Thermokarst Lakes as a Source of Atmospheric CH4 During the Last Deglaciation

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Thermokarst Lakes as a Source of Atmospheric CH_4 During the Last Deglaciation

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Polar ice-core records suggest that an arctic or boreal source was responsible for more than 30% of the large increase in global atmospheric methane (CH_4) concentration during deglacial climate warming; however, specific sources of that CH_4 are still debated. Here we present an estimate of past CH_4 flux during deglaciation from bubbling from thermokarst (thaw) lakes. Based on high rates of CH_4 bubbling from contemporary arctic thermokarst lakes, high CH_4 production potentials of organic matter from Pleistocene-aged frozen sediments, and estimates of the changing extent of these deposits as thermokarst lakes developed during deglaciation, we find that CH_4 bubbling from newly forming thermokarst lakes comprised 33 to 87% of the high-latitude increase in atmospheric methane concentration and, in turn, contributed to the climate warming at the Pleistocene-Holocene transition.

Methane is an important greenhouse gas, whose sources to the atmosphere during the last deglaciation have yet to be reconciled with geological and paleoecological evidence. In northern high latitudes, ice-core records show that abrupt (decadal-scale) increases in temperature and precipitation were followed by a slower (100- to 300-year) rise in atmospheric methane concentration (AMC) (*1–3*), likely reflecting a lag in the terrestrial ecosystem response to rapid climate change. Values of the interpolar methane gradient, an indicator of the latitudinal distribution of CH_4 sources computed from the difference in CH_4 concentration between ice cores from Greenland and Antarctica, suggest that a new arctic/boreal source contributed substantial amounts of CH_4 from 14 thousand calendar years before present (kyr B.P.) through the Younger Dryas (YD) (~13 to 11.5 kyr B.P.) and accounted for >30% (30 to 40 Tg CH_4 year^{-1}) of the rapid rise of CH_4 emissions (83 to 99 Tg CH_4 year^{-1}) during the early Holocene (11.5 to 9.5 kyr B.P.) (*1–5*).

Two main hypotheses have been advanced to explain millennial-scale variations in AMC: a catastrophic release of methane hydrates in seafloor sediments ["clathrate gun hypothesis" (*6*)] and an increased CH_4 emission from northern wetlands in response to climate warming [wetland hypothesis (*7–9*)]. Reservations remain in the literature about attributing early Holocene CH_4 to a single source (*3*, *4*, *10–12*). Recent evidence of widespread northern peatland formation during the early Holocene suggests that wetlands may have contributed 4 to 9 Tg CH_4 year^{-1} (*8*, *9*). There is a marked paucity of peatland initiation dates for the vast region of north Asia that was not ice-covered during the Last Glacial Maximum (LGM) (*9*). It was in the lowland areas of this region that an extensive initiation of deep "thermokarst" lakes occurred at the beginning of the last deglaciation [(*13–15*) and table S1] and may have been a source of atmospheric CH_4 at that time (*16*). When ice-rich frozen ground thaws, the loss of volume from melting ice creates depressions in the land surface: a process called thermokarst (*13*). Ponding of water in depressions creates thermokarst lakes, which may expand as a result of both thermal and mechanical erosion over time scales of decades to centuries (*13*).

We develop this third alternative hypothesis (thermokarst-lake hypothesis): CH_4 ebullition (bubbling) from newly formed thermokarst lakes occurred extensively across large unglaciated regions in northern high latitudes, particularly in Siberia, as the climate became warmer and wetter. Thermokarst-lake CH_4 emissions are distinct from those of wetlands because thermokarst lakes are a distinctive ecosystem type (*13*) not typically included in wetland emission estimates (*17*) and because ebullition, which dominates CH_4 emissions from thermokarst lakes, is a substantially larger source of CH_4 than previous-

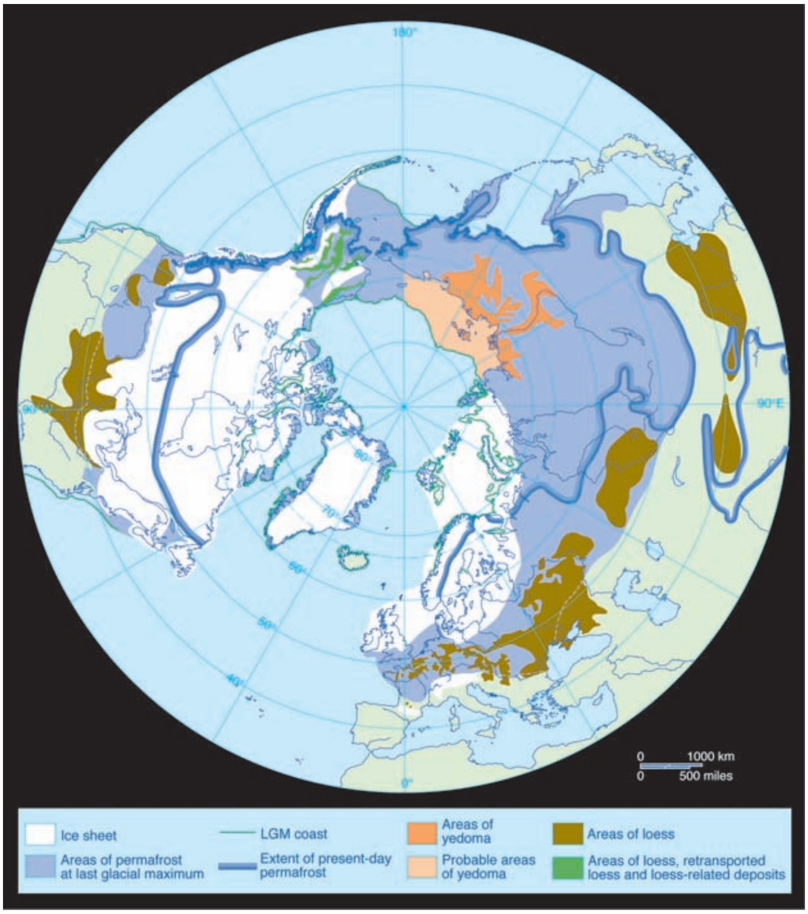

Fig. 1. Current and probable LGM regions of loess, loess-related deposits, and yedoma mapped in relation to the modern and LGM distribution of permafrost. Information sources are provided in the SOM text. Modern and LGM coasts are shown, the latter approximated from the modern 120-m isobath (*30*). The map indicates that considerable areas of loess would have been frozen at the LGM and subsequently thawed, and yedoma would have extended northward on the exposed Siberian shelf.

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ly thought (*18*). We provide three lines of evidence in support of this hypothesis: (i) A reconstruction of late Quaternary paleogeography documents the areal extent over which this process likely occurred, and a synthesis of basal radiocarbon-dated thermokarst-lake sediments indicates that many thermokarst lakes were initiated ~14 kyr B.P. and that thermokarst activity accelerated during 11.5 to 9 kyr B.P., coinciding with the CH_4 emissions increase from arctic/boreal sources; (ii) Laboratory incubations show that Pleistocene-aged frozen sediments support high rates of CH_4 production; and (iii) Thermokarst lakes that are currently expanding in areas of frozen Pleistocene sediments have high ebullition rates of Pleistocene-aged CH_4 (just as they would have had at the onset of their formation in the early Holocene). To estimate post-Pleistocene CH_4 emissions from lakes, we integrate the information on CH_4 production rates from sediments, carbon (C) loss from drained thermokarst-lake sediments that refroze, flux rates from modern thermokarst lakes, and the areal extent of Pleistocene sediments subject to thermokarst-lake development. We show that these emissions could have contributed up to ~87% of the boreal contribution to AMC increases recorded in ice cores.

During the late Pleistocene, extensive loess and loess-related deposits formed throughout unglaciated regions of northeast Siberia, Europe, and North America (Fig. 1). In northeast Siberia, these deposits, which have a particularly high ice content and a large volume of labile organic C, are referred to as the "yedoma ice-complex" [(*19*–*22*) and supporting online material (SOM)]. Yedoma has remained largely frozen throughout the Holocene, currently occupies an area of >1 × 10^6 km^2, and in many regions is tens of meters thick (*14*, *21*). During the LGM, when the global sea level was 120 m lower than that of today, similar deposits covered substantial areas (0.9 × 10^6 km^2) of the exposed northeast Eurasian shelves (*19*, *22*) (Fig. 1).

In northeast Siberia, thaw of yedoma makes organic matter available in anaerobic lake bottoms, fueling methanogenesis (*18*, *23*). Once initiated, thermokarst lakes deepen and can persist for thousands of years (*13*, *14*, *24*) (SOM text). In certain areas of Siberia and northern Alaska where thermokarst lakes are prominent, as much as 50% of the landscape is covered with lake scars (*13*, *25*, *26*). In several major Siberian lowlands, nearly 100% of the yedoma ice-complex has been reworked by lakes (*13*, *14*).

Patterns of thermokarst-lake formation based on a compilation of basal radiocarbon dates appear broadly consistent with the climate evolution of northeast Siberia, Alaska, and northwestern Canada, as well as with patterns of increase in boreal CH_4 sources to the atmosphere after the LGM (Fig. 2). There are few records of thermokarst during the glacial period. Data suggest that thermokarst-lake formation occurred as early as ~14 kyr B.P. in Russia, Alaska, and northwestern Canada (table S1), coincident with increases in boreal CH_4 sources, temperature, and moisture (*27*). Some data suggest a climate reversal at the time of the YD, but its expression is greatly muted in northeast Siberia and Alaska when compared with the Greenland temperature record (*15*, *27*–*29*). Geological evidence suggests that thermokarst lakes persisted (*14*) and continued to form through the YD, which is consistent with sustained sources of boreal CH_4 (Fig. 2). Multiple proxies indicate that the warmest period of the current interglacial in northeast Siberia (11 to 9 kyr B.P.) occurred in concert with peak summer insolation (*27*, *28*). During this period, many new thermokarst lakes formed in Siberia (Fig. 2, C and D); 45% of the compiled dates of thermokarst-lake formation fall between 11.5 to 9 kyr B.P. (table S1). Subsequently, the number of reported dates decreases throughout the Holocene, as relatively stable drainage patterns became established. Thermokarst lakes continue to develop today as evidenced, for example, by remote sensing analyses of a yedoma area in northeast Siberia that shows a ~14% increase in lake area during recent decades (*18*).

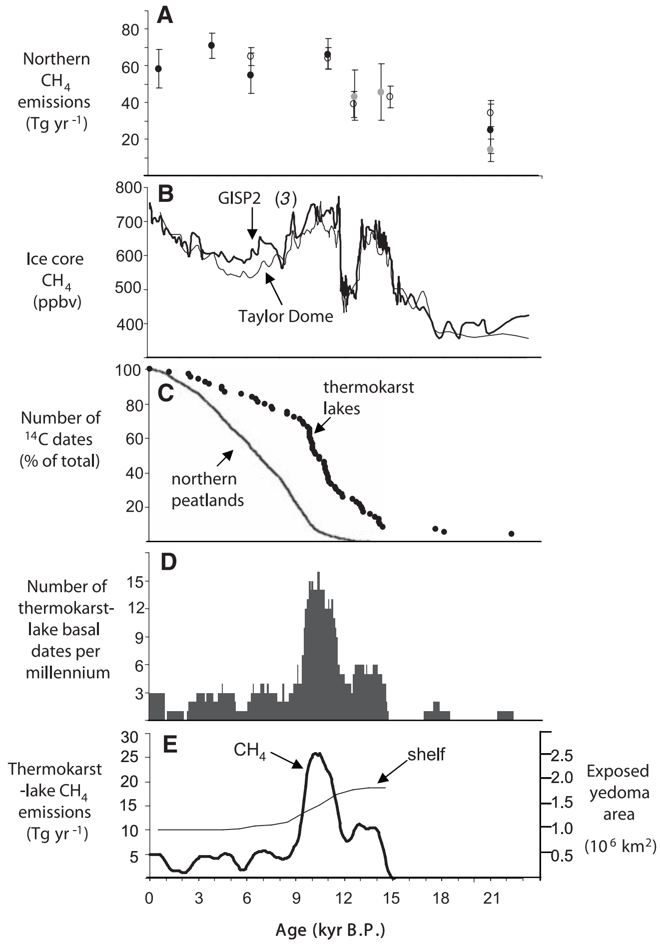

Fig. 2. Thermokarst-lake development during deglaciation as a northern source of atmospheric CH_4. (**A**) Three independent estimates of Northern Hemisphere CH_4 emissions derived from the interpolar CH_4 gradient [open circles (*3*), solid black circles (*4*), and solid gray circles (*5*)] suggest that a modest northern CH_4 source appeared by ~14 kyr B.P., was sustained through the YD, and increased substantially after 11.5 kyr B.P. Error bars indicate uncertainties in three-box models propagated from SEs in CH_4 concentrations in ice cores for selected time intervals and uncertainties in the calculation of the interpolar CH_4 difference. (**B**) The interpolar CH_4 gradient is modeled based on the difference in ice-core CH_4 concentrations in Greenland [Greenland Ice Sheet Project 2 (GISP2), black line] and Antarctica (Taylor Dome, gray line) (*3*). The AMC drop recorded during the YD in these global records is attributed to decreases in tropical (as opposed to northern) CH_4 sources (*4*, *5*). ppbv, parts per billion by volume. (**C** and **D**) The pattern of northern hemisphere CH_4 emissions in (A) is consistent with the formation of CH_4-emitting northern thermokarst lakes shown as a cumulative curve (C) and as the number of documented thermokarst-lake initiation dates per millennium occurring within time steps of 100 ± 500 calendar years B.P. according to table S1 (D). The cluster of lakes initiated between 11.5 to 9 kyr B.P. coincides with the steepest part of the cumulative curve of 69 thermokarst initiation dates in (C) and with the peak of AMC recorded in ice cores after abrupt warming and wetting. The cumulative curve of 1516 peatland initiation dates from (*9*), shown also in (C), suggests that northern peatlands would also have been a source of early Holocene atmospheric CH_4, though acceleration of peatland initiation lags behind that of thermokarst lakes by several millennia. (**E**) Methane emissions for the Siberian yedoma region, modeled according to rates of thermokarst activity, suggest that the expansion of yedoma thermokarst lakes on the exposed yedoma surface could have released as much as 20 to 26 Tg CH_4 $year^{-1}$ after abrupt warming around 11.5 kyr B.P. The curve labeled "shelf" indicates the decline in the area of yedoma exposed on the continental shelf as sea level rose during the early Holocene. The text describes a second independent scenario that yields the estimate of early Holocene thermokarst-lake emissions (13 to 20 Tg CH_4 $year^{-1}$). Together, these scenarios suggest that thaw of yedoma would have been an immediate and substantial contribution to the new boreal CH_4 source (~30 to 40 Tg $year^{-1}$) observed in ice-core records.

Until recently, thermokarst lakes were not recognized as a globally important source of atmospheric CH_4. Bubbling from thermokarst lakes, which currently cover a large proportion (>10%) of yedoma territory in Siberia, contributes ~4 Tg CH_4 annually to regional sources (*18*, *23*). Given the extensive degradation of yedoma permafrost since the LGM (Fig. 1), observed CH_4 emissions from lakes associated with yedoma degradation today, and geological evidence of thermokarst-lake formation at the start of the Holocene (Fig. 2), we propose that CH_4 bubbling from Siberian thermokarst lakes contributed substantially to the rapid increases in AMC during deglaciation (*22*).

To assess this thermokarst-lake hypothesis, we applied rates of CH_4 emissions measured in modern thermokarst lakes to the pattern of post-LGM lake development implied by basal-date records that serves as a proxy for thermokarst activity, as a function of exposed yedoma terrain in 1000-year time steps during deglaciation (fig. S1). Details of measured parameters and transfer functions are given in (*30*). In this scenario, thermokarst lakes appeared on the exposed yedoma land surface in northeast Siberia between 14 to 13 kyr B.P., contributing ~11 Tg CH_4 $year^{-1}$. Lake emissions of ~8 to 9 Tg CH_4 $year^{-1}$ continued through the YD until 11.5 kyr B.P., when a spike in basal dates represents an acceleration of thermokarst activity and new lake formation, contributing up to 26 Tg CH_4 $year^{-1}$. After 9 kyr B.P., our scenario depicts a decline in lake emissions as thermokarst activity decelerated and total yedoma area available for new thermokarst continued to decrease. Average lake emissions from 9 kyr B.P. to the present were 2 to 6 Tg CH_4 $year^{-1}$. Our calculations do not include CH_4 that would have been released from CH_4-producing submarine habitats created by sea-level rise or from North American lakes (*14*, *22*).

We provide a second independent estimate of CH_4 emissions using C mass balance based on the C lost from yedoma beneath former thermokarst lakes (*30*). Yedoma beneath thermokarst lakes that formed in the Holocene and subsequently drained and refroze has ~33% less C [18.0 ± 1.4 kg C m^{-3} (mean ± SE), $n = 15$ samples] than yedoma that never thawed (26.8 ± 1.5 kg C m^{-3}, $n = 54$ samples) (*18*). At the beginning of the Holocene, yedoma contained ~500 Gt C (*26*). Assuming that if 15 to 25% of the yedoma C beneath lakes, whose scars cover 50% of the yedoma territory, was emitted as CH_4 (*21*, *23*) during the Holocene and that if 65% of these emissions occurred between 14 to 9 kyr B.P., based on geological evidence (table S1), then thawing yedoma beneath lakes would have contributed (on average) 8 to 12 Tg CH_4 $year^{-1}$ during deglaciation. This estimate is conservative because it ignores Holocene organic detritus accumulating on lake bottoms (*31*) that would also produce CH_4. Pleistocene-aged organic C fuels ~60% of the CH_4 emitted from modern yedoma thermokarst lakes in northern Siberia (*18*), suggesting that contributions of Holocene substrates for methanogenesis could also have been large (~40%), yielding a total lake-emissions estimate of 13 to 20 Tg CH_4 $year^{-1}$.

Finally, we used CH_4 production potentials (145 ± 31 g CH_4 m^{-3} $year^{-1}$, $n = 23$ samples) of thawed northern Siberian yedoma in laboratory incubations to provide an additional independent confirmation of thawing yedoma contributions to the AMC rise at the onset of this interglacial period (*30*). Based on (*32*), if we assume that abrupt warming and wetting transformed 10% of the dry, unglaciated landscape (1.9×10^6 km^2) into a ponded surface regime dominated by shallow pools for 3 to 4 months of the year, then anaerobic decomposition in the surface (1-m depth) of the locally deepening active layer might have produced CH_4 on the order of 7 to 9 Tg $year^{-1}$. Although microbial oxidation in pools might have reduced total CH_4 emissions during the early stages of pond formation, our incubation-based calculation demonstrates that the CH_4 production potential of yedoma sediments was high enough to contribute immediately upon thaw to the abrupt rise in AMC.

Our two independent estimates (20 to 26 and 13 to 20 Tg CH_4 $year^{-1}$) of yedoma thermokarst-lake contributions to the rise in AMC are similar to one another and within the ~30 to 40 Tg CH_4 $year^{-1}$ boreal-source constraint from the interpolar CH_4 gradient recorded in ice cores (*4*). Formation and expansion of thermokarst lakes at the onset of Holocene warming appear to have led to a large new AMC source: bubble emissions from lakes. Our estimate of CH_4 derived largely from the Pleistocene-aged C reservoir can account for a substantial proportion (33 to 87%) of northern AMC sources during the last deglaciation. If this conservative estimate is roughly correct, other northern sources [such as peatlands (*8*, *9*), hydrates, and/or wildfires, or natural gas seeps (*11*, *12*)] are also required as inputs to AMC during deglaciation. Isotope ratios of $^{13}C/^{12}C$ of CH_4 [–58 to –83‰ (per mil)] and D/H (–338 to –420‰) from modern Siberian thermokarst lakes (*18*) are similar to those of boreal wetlands and are consistent with multisource scenarios proposed to explain CH_4 isotope ratios in ice cores during the latest deglaciation [(*11*, *12*) and SOM text].

Records of AMC in ice cores show that a moderate arctic/boreal source appeared at 14.8 kyr B.P. and was sustained throughout the YD (*5*). In the early Holocene, there was a rapid rise in boreal emissions that demands a rapid ecosystem response. Estimates of early peatland emissions are insufficient to account for this northern source alone (*9*). Here we provide a first approximation of paleo-CH_4 flux from a new terrestrial source, based on what is known about patterns of yedoma thermokarst-lake ebullition emissions and the timing of thermokarst-lake formation during deglaciation. Our compilation of thermokarst-lake basal ages suggests that lakes formed extensively in Alaska, northwestern Canada, and Russia as early as 14 kyr B.P. Thermokarst lakes would have contributed modestly to atmospheric CH_4 through the YD, explaining the overshoot in AMC relative to temperature in ice core records during the YD (*33*). Finally, an expansion of thermokarst lakes in the early Holocene contributed considerably to the spike in AMC recorded in ice cores.

About 500 Gt C remain preserved in the yedoma ice-complex in northeast Siberia (*21*). If the yedoma territory with its high ice–content permafrost warms more rapidly in the future, as projected (*34*), ebullition from thermokarst lakes could again become a powerful positive feedback to high-latitude warming, as it appears to have been during deglacial climate warming at the onset of the Holocene. Expansion and formation of yedoma thermokarst lakes in northeast Siberia during the era of satellite observations suggest that this positive feedback is already underway (*18*). This important source of atmospheric CH_4 is not currently considered in climate-change projections.

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Holocene. However, CH_4 emissions are not well known for lakes in these regions and are not included in our thermokarst-lake CH_4 emission estimate. Our calculations of CH_4 emission from thermokarst lakes are based on a conservative estimate of the extent of yedoma, namely its current distribution in north Siberia and the previously exposed adjacent continental shelves (total area: 1.9×10^6 km^2 at 15 kyr B.P.). Additional details are provided in the SOM Materials and Methods.
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Supporting Online Material
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Materials and Methods
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The Coevolution of Parochial Altruism and War

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Altruism—benefiting fellow group members at a cost to oneself—and parochialism—hostility toward individuals not of one's own ethnic, racial, or other group—are common human behaviors. The intersection of the two—which we term "parochial altruism"—is puzzling from an evolutionary perspective because altruistic or parochial behavior reduces one's payoffs by comparison to what one would gain by eschewing these behaviors. But parochial altruism could have evolved if parochialism promoted intergroup hostilities and the combination of altruism and parochialism contributed to success in these conflicts. Our game-theoretic analysis and agent-based simulations show that under conditions likely to have been experienced by late Pleistocene and early Holocene humans, neither parochialism nor altruism would have been viable singly, but by promoting group conflict, they could have evolved jointly.

Late 19th-century scientists as diverse as Charles Darwin (*1*) and Karl Pearson (*2*) recognized war as a powerful evolutionary force that might foster social solidarity and altruism toward the fellow members of one's group. But despite Hamilton's speculation about how this could occur (*3*), neither the process by which war might have become sufficiently common to support the evolution of altruism nor the possibility that altruism conditioned on group membership might have contributed to the unusually high level of lethal intergroup conflict among humans has been subjected to systematic investigation.

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The empirical importance of both altruism and hostility to members of other groups is well established. Experimental and other evidence demonstrates that individuals often willingly give to strangers, reward good deeds, and punish individuals who violate social norms, even at a substantial personal cost (*4*), while favoring fellow group members over "outsiders" in the choice of friends, exchange partners, and other associates and in the allocation of valued resources (*5*). For example, a recent "third party punishment" experiment in Papua New Guinea revealed strong favoritism toward a subject's own linguistic group in giving to others, and significantly greater punishment of individuals from another linguistic group (by comparison to the subject's own group) who acted ungenerously toward the subject's fellow group members (*6*).

Intergroup hostility and aggression are similar to altruism in that an individual adopting these behaviors incurs mortal risks or foregoes beneficial opportunities for coalitions, co-insurance, and exchange, thereby incurring a fitness loss by comparison to those who eschew hostility toward other groups. When this is the case, and when the members of the actor's group benefit as a result of one's hostile actions toward other groups, we term the behavior "parochial altruism." The experimental subjects in Papua New Guinea provide an example.

Neither parochialism nor altruism would seem likely to survive any selection process that favors traits with higher payoffs. But parochial altruism could have emerged and proliferated among early humans because our ancestors lived in environments in which competition for resources favored groups with substantial numbers of parochial altruists willing to engage in hostile conflict with outsiders on behalf of their fellow group members. These group benefits could have offset the within-group selection against both parochialism and altruism. Unlike multilevel selection models in which group conflict is simply assumed (*7*–*9*), we thus provide an explanation of warfare itself and its uniquely lethal nature among humans. Whether this account is plausible is an empirical question.

The ethnographic and archaeological record suggests that warfare was a frequent cause of death among some hunters-gatherer groups and early tribal societies (*10*, *11*). Mortality in intergroup conflicts as a fraction of all deaths may have been an order of magnitude greater among early humans than among Europeans during the bellicose 20th century. Most hostile intergroup contact was probably ongoing or intermittent, with occasional casualties, more akin to boundary conflicts among chimpanzees (*12*) than to modern warfare. However, "pitched battles" did occur