camouflaged clothing and came bare-footed to minimize the chance their approach would be heard. However, they were spotted, and the Point Hope villagers poured out and attacked the raiders who retreated onto a field studded with caribou spikes rendering many of them helpless. Their comrades fled leaving the injured to be killed by the defenders.[116:103–104]

Sometimes the Iñupiaq engaged in large open battles. This could occur when a large raiding party was detected or when the animosity between two nations had reached a boiling point.[116:104–105] In open battles, the two sides formed battle lines with the best archers on the flanks. Then, the two sides would exchange archery fire, sometimes for hours. If one side was getting the worst of it, they might flee, experiencing serious casualties. Sometimes the two sides would close and engage in hand to hand combat armed with lances and knives.

6.3 | Peacemaking and alliance formation

We don't have the space to treat this topic in the detail of the preceding ones, but we think it important to make the point that people in small-scale foraging societies can cooperate on cross-cultural scales. Small-scale societies seek to reduce the harm caused by warfare and realize the benefits of cross-cultural trade. They are capable of operating a fairly sophisticated "foreign policy" aided in part by cross-cultural institutions such as law and money.

In his classic book on warfare and diplomacy Thomas Schelling[117] wrote "The power to hurt is bargaining power. To exploit it is diplomacy—vicious diplomacy but diplomacy." He described the complex strategies that modern nations use to exploit the coercive power of arms to gain advantages over other nations, ideally by coercion and deterrence short of actual warfare. Warfare is costly. People are killed and injured, property is destroyed, and survivors experience anxiety, suffering, and grief. The weak can drive up the costs of victory for the strong. As Curtin[118] notes in his classic book on cross-cultural trade, traders only operate if they are reasonably certain that they and their goods are safe from violence and theft. Open warfare also disrupts trade and other productive intersocietal activities. Peace favors trade and makes possible the formation of alliances that can help deter and coerce rivals. Peace and alliances require a polity to credibly commit to policy that prevents behavior that would disturb the peace. Local groups can't act as bandits and steal from peaceful traders. Ambitious warriors can't conduct free-lance raids against neighboring societies who are party to a peace. The same basic collective action problem that has to be solved for a polity to make war has to be solved to make peace and alliances. A frequent assumption is our Pleistocene ancestors lived in small, mutually hostile bands.[119] We think the historical, archaeological and ethnographic evidence suggests that diplomacy on the part of such societies can hold together large alliances and maintain peace over large areas.

Western North America has many examples of peace and trade. Northern California was entirely occupied by hunter-gatherers at the time of European conquest in the middle of the 19th century. In the early 20th century, ethnographers were able to interview elderly people with some first-hand experience with their still-intact societies and who had substantial second-hand knowledge from people of their parents' and grandparents' generations. Individual ethnographies based on such interviews have limitations, but the large number of groups for which ethnographies are available give a fairly comprehensive portrait of aboriginal life.[120–122] Furthermore, the archaeological record in Northern California is relatively good so that we have a general idea about the prehistory of trade and warfare.[123,124] However, these groups lived at much higher population densities (180 persons per 100 km^2 for the Yurok, for example[18]) than most foragers and had substantial differences in wealth, so they may not be representative of Pleistocene foragers.[18]

Peace-making in Northern California was similar across the region. Northern California peoples tended to be suspicious of others, especially strangers and foreigners. They accumulated property, guarded it zealously, were jealous of people richer than themselves, and energetically pursued grievances. If possible, they would enlist relatives and allies in their quarrels. At the same time everyone recognized that this mind set was a recipe for costly feuds and wars. Third parties could get hurt and hostilities disrupted normal social and economic life. Hence, a set of rules evolved that parties not directly involved in a dispute could use to encourage hotheads to calm down and settle their differences. The basic principle is that people own their own fights. This is most formalized in the Yurok-Hupa-Karok legal system.[120] These three tribes live in the northwest corner of California and the southwest corner of Oregon. The first principle of this system is that all rights, claims, possessions and privileges are individual, not collective. Families and communities have no standing in the system. The second is that there is no legitimate punishment. Any punishment by an individual is an offense itself. The third principle is that any injury or offense can be valued in material terms. Immaterial (insults) and material (theft) transgressions can both be valued. Aggrieved individuals shunned those with whom they had a dispute. Shunning also affected relatives and friends of the shunned individual, disrupting the local economy and social life. Aggrieved individuals generally fell under pressure to resolve the dispute through negotiations aided by a legally knowledgeable "judge" who acted as a mediator. Once the two individuals reach a mutually agreeable compensation and the agreed upon goods have been exchanged, the grievances were considered to be settled. To harbor any detectable grudge or lingering ill will would be a fresh offense. Compensation was often substantial and individuals could be in debt for years before meeting their full obligation.

These concepts of individual responsibility and compensation for offenses were widespread in Northern California, but were not as fully formalized as in the Yurok-Hupa-Karok cluster. In other societies senior male chiefs were recognized, and had the power to encourage settlements, but the autonomy of individuals tended to be substantial. This system meant that aggrieved parties could not recruit friends or kin to retaliate directly for offenses committed against them, and this prevented individual conflicts from expanding into collective feuds. Bettinger[122] argues that over the past few centuries, Northern California societies evolved from patrilineal clans in which chiefs had considerable power to a more individualistic system that reached its extreme with the Yurok-Hupa-Karok.

The same principles that applied to within-community dispute settlement applied to between-community grievances, such as trespass on a neighboring group's territory. Goldschmidt[125] describes the situation of the Nomlaki, the Inner Coast Range branch of the Central Wintun. The usual causes of intertribal conflict were transgressions on property rights of individuals (i.e., over a woman) or groups (i.e., encroachment on another tribe's territory). In the former case, attempts were made to settle the affair by negotiated compensation of the aggrieved parties, as in within-community conflicts. The latter type of transgression generally resulted in a war party from the aggrieved group being organized. Many men in Northern California groups trained as warriors, but there were no formal war leaders. Tactics included surprise raids and short pitched

battles. Older men accompanied the warriors, and served as peacemakers. Peacemakers exhorted warriors to consider settlement of the dispute instead of fighting. This might work or the opposing parties might be too angry to settle immediately and fighting would ensue. The desire of warriors to continue fighting was undermined by the knowledge that peace would have to be negotiated eventually and the more killing, the more costly the compensation. The contending parties brought goods to use in compensation in expectation that the dispute would be resolved on the day of the battle. Fighting usually stopped after one or a few casualties and compensation for the original transgression was negotiated among the relevant parties. The same was true for the injuries sustained in the fight itself. Once compensations were worked out, remaining goods and money were traded.

Thus, although Northern California tribes were wary of strangers from other groups, active hostilities were infrequent, and casualties usually few. In times of peace, those with goods to trade could approach a village of another tribe, announce themselves, and request to speak to their trade partners. Molesting, robbing, or killing such individuals would constitute a grievance that eventually would have to be compensated, perhaps after a costly war. So, traders could feel reasonably safe in conducting their business.

California was dense with trade routes.[126] Most tribes traded with their neighbors for a wide variety of goods. For example, the Coast Range Nomlaki had a surplus of acorns and traded them to their Valley floor neighbors for fish caught in the Sacramento River. Localized sources of important items like salt motivated trade in everyday necessities between neighboring groups. There were also valuables that moved long distances, such as high-quality obsidian, marine shells, shell bead money, and exotic items from the Pueblo region. These were almost always relayed from one trader to the next, no one trader moving more than a few kilometers. Thus, both subsistence and the prestige economies benefitted from trade.

Archaeologists recover shell beads and stone used to make tools and analyses of these materials allow them to reconstruct trade networks deep in time. Hughes and Bennyhoff[123] describe the history of trade in shell beads for California and the Great Basin. Pacific Coast shells moved in considerable quantity across the Sierra Nevada Mountains, especially in the time period between 4000 and 2200 years before present, supported by four distinct trade networks. Trade networks in Aboriginal Australia were as extensive as in Western North America and in the north included exchanges with maritime voyagers from New Guinea and Indonesia.[127]

The technology and the art of the Upper Paleolithic people of the last ice age suggest that they were behaviorally modern in important respects. Whether the similarity to ethnographically known people extends to social organization is a harder problem. One of the best understood Upper Paleolithic cultural phenomena is the Gravettian Culture that occupied all of Europe from about 30 to 21 ka.[128] There was considerable stylistic uniformity across the whole region from the Urals to the Atlantic and from the ice margins to the Mediterranean. As in Western North America long distance movement of stone used to make tools and marine shells testifies to trade system that spanned the continent.[129] The ethnic frontiers where conflict was most likely appear to have been far to the east of France and Spain beyond the Urals and south of the Ukraine. Gamble[130] argued that the stylistic similarity of the Gravettian across such a large area could only be maintained by open interaction networks in which ideas and probably people could flow with little hindrance. Stone and bone plaques elaborately marked with rows of small pits have been interpreted as calendrical devices used to coordinate the movement of dispersed groups.[131] Gravettian burials indicate significant inequality in status[20] as if, at least in some circumstances, strong leadership roles existed perhaps for organizing communal hunts, feasting, or long-distance trade.

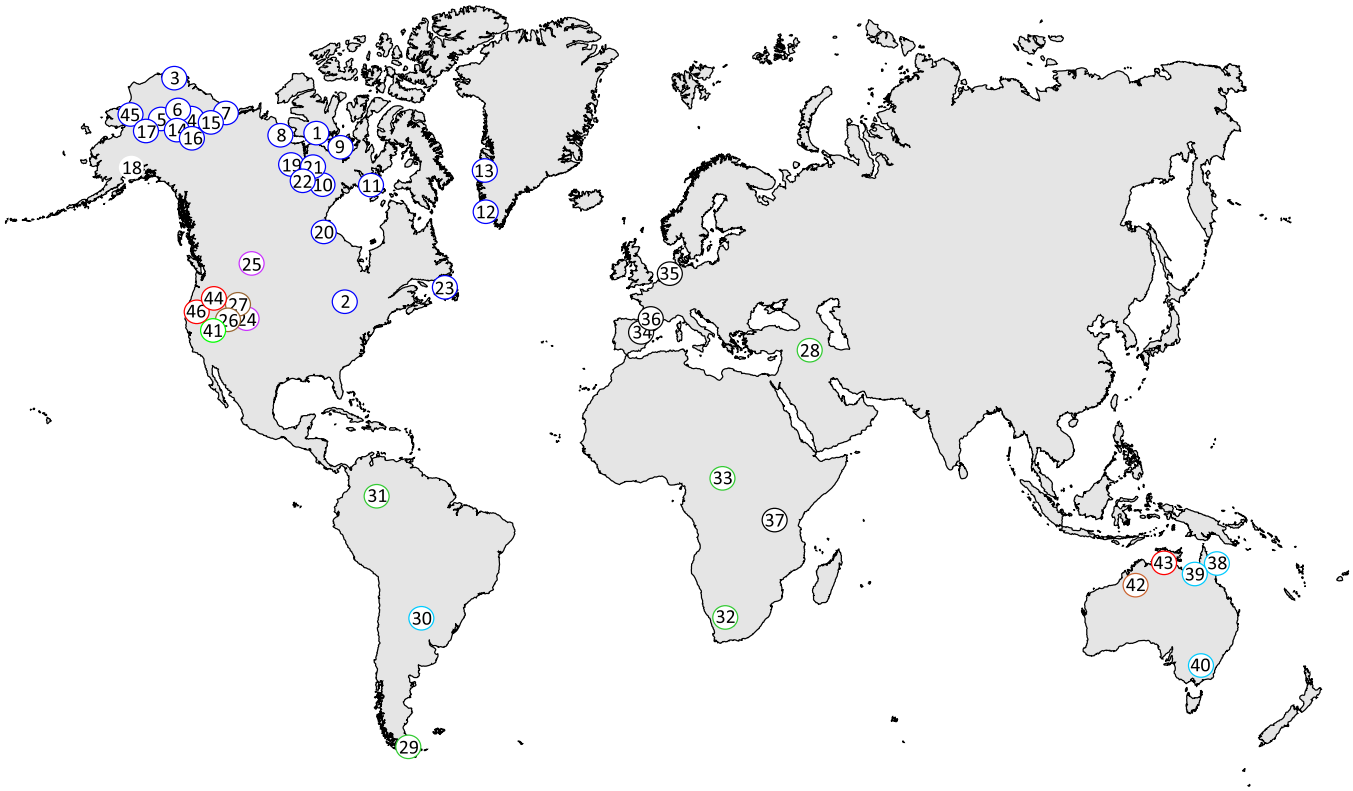
7 | DISCUSSION

Hunter gatherer groups observed over the last century vary widely in social complexity. At one end of the continuum, there are “simple” foragers who live in small mobile egalitarian bands at low population density, and at the other end of the continuum there are “complex” foragers who live in sedentary groups with sizable permanent settlements and substantial social hierarchy. Holocene climates, new technologies, and the influence of food producing neighbors mean that Holocene foragers likely differ from Pleistocene people in important ways. Many authors think that only societies on the simple end of the continuum provide a useful model for the ancestral societies in which human physiology and psychology evolved. Such groups live in small egalitarian bands in which food is widely shared, sick and injured are cared for, and other kinds of mutually beneficial small-scale cooperation are common. Many scholars[2–10] believe that large-scale collective action is rare among simple foragers, and could have not had much effect on the evolution of our cooperative psychology.

The evidence we have reviewed indicates that Holocene hunter-gatherers cooperated on tribal scales to produce collective goods. Sometimes, hundreds of people worked together to build drivelines and harvest game, construct substantial irrigation works, make shared habitat improvements, participate in large-scale conflicts, and maintain peace within large groups. Much of this occurred in groups living at relatively low population densities at the simple end of the continuum of social complexity. Given the logistical difficulties of assembling large groups in such low-density populations, fairly sophisticated planning and coordination must have been required. In some cases, such cooperation occurred regularly, and was an important component of subsistence economies. Evidence for large-scale collective action is geographically widespread, coming from most parts of the world where foragers maintained a substantial presence during the Holocene (Figure 4). Of course, Holocene foragers are not human fossils, and likely differ from Pleistocene hominin populations in which the psychological machinery that underpins human cooperation evolved. However, this evidence does indicate that the economics of mobile hunting and gathering do not

preclude large-scale cooperation even in mobile societies in which people lived in small groups most of the year.

There is also archaeological evidence for large-scale cooperation in middle Pleistocene societies in Europe and Africa. Faunal assemblages at a number of Middle Paleolithic sites in Europe suggest that Neanderthals engaged in communal hunting of large mammals, reindeer, bison, and horses, and evidence from two MSA sites in East Africa provide circumstantial evidence for communal foraging. Finally, Upper Paleolithic cave art seems to portray drivelines and corrals like those used in Holocene North America.



	Site/Group	Activity
1	Victoria Is	Caribou stone driveline
2	Lake Huron	Caribou stone driveline
3	Pt. Barrow	16km willow caribou driveline
4	Anaktuvuk	8lm stone caribou driveline
5	Kobuk	Caribou drive
6	NE Alaska	Caribou drivelines
7	Mackenzie River	Caribou drive
8	Central Arctic	Caribou drive
9	Central Arctic	Caribou drivelines
10	W. of Hudson Bay	Caribou drivelines
11	Southhampton Island	Caribou drive
12	Saputit Fjord	Caribou driveline
13	Aasivissuit	4km stone caribou driveline
14	E. Alaska, Yukon	Caribou corral and drivelines
15	Old Crow Flats	70–100 person caribou drive
16	Tanana & Yukon Rivers	48 km caribou driveline
17	Upper Koyukuk River	30 km caribou driveline

FIGURE 4 Locations of sites and observations mentioned in the text

18	Cook Inlet	16 km caribou drivelines
19	S. of Artillery lakes	3–5 km caribou drivelines
20	Fort Prince of Wales to Bloody Falls	300-650 person caribou drives
21	Thelon River	3.3 km caribou driveline
22	S. of Thelon River	2 km caribou driveline
23	Slaughter & Faithful Isles Newfoundland	50 km caribou driveline
24	Olsen Chubbuk E Colorado	Bison hunt, 26,000 kg meat harvested
25	Head-smashed-in, s. Alberta	Bison cliff drives 5500–500 ka
26	Nevada	Many pronghorn pens/drivelines
27	Rollins Pass, CO	High elevation driveline, probably sheep
28	SW Asia	Many drivelines, called kites
29	E. Tierra Del Fuego	2 guanaco drives
30	Paraguay	Communal Fishing
31	W. Venezuela	Capybara drive
32	Nama Karoo, S. Africa	Stone drive lines
33	Congo Basin	Net hunting
34	Gran Dolina, Catalonia	Communal bison hunts
35	Salzgitter Lebensted, N Germany	Communal caribou hunt
36	Mauran, S. France, Lascaux, Altimira	Communal bison hunts, images of drivelines
37	Bovid Hill, Kenya, Lukenya Hill	Communal antelope hunt
38	Queensland	Many coastal fish weirs
39	Sweers Betnick Is Gulf of Carpenteria	Coastal fish weirs
40	Murray/Darling R. S.W. Australia	Eel traps, extensive canals
41	Owens Valley	Canals, habitat improvement
42	Burning W. Desert	Burning
43	Murngin Arhnemland	Warfare
44	fortifications, Modoc, E. Oregon	Warfare
45	warfare Koetzebue Sound	Warfare
46	Yurok, Hupa, Karok, Nomlaki, NW California	Warfare/peacemaking

FIGURE 4 (Continued)

So, it is plausible that people in the Pleistocene societies that formed the basis for the evolution of human behavior also cooperated in large groups.

This evidence weighs against the hypothesis that cooperation among Pleistocene hominins was limited to small band-sized groups. This hypothesis is rooted in ethnographic descriptions of Holocene foragers like the Ju/'hoansi and the Hadza where large-scale cooperation has not been observed. The evidence we have reviewed here suggests that this picture of Holocene foragers should be amended; cooperation among small-scale nomadic foragers often extended to large-scale groups, even to cross-cultural scales in the case of military alliances and trade partnerships. This suggests that the psychological mechanisms that support large-scale cooperation in contemporary societies evolved to support large-scale cooperation in Pleistocene societies of mobile hunter-gatherers, and explanations of contemporary cooperation based on mechanisms evolved to support only small-scale cooperation are less plausible.

A number of important objections can be raised. First, there are few published ethnographic descriptions of large-scale cooperation among well-studied 20th century foragers. Why should this be the case? Moreover, given the high quality of modern ethnographies, perhaps we should be skeptical about the historical and archaeological evidence we have assembled.

A number of factors have conspired to reduce reports of large-scale collective action among contemporary foragers. Few anthropologists have focused on explaining large-scale collective action among foragers. Behavioral ecologists understand the problem, but those studying foragers have focused on smaller scale within-group cooperation, especially food sharing, mutual aid and small-scale collective action. Such behaviors occur frequently and can be studied using the rigorous quantitative methods of behavioral ecology more

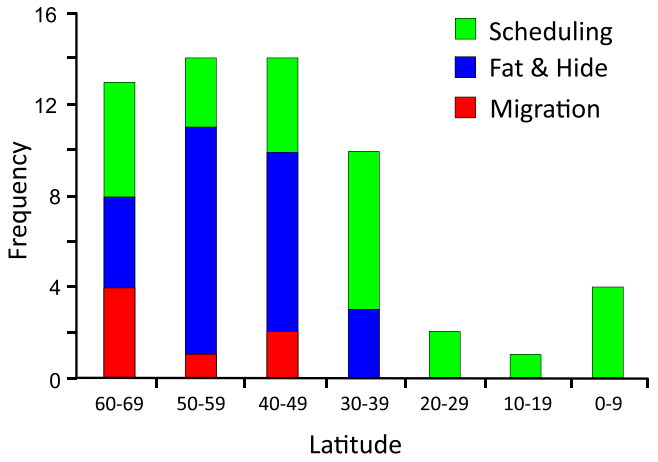


FIGURE 5 Frequency communal hunts as a function of latitude for 60 societies, including food producing societies.[48] The height of the bars gives the number of societies in that latitude bin, and the colored subdivisions gives the number of societies with different reasons for communal hunting. Communal hunts were more common in Arctic and temperate environments. In these environments, communal hunts were motivated by seasonal migrations, the quality of hides, and the fatness of the prey

easily than rarer and harder to quantify behaviors. Two recent cross-cultural surveys of hunter-gatherer behavior by behavioral ecologists do not mention large-scale communal foraging[3,19] even though they include societies like the Inuit, Athabascans and Iñupiaq where large-scale communal foraging and warfare have been reported, especially in earlier accounts. Another influential synthesis[18] does not treat large-scale communal foraging in any detail and its treatment of warfare does not discuss free-riding. Scholars outside of human behavioral ecology have not emphasized the free-rider problem inherent in communal hunting, investment in shared facilities like drivelines and fortifications, and participation in large-scale conflict. For example, many archaeologists emphasize the level of cognition necessary to coordinate large hunts and take it for granted that if large hunts pay on average and if people are smart enough to organize them, they will occur. Similarly, anthropologists working in the cultural ecology tradition often start with the assumption that behavior is adaptive at the group level.

It could also be argued that there is little evidence for large-scale cooperation in Africa the region in which modern humans likely evolved. Modern humans emigrated from Africa about 60ka and spread rapidly across the globe. This strongly suggests that the shared psychology that gives rise to large-scale cooperation must have been present in African populations before that date. Moreover, neither large-scale communal foraging nor warfare has been observed among Ju/'hoansi or the Hadza, the canonical open country African foragers. However, observations of African foragers have mainly been limited to very dry environments or very moist environments. Less arid tropical grasslands in which large, migratory herds of ungulates create natural targets for communal hunting[86] have been dominated by pastoralists for many thousands of years. We know much less about foraging behavior in such environments than in high latitude environments. Such tropical grasslands have more resident, non-migratory species and greater availability of plant resources suggesting that communal foraging might be less common.[86] However, two of the three MSA sites in East Africa with sufficient evidence to reconstruct foraging methods suggest communal foraging did occur.[59] In some dry environments, like those found in southern Africa, large migratory herds of springbok were common until recently and may have been harvested using drivelines.[75] In forest environments, communal net hunting has been widely observed, although limited to groups less than 60 individuals. Moreover, large-scale communal hunting and warfare have been observed in open dry habitats in Australia and North America.

More generally, communal hunts are more common above latitude 30 (Figure 5), but most foragers described in mid-20th century ethnography lived at low latitudes in habitats where communal hunts may not have been profitable or at very high latitudes where the availability of rifles made individual hunts for arctic reindeer more profitable than communal hunts. In other areas, horses provided a better way to hunt bison. Modern hunter gatherers are often surrounded by more powerful food producing neighbors and often live within modern states that suppress intergroup conflict.

It also could be argued that the Holocene is different from the Pleistocene. Warmer, more stable Holocene climates and higher atmospheric CO_2 levels likely made agriculture possible and it could be that large-scale collective action was also made possible by the same environmental changes. For example, Eric A. Smith suggested to us that harsh, chaotic Pleistocene climates prevented people from establishing bounded social groups necessary for organizing large-scale cooperation. Or it might be that higher population densities made possible by more plant productivity made cooperation more profitable. The archaeological evidence for communal foraging by Middle and Upper Paleolithic hominins is not extensive so we cannot know for sure that they engaged in large scale cooperation. However, communal foraging and warfare are difficult to detect in the archaeological record so the absence of evidence is not determinative. Also, the argument that Holocene foragers cannot be used as models for Pleistocene foragers applies with equal force to ethnographic evidence about 20th century foragers, and we are left with no behavioral data to illuminate Pleistocene archaeology. It seems more reasonable to cautiously accept convergent evidence from ethnographic, historic and archaeological sources.

Finally, it could be argued that large-scale cooperation occurred during the Pleistocene but was infrequent compared to food sharing and other forms of within group cooperation, and had little influence on the evolution of human psychology. You can think of this as the Paleolithic mismatch hypothesis. According to this argument, Pleistocene foragers sometimes cooperated in large groups, but they did so because, like modern people, their evolved psychology was tuned to a world of small group cooperation, and this psychology led them to occasionally cooperate in large groups. For example, cues of group membership did not respond correctly to interactions in larger groups. However, they did not find themselves in this situation often

enough for natural selection to have reorganized their group membership psychology to prevent it. This argument suffers from several weaknesses. First, there are good reasons to think that warfare may have been fairly common in some environments. Second, even though communal hunting was often seasonal, it played a crucial role in yearly subsistence of mid and high latitude peoples by providing hides and fat crucial for survival. Third, the evidence we have reviewed suggests that cooperative mass hunting may be a few hundred thousand years old, leaving plenty of time for selection to act to reduce participation in large-scale cooperation if such cooperation was maladaptive.

The evidence we have presented indicates that low density, mobile foragers regularly engaged in large-scale cooperation during the Holocene, and there is evidence that hints that this has been going for a long time. This in turn supports the hypothesis that the psychological mechanisms supporting large-scale cooperation in contemporary environments evolved because they supported large-scale cooperation in ancestral environments in which people lived as mobile foragers. Residential group sizes, degrees of relatedness, and some other aspects of population structure of mobile foragers are similar to those seen in other social mammals, especially social carnivores and other primates. The mechanisms used to explain the evolution of cooperation in such species, kinship, reciprocity, and direct sanctions suggest that large-scale cooperation among unrelated individuals is an unlikely to evolve.[1,7] However, humans are unusual in a number of ways. Although interspecies comparisons of intelligence are notoriously difficult, it does seem likely that humans have exceptional abilities in the domains of causal reasoning and theory of mind. Combinatorial language allows the spread of information about individual behavior beyond those who were able to observe the behavior. This ability would seem to be essential for both norm and signaling-based explanations of large-scale cooperation. Language also allows us to plan and negotiate in ways that are not available to other creatures. Institutional explanations of large-scale cooperation are based on the idea that people bargain about norm content, intelligently choosing institutional arrangements that are mutually beneficial. Leadership requires followers and the leader to bargain in advance about the share of the group output the leader receives in return for imposing sanctions. Human societies are regulated by shared, culturally transmitted moral norms that allow human societies to gradually evolve norms and institutions that can support cooperative social behavior appropriate to local conditions.[11] Cultural norms can also amplify the effects of genetic relatedness in subtle ways to allow the spread of genes leading to altruism.[132,133]

We think that the historical and archaeological evidence supports the idea that human foragers engaged in large-scale cooperation with unrelated individuals during the Holocene and perhaps much further back in time. There is strong evidence that our species has been fully modern technologically and cognitively for several hundred thousand years, and it is plausible that we have been cooperating on large-scales for a good part of this time interval. This, in turn, suggests that our psychology evolved in such a world and that mechanisms like other-regarding preferences and norm psychology that support large-scale-cooperation in the contemporary world are adaptations shaped by natural selection because they supported large-scale cooperation in ancestral environments.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data sharing not applicable—no new data generated.

GLOSSARY

Bands	Ethnographically known hunter-gatherers live on a day-to-day basis in groups as small as one extended family but averaging perhaps 30 people. Bands are the constituent parts of larger scale ethnolinguistic units often called maximal bands or, less formally, tribes. Membership in bands is quite fluid compared to tribes. Individuals and families often switch bands based on utilitarian considerations and ties of kinship and friendship.
Communal hunting	Hunts in which large numbers of personnel are recruited to drive herds of game into nets, enclosures, water bodies, or difficult terrain where they could be killed in quantity.
Drive lines	Long fence like structures designed to channel herding animals to corrals, blind canyons, or drop-offs where they could be taken in significant numbers. Aside from the labor of construction, whole communities often backed up the physical barrier to stampede the herds into the enclosures or over the drop-offs.
Ethnolinguistic groups (tribes)	Social units on the order of a thousand people in hunting and gathering societies. These groups are symbolical marked and attract emotional affinity. Usually substantially endogamous.
Fish traps and weirs	Often substantial structures used to trap fish in intertidal zones or on rivers to channel migrating fish into situations where they can be netted or speared.

Gravettian culture	Geographically extensive cultural phenomenon of Upper Paleolithic Europe 33,000–22,000 years ago. Some authorities think that Gravettian people were political organized on larger scale than typical of ethnographic hunter-gatherers including having systems of institutionalized political power, as some ethnographically known hunter-gatherers do.
Holocene	The geological Epoch since the end of the last major glacial episode 11,700 years ago.
Institutions	More or less formalized sets of culturally inherited rules that govern social life in human societies. Marriage and kinship are familiar examples. In most human societies, wives, husbands, and children have roles governed by explicit social norms. Typically, grandparents, adult siblings and other kin have normative roles in family life. Institutions mandate rewards and punishments for behavior that conforms or does not conform to the rules, thus tending to align private incentives with collective goals, minimizing the need for individual altruism (self-sacrifice) to sustain cooperation.
Large scale cooperation	Cooperation on a scale larger than can be sustained by non-altruistic voluntary punishment, giving rise to the so called second order dilemma of cooperation. This is approximately the same scale as hunter-gatherer bands, about 30 people. Above this scale, more sophisticated social institutions are required to sustain cooperation. Large scale cooperative enterprises are usually organized by leaders. In ethnographically known cases in hunter-gatherers, leaders are usually respected persons who could lead by persuasion, without institutionally defined coercive power or with coercive power strictly limited to project at hand. Thus, a "boss" typically organized and supervised a communal hunt and a "war chief" a raiding expedition.
Mismatch hypothesis	The inheritance of genes and culture creates lags in the evolution of adaptations. After abrupt environmental change maladaptations will persist for some time. The earth's climates rapidly switched from cold, dry and highly variable to warmer, wetter and much less variable about 11,700 years ago. A prominent mismatch hypothesis holds that even today it is likely that much human behavior is maladaptive because gene-based cognitive adaptations evolved during humans' 2 plus million year adaptation to Pleistocene conditions. Skeptics point out that humans have been more successful in the Holocene than the they were in the Pleistocene.
Other regarding preferences	Social emotions like empathy and loyalty cause humans to bond to other individuals. Such bonds cause people to weigh the welfare of others in their preference set, leading to the provision of material aid and social support to such valued others. Social norms and institutions often promote attachments to abstract groups and enjoin consideration for the welfare of strangers, at least strangers belonging to one's own symbolically marked group.
Pleistocene	The geological Epoch dominated by high amplitude glacial-interglacial cycles. Began 2.6 million years ago and ended with the Holocene. The biocultural evolution of the human genus *Homo* occurred mostly in this Era.
Public goods (collective goods)	Goods produced by the joint activity of a community, usually requiring cooperation to produce. Producers of public goods cannot prevent non-producers from sharing in their consumption, potentially giving non-producers an evolutionary advantage that will tend to undermine their production. For example, big game hunters produce carcasses that contain more meat than they can eat before it spoils. They therefore share their kills with their campmates when they are successful and in turn share in the kills of successful campmates, forming a collective risk pool to finesse the high variance of returns to big game hunting. Selfish members of such camps can share in the kills without producing any, tending to undermine cooperation in the evolutionary long run if selfishness has a hereditary basis.
Small scale societies	Societies of roughly 1000 people, usually symbolically marked by dialect or similar distinctive features. Social systems are egalitarian with leadership based on prestige rather than coercive power. Known to ethnography mainly from the Americas and Australia. Generally regard as the dominant type of human society until the evolution of larger scale, structurally more complex, societies in the Holocene.
Upper Paleolithic societies	About 50,000 years ago, with deeper roots in Africa, modern humans dispersed to Eurasia and began to make a distinctly advanced toolkit and rather sophisticated art. Originally best documented in Europe, this phenomenon seems to have occurred more or less coincidently all over the Old World.

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