www.sciencemag.org/cgi/content/full/324/5932/1293/DC1

Supporting Online Material for

Did Warfare Among Ancestral Hunter-Gatherers Affect the Evolution of Human Social Behaviors?

Samuel Bowles

E-mail: samuel.bowles@gmail.com

Published 5 June 2009, *Science* **324**, 1293 (2009)
DOI: 10.1126/science.1168112

This PDF file includes:

Supporting on line materials for

Did Warfare among Ancestral Hunter-gatherers Affect the Evolution of Human Social Behaviors?

Samuel Bowles

Contents

1. Methods: Contest Success Functions

Figure 2A shows the probability of success for group j when matched with another group with a fraction *p* of altruists, or $\lambda^j(p_j, p) = \lambda^j(p_j, \frac{1}{2})$ This depends on the difference in the number of altruists in each group (*1*): $\lambda^j(p_j, p_i) = \frac{e^{4\mu p_j}}{e^{4\mu p_j} + e^{4\mu p_i}}$, so

$$\lambda^j(p_j, \frac{1}{2}) = \frac{e^{4\mu p_j}}{e^{4\mu p_j} + e^{2\mu}} \quad \text{and} \quad \lambda_A(\tfrac{1}{2},\tfrac{1}{2}) = \mu.$$

To illustrate the consequences of differing values of λ_A consider the differential expected wartime mortality when two groups with differing numbers of altruists meet. Suppose that the two groups differ in the fraction of altruists by ten percent, and that the mean of the two is one-half (which will maximize the mortality effect of the differences in frequency of altruists, as can be seen from Figure 2). Let δ^-, δ^+ and λ^-, λ^+ be the expected δ (fraction of deaths due to warfare) and λ (the probability of survival) for the group with fewer and more altruists, respectively. Then we have

$$\delta^-/\delta^+ = \lambda^+/\lambda^- = (\tfrac{1}{2} + 0.05\,\lambda_A)/(\tfrac{1}{2} - 0.05\,\lambda_A)$$

which gives the values cited in the text.

2. Materials and Methods: The extent and lethal nature of war.

Despite very low population densities (*2*) Late Pleistocene groups were not isolated reproductively or in other ways. This is evident from the early emergence of trading relationships over very long distances (*3*) and the rapid diffusion of tools, ornaments, and rituals even among the scattered Aboriginal Australians (*4*). Thus it seems safe to conclude that all but the most isolated forager groups sometimes interacted with other groups. Groups that avoided hostile interactions benefited from greater access to the resources in what would otherwise have been non-productive defensive buffer zones (*5, 6*), as well as from exchange and co-insurance against risk, often over substantial distances (*7, 8*). However these mutually beneficial relationships must have been frequently disrupted.

The challenges of interpreting the archaeological evidence on mortality in group conflict are illustrated by the site at Vasiliv'ka studied by D. Telegin (*9*). It is estimated that the site initially contained 60 to 70 individuals, but was disrupted during the Second World War by the construction of a trench bisecting it. Only 44 of these individuals were available for study (32 of them adults), one represented by a head only. None of those who apparently died violently perished from head injuries, so we cannot be confident that this individual died of some cause other than interpersonal violence. Seven males are buried in identical fashion (facing east) and could well have died in warfare. One individual appears to have been bound (or the tendons severed) when interred and is buried with a second individual who had multiple points close to the jaw, scapula, and taxal bone, indicating a violent death. I count the head-only individual as part of the assemblage and exclude that individual and the seven east-facing males from those estimated to have died violently. Without exception the other sites present similar challenges.

Tables S1 – S3 present (respectively) the 15 archaeological, 8 ethnographic data used here, and 14 cases (excluded from this study or re-estimated) in which data were either incorrectly thought to pertain to hunters-gatherers, were misestimated, or are not sufficient to provide an estimate of δ.

Table S1. Sources for Archaeological Evidence in Table 2

Site, source	*Comments*
British Columbia Cybulski (1994) (*10*) **0.23**	30 sites. Including all areas, all pre-contact dates. Percent adult violent trauma indicated: 5500-3500 bp: 21%; 3500- 1500bp 32% (Prince Rupert) 6.2% (Strait of Georgia) 1500 – 234 bp 28% (745 individuals total) p. 82 simple average 0.227 (averaging middle period's regions)
Nubia Site 117 (Jebel Sahaba) Wendorf (1968) (*11*):993 **0.46**	Adults: 9/20 females; 10/21 males Embedded (4) or associated points only.
Nubia (near Site 117) Wendorf (1968) (*11*):993 **0.03**	1/39 = 0.026. If 21% of these 39 are immature (same as site 117) then 1/39(0.79) = 0.032
Ukraine (Vasiliv'ka) Telegin (1961) (*9*) **0.21**	44 individuals, 32 adults among which embeded points in individuals 5,12,33-36. Individual 6 was burried (along with 5) bound or with tendons cut. 7/32 Date from Guilaine and Zammit (2005) (*12*): 75-76
Ukraine (Volos'ke) Danilenko (1955) (*13*) **0.22**	3 (individuals 3, 5, and 10) with embedded points of 18 adults (two with very partial skelatal recovery). Others with severed limbs (15 probable, 16 definite). Included individuals 3,5,10 and 16: 4/18
Algeria (Calumnata) Dastugue (1970), Chamla (1970), Biraben (1970) (*14-16*) **0.04**	Of 53 age > 14 yrs, individuals 26 (traumatic fracture, p. 122) and 33 a (embedded point p. 123) Excluding a possible head wound p.124
S. California Lambert (1997) (*17*) **0.06**	54 /840 adults had projectile injuries excluding the Late Period (calibrated dates 1380-1804, contact was in 1542) that 'saw a coalescence of the traits we associate with chiefdoms' p. 102.
Central California Moratto (1984) (*18*) **0.05**	Disarticulated skeletons, points embedded in bone only p183 (> 5%) Total individuals not given. This estimate was given the average weight in the weighted means in Table 1.

Sweden (Skateholm I) Price (1985) (*19*) **0.07**	Points embedded in bone only 2/30 (adults, excluding 2 cremated individuals) p.350
France (Ile Teviec) Newell et al. (1979) (*20*) **0.12**	Of 16 adult individuals, individual 2 (blows) and 16 (embedded points).(pp 132-137)
Denmark (Bogebakken) Newell et al. (1979) (*20*) **0.12**	Of 17 adults (including non-aged), embedded points (individuals 7 and 19A (pp. 46-50)).
Central California Andrushko et al. (2005) (*21*) **0.08**	Young adults severed forearms 10/59 males 2/86 females. May have coincided with the 'emergence of more hierarchical social system" 383
Central California Jurmain (2001) (*22*) **0.04**	Adults at Yakima (SCI-038); 4 embedded and 3 associated points p. 19 excluding extensive craniofacial injuries (162 adults) plus Adults at Ala-329 10/248 p 19 excluding extensive craniofacial injuries
Gobero, Niger. Sereno et al. (2008) (*23*) **0.00**	Based on 35 of the approx. 200 burials at the site.
Sarai Nahar Rai (N.India) Sharma (1973), Kennedy et al. (1986) (*24, 25*) **0.30**	V, X and XIII (all from 1972 excavation by Sharma (1973) (*24*):138-9) with embedded or piercing microlithic points, of a total of 10 adults (including the Kennedy et al assemblage) Revised date from Kennedy (2000) (*26*) p. 197

Table S2. Sources for Ethnographic Evidence in Table 2. Notes: Based on data on forager demographics (from !Kung, Hadza, Hiwi and Ache populations in (*27*)) where explicit data are not available, estimates assume that 60 percent of the total population are 15 years or older and that the annual mortality among this group is 0.025 (estimated as the inverse of the life expectancy at age 15 for these four groups).

Population/ region/ dates/ δ	*Livelihood and society*	*Comment* (n = total population (census size), d = annual war deaths, D = total annual deaths of adults (15 years and older))
Ache, Eastern Paraguay pre-contact (1970) **0.30**	Forager: peccaries, tapir, deer, pacas armadillos capuchin monkeys, coatis, edible palms, fruit. Hill and Hurtado (1996) (*28*)	Total (aged >14) adult deaths due to violence from non-Ache in precontact period:: 46, total deaths in this group 153. p. 173. "During the 400 years since the first arrival of the Spaniards, the Ache have engaged in only hostile relations with outsiders. They did not trade, intermarry or visit..."p 41 Most war deaths were in conflicts with horticultural Guarani. Mortality in (inter Ache) club fights accounted for 8 percent of deaths of males > 15 years. (p.164) Other within group killing very rare.
Hiwi, Venezuela-Colombia pre- contact (1960) **0.166**	Forager: riverine mammals, turtles and fish, wild roots and fruit. Hill et al. (2007) (*29*)	Fraction of 76 pre contact adult (aged >14) deaths due to warfare and homicide committed by non-Hiwi; if both between Hiwi hostilities and conflicts with non Hiwi are included the fraction is 36%. Of these 46% of these are due to non Hiwi (p. 451). "Warfare/homicide" deaths committed by other Hiwi are excluded as possibly these are within group (i.e homicide not warfare).
Ayoreo Bolivia-Para-guay 1920-1979 **0.152**	Seasonal forager-horticulturalists. Bugos (1985) (*30*)	Deaths of known causes among the Direkendai Gosode populations: 1301 Total killed by members of other populations: 198. (p.89). This may be a substantial underestimate of earlier conditions given that "very few Ayoreo have died violently since 1950" p. 90.

Murngin NEArnhem Australia 1910-1930: **0.207**	Forager (honey, plant foods), hunting (kangaroo, emu, small/large birds), fishing (shellfish, misc. fish, freshwater tortoises, snakes). Warner (1931) (*31*)	n = 3,000 (p481). Recorded deaths from conflicts with other groups over the period: *gaingar* (29), *milwerangel* (3), *maringo* (35), *narrup* (27); total 93.Total deaths from 'fight within group' i.e. *nirimaoi yolno*: 2. p 457 (These were excluded.) Warner estimates that due to missing regions and other non-reporting, the actual number is twice this or d = 9.3 (p. 482). D = 3000x0.6x0.025 = 45. d/D = 0.207
Casiguran Agta Philippines 1936-1950 **0.049**	Semi-nomadic hunter gatherers: deer, pig, monkey, forest products fish. Headland (1989) (*32*)	Interpolating from population in 1936 and 1977, the average population in 1936-1950 was 894, of which an estimated 536 were adults. Excluding children and non-Casiguran Agta an estimated 10 were killed in four raids (2 of them by Ilokano farmers). D = 0.025x536; d = 10/14
Tiwi N.Australia 1893-1903 **0.100**	Hunting fishing (shellfish), foraging (roots, seeds, turtle eggs). Substantial reproductive skew. Pilling (1968) (*33*)	"In one decade at least 16 males in the 25-45 age group were killed in feuding either in sneak attacks or in arranged pitched battles. .. .over 10 percent ...males in that age category." Assuming this age-sex group is 1/4 of the adults we have 640 adults and d = 1.6, D = 640x0.025 = 16
Anbara , N. Arnhem Land, 1940-1960 **0.045**	Recently settled formerly nomadic maritime foragers. Hiatt (1965) (*34*)	n = 149 p.19. Anbara men killed by other groups: 2 (p. 121). D = (149x0.6x0.025 = 2.235 d = 0.1

Modoc California 1934 field work re 'aboriginal times.' **0.126**	Forager (hunting, fishing, roots); seeds of wocus (pond lily) was primary staple. seasonal foragers. Ray (1963) (*35*)	n estimated (by this author) from settlement data (p.201-111): 2384. Single battle seldom more often than once a year against Pitt Rivers tribes (p 134) in which 5 or 10 percent were killed 143; fighting unit consisted of ten to a hundred men 135. Midranges of above data d= 0.075x60 = 4.5 D = 0.025x0.6x2384 = 35.76

Table S3. Additional sources judged to be un-representative or unreliable.

Population	*Cited in*	*Origin*	*Comment*
Nubia Qadan	Keeley (1996) (*36*)	Wendorf (1968) (*11*)	No relevant data for a figure of 21 % of deaths due to warfare on the cited pages (or in the entire chapter). The only site other than 117 had evidence of violent death in 1/38 = 3% of the individuals (p. 993). This page is cited but these much lower figure is not.
Central Ca.	Keeley (1996) (*36*)	Walker and Lambert (1989) (*37*)	Selective use of data. Reported data (10 % of deaths due to warfare) refer to a sub period of the Walker-Lambert data set. Using the entire data set the figure is 6 %.
British Columbia	Keeley (1996) (*36*)	Cybulski (1994) (*10*)	Selective use of data.The two numbers cited (32 and 28 percent of all deaths due to warfare) refer to sub periods and regions of the Cybulski data set. The average over the entire data set is 23%.
Senoi Semai	Keeley (1996) (*36*)	Dentan (1979) (*38*)	Not hunter-gatherers. Described as "semi-sedentary horticulturists" ((*38*):vii) who keep chickens and in irrigated rice growing areas, water buffalo (p.33-4) and grow maize, tapioca, sweet potatoes and tobacco these acquired "sometime after the Portuguese first contacted Malaya in the 15th century." (p.47) "Present day Semai rarely dig up wild roots except in emergencies" when "crops fail." P. 47
Casiguran Agta	Wrangham et al. (2006) (*39*)	Headland (1989) (*32*)	Homicide, not warfare. The data (326 per 100,000) reported are for the homicide rate (p. 69) not for intergroup violence (on which evidence is presented (also on p. 69). The latter rate is much lower (75 per 100,000). See Table S2.
Yahgan	Wrangham et al. (2006) (*39*)	Cooper (1917) (*40*)	Homicide, not warfare.Cooper (p. 174) cites 22 cases of homicide among the Yahgans (1871-1884) but provides no data on intergroup conflict.
Andamanese	Keeley (1996) (*36*)	Radcliffe-Brown (1922) (*41*) via Wright (1942) (*42*)	Selective use of data, heavily impacted by colonial rule. 'The diminution of population has combined with other causes to alter considerably the mode of life of the islanders. What were formerly distinct and often hostile communities are now merged together.' Radcliffe-Brown (1922) (*41*) p. 19 Jarawa killed 4 in attacks (p. 86) on Andamanese friendly to the British (A-Pucikwar, Akar Bale and Aka Bea had a total of 96 members. p.16). The losses of these tribes were hence about 4/96 in a generation or 4/(96x30) per year, However most of Jawara attacks were against non-Andamese of whom they killed 29 (p.86).
Dobe !Kung	Wrangham et al. (2006) (*39*)	Lee (1979) (*43*)	No warfare data in Lee. (*44*):69 gives 15% (males) 8% (females) for 'violent causes of death" which from Lee are homicides. Description (without mortality estimates) of inter

			group lethal hostilities among Kung, Koisan in (*45*):pp 155-159
Canadian Eskimo	Wrangham et al. (2006) (*39*)	Graburn (1969) (*46*)	No warfare data. Graburn's "Causes of Death, 1945-1960" p. 150 include 'accidents' and 'other, and unknown' but not warfare.
Yorok	Keeley (1996) (*36*)	Kroeber (1953) (*47*)	Unrepresentative (bellicose) period. Based on a census in 1852 following "the greatest war of which the Yurok have recollection" Kroeber (1953) (p.126) that took place in 1830 or 1840. The Yorok had chiefs
Modoc	Keeley (1996) (*36*)	Ray (1963) (*35*)	Mis-estimated population size. Keeley's estimate of n = 1000 appears a substantial underestimate leading to an estimated rate of morality more than double what is likely. (See Table S.3). An estimate of n = 3000 (based on Kroeber) is in Cook (1971)p. 69
Piegan	Keeley (1996) (*36*)	Ewers (1955) (*48*) via Livingstone (1968) (*49*)	Unrepresentative and insufficient data. Based on a partial account of raids and battles involving Piegan, Ewers reports that "There must have been a number of years in which more than 1 percent of the total Piegan population died in battles large and small'(p. 212.) The relevant data (Table 7, p. 195) provide no way deriving an average over a span of years; and it is unclear how Ewers arrived at the above statement.
Kato	Keeley (1996)	Kroeber (1953) (*47*), Kroeber (1965) (*50*)	Data are from what appears to be a particularly bellicose (pre-contact) conflict with the Yuki (hence not representative). "The story refers to certain events in a bitter embroilment between Kato and Yuki." (*50*):395. Kato had chiefs. Related data for the Yuki are unrepresentative for the same reason.
Gidjingali	Wrangham et al (2006) (*39*)	Hiatt (1965) (*34*)	Hiatt provides data only on the Anbara community, not all Gidjingali (deaths in inter group conflicts, p. 121, population size, p.19). Using these numbers, 100,000(d/n) = 67, not the 148 reported.

3. Genetic differentiation among hunter gatherer populations

Table S4 gives presents the estimates of genetic differentiation among hunter-gatherer groups.

Population	*Index*	*F*	*SEE*
Indigenous Circumpolar Eurasian populations	F_{DT}	0.076	0.013
Native Siberian populations	F_{DT}	0.170	na
Native Siberian populations	F_{DG}	0.114	na
Ainu-Chukchi (*51*)	F_{GT}	0.075	0.037
Ainu-Eskimo (*51*)	F_{GT}	0.109	0.023
Chukchi-Eskimo(*51*)	F_{GT}	0.047	0.020
!Kung demes (Southern Africa)	F_{DG}	0.007	na
Southern African groups	F_{GT}	0.075	0.067
Southern African populations (from 18 groups)	F_{DT}	0.081	na
Aboriginal Australians (7 Arnhem Land populations(*52*)) [a]	F_{GT}	0.040	$p < 0.0001$
Aboriginal Australians (14 groups)	F_{GT}	0.042	0.025
Kaiadilt-Lardiil groups (Australia)	F_{DT}	0.081	na
Asmat-Mappi (Lowland Western New Guinea)	F_{DT}	0.056	na
Mbuti (Central Africa)-San (Southern Africa)	F_{GT}	0.149	0.046
Aka (between 'villages' in the same group)	F_{DG}	0.042	0.041
Aka (between groups)	F_{GT}	0.057	0.034
Aka (between 'villages' in all groups)	F_{DT}	0.097	na
Pygmy (between language groups) (*53*)[a]	F_{GT}	0.022	0.004

Table S4: Genetic differentiation among hunter-gatherer populations Except where noted, the data are from (*54*) where complete sources and methods are given. F_{DT} , F_{GT} , and F_{DG} are respectively between demes (the smallest groups) in the total population, between ethno-linguistic groups in the total population and between demes in the ethno-linguistic group. The mean F_{ST} of the 18 estimates is 0.074 (standard deviation: 0.042), while that for the 15 estimates between ethno-linguistic groups is 0.078 (0.040). Standard errors of the estimates (SEE) are not available (na) for some groups. Notes: a: These microsatellite-based estimates may underestimate the degree of genetic differentiation (*55-57*).

.

Additional data on genetic differentiation is available for the pairs of more geographically-separated hunter gatherer groups in Table S5. So as not to over-estimate the genetic differences among groups that in the distant past may have engaged in conflicts, these measures of genetic differentiation are not used in the paper (Table S4).

Two data sets – for Pygmies and Aboriginal Australians—provide microsatellite-based estimates of differentiation that are not directly comparable with the other measures and are likely to be underestimates (*55-57*)

The Pygmy estimate is based on recently collected data from 266 individuals at 15 autosomal microsatellite loci and is the mean of 24 estimates for pairs of populations in distinct language groups (*53*). The mean for all 36 pairs (including within language group estimates) is 0.019. The studied populations appear to have had extensive asymmetric gene flow from surrounding Bantu speaking farmers for at least the past 100 generations while being relatively reproductively isolated one from another by the surrounding Bantu populations. The mean effective group size is 3923.

A total of 8868 Aboriginal Australian individuals' genetic information at15 hypervariable autosomal microsatellite loci were studied (*52*). The information was collected for forensic purposes by the Australian Federal Police. It is unlikely that many of these individuals were engaged in hunting and gathering. Only 26 percent of Australia's Aboriginal population live in "remote areas" and the "non remote" individuals are of course much more likely to have been engaged in an offense that got the attention of the Australian police. The reported estimate Table S4 was selected because data on wartime mortality was also available from this region and because these are among the least acculturated populations most likely to resemble Pleistocene hunter gatherers.

Blood samples were available because each of these individuals was "associated" with an "offense" and the data are from Forensic and Technical Services of the Australian Federal Police. Only in the Northern Territories were "pure" and "declared" individuals identified. "The pure data set ...met a number of criteria: they live in a remote district, have a skin name, or were assigned as pure blood on the basis of information from the investigating officers. The declared data set comprises those who self-declared themselves as Aboriginal" (p.715). Table 1 "summary of Aboriginal data used in the analysis of genetic differentiation..." lists 6 tribes in which there are "pure" identified, a total of 359 individuals, and in these tribes the numbers of declared are 3055. So we may assume that mating among the pure and declared is significant, and that the designation pure may be more cultural than genetic.

Ethno-linguistic unit identification was done as follows. "All samples were provided with an accompanying geographic placeholder [that]...most commonly indicated the place of residence or the location of the forensic matter with which the individual was associated..." These locations were then associated with "a traditional region and also a tribal territory." The authors remark: "It is unlikely that all samples come from the regional or tribal populations assigned to them... It would be wrong to suppose ... that the location of the forensic matter corresponds exactly with the birthplace or homeland of the donor." 715. The resulting regional or tribal mis-assignment of individuals is the equivalent of heightened intergroup migration from the standpoint of measurement of genetic differentiation. The authors note additional reasons to think that genetic differentiation is underestimated in the Arnhem Land data (*58*).

Table S.5. Genetic differentiation among geographically separated hunter-gatherer populations Note F_{ST} estimates are above the diagonal, SEE's are below(*51*).

	San	Mbuti	Ainu	Eskimo	Chukchi	Australian
San			**0.244**	**0.222**	**0.165**	**0.270**
Mbuti			**0.323**	**0.333**	**0.255**	**0.429**
Ainu	0.052	0.087				**0.147**
Eskimo	0.046	0.075				**0.123**
Chukchii	0.053	0.078				**0.174**
Australian	0.055	0.103	0.026	0.031	0.058	

References and Notes

1. J. Hirshleifer, *Public Choice* **63**, 101 (1989).

2. J.-P. Bocquet-Appel, P.-Y. Demars, L. Noiret, D. Dobrowsky, *Journal of Archaeological Science* **32**, 1656 (2005).

3. S. McBrearty, A. Brooks, *Journal of Human Evolution* **39**, 453 (2000).

4. H. Lourandos, *Continent of Hunter-gatherers* (Cambrdige University Press, Cambridge, 1997), pp. 390.

5. R. C. Kelly, *Warless Societies and the Origin of War* (University of Michigan Press, Ann Arbor, 2000), pp.

6. S. A. LeBlanc, *Constant Battles* (St. Martins Press, New York, 2003), pp. 271.

7. P. Wiessner, *Evolution and Human Behavior* **23**, 407 (2002).

8. D. Nettle, *Journal of Anthropological Archaeology* **15**, 403 (1996).

9. D. Telegin, *Arkheologiya* **XIII**, 3 (1961).

10. J. Cybulski, in *In the wake of contact: Biological responses to conquest* C. S. Larsen, G. Milner, Eds. (Wiley-Liss, 1994) pp. 75-85.

11. F. Wendorf, in *The Prehistory of Nubia* F. Wendorf, Ed. (Southern Methodist University Press, Dallas, 1968), vol. 2, pp. 954-998.

12. J. Guilaine, J. Zammit, *The origin of war: violence in prehistory* (Blackwell, Oxford, 2005), pp. 282.

13. V. N. Danilenko, *Sovietskaya Etnografia* **3**, 54 (1955).

14. J. Dastugue, *Memoires du Centre de Recherches Anthropologiques, Prehistoriques, et Ethnographiques* **XV**, 119 (1970).

15. M.-C. Chamla, *Memoires du Centre de Recherches Anthropologiques, Prehistoriques, et Ethnographiques* **XV**, 1 (1970).

16. J.-N. Biraben, *Memoires du Centre de Recherches Anthropologiques, Prehistoriques, et Ethnographiques* **XV**, 127 (1970).

17. P. Lambert, in *Troubled Times: Violence and Warfare in the Past* D. L. Martin, D. W. Frayer, Eds. (Gordon and Breach, Amsterdam, 1997) pp. 77-109.

18. M. Moratto, *California Archaeology* (Academic, Orlando, 1984), pp.

19. T. D. Price, in *Prehistoric Hunter-Gatherers: The emergence of cultural complexity* T. D. Price, J. A. Brown, Eds. (Academic, Orlando, 1985) pp. 341-363.

20. R. R. Newell, T. S. Constandse-Westerman, C. Meikeljohn, *Journal of Human Evolution* **8**, 29 (1979).

21. V. Andrushko, K. Latham, D. Grady, A. Pastron, P. Walker, *American Journal of Physical Anthropology* **127**, 375 (2005).

22. R. D. Jurmain, *American Journal of Physical Anthropology* **115**, 13 (2001).

23. P. Sereno *et al.*, *PLoS ONE* **3**, 1 (2008).

24. G. R. Sharma, *Proceedings of the Prehistoric Society* **39**, 129 (1973).

25. K. Kennedy, N. Lovell, C. Burrow, "Mesolithic Human Remains from the Gangetic Plain: Sarai Nahar Rai" (Cornell University, 1986).

26. K. Kennedy, *God-Apes and Fossil Men: Paleoanthropology of South Asia* (University of Michigan Press, Ann Arbor, 2000), pp. 480.

27. M. Gurven, H. Kaplan, *Population and Development Review* **33**, 321 (2007).

28. K. Hill, A. M. Hurtado, *Ache life history: the ecology and demography of a foraging people* (Aldine de Gruyter, 1996), pp. 561.

29. K. Hill, A. M. Hurtado, R. S. Walker, *Journal of Human Evolution* **52**, 443 (2007).

30. P. E. Bugos, Doctoral Dissertation inAnthropology,Northwestern University (1985).

31. W. L. Warner, *Oceania* **I**, 457 (1931).

32. T. N. Headland, *American Journal of Human Biology* **1**, 59 (1989).

33. A. Pilling, in *Man the Hunter* R. Lee, I. DeVore, Eds. (Aldine, Chicago, 1968) pp. 157-158.

34. L. R. Hiatt, *Kinship and Conflict: A Study of an Aboriginal community in Northern Arnhem Land* (Astralian National University, Canbera, 1965), pp.

35. V. F. Ray, *Primitive Pragmatists: The Modoc Indians of Northern California* (University of Washington Press, Seattle, 1963), pp.

36. L. Keeley, *War Before Civilization* (Oxford University Press, New York, 1996), pp. 245.

37. P. Walker, P. M. Lambert, in *Advances in Paleopathology, Journal of Paleopathology: Monographic Publication No. 1* L. Cappasso, Ed. (Marino Sofanelli, Chieti, Italy, 1989) pp. 207-212.

38. R. Dentan, *The Semai: A non violent people of Malaya* (Holt, Rinehart and Winston, New York, 1979), pp.

39. R. W. Wrangham, M. L. Wilson, M. N. Muller, *Primates* **47**, 14 (2006).

40. J. M. Cooper, "Analytical and critical biography of the tribes of Tierra del Fuego" (1917).

41. Radcliffe-Brown, *The Andaman Islanders* (Cambridge, 1922), pp.

42. Q. Wright, *A Study of War* (University of Chicago Press, Chicago, 1942), pp.

43. R. B. Lee, *The !Kung San: Men, Women and Work in a Foraging Society* (Cambridge University Press, Cambridge, 1979), pp.

44. N. Howell, *The Demography of the Dobe!Kung* (Aldine de Gruyter (Second Edition), Hawthorne New York, 2000), pp.

45. I. Schapera, *The Khoisan Peoples of South Africa* (Routledge and Kegan Paul, London, 1930), pp. 450.

46. N. Graburn, *Eskimos without igloos* (Little, Brown and Company, Boston, 1969), pp.

47. A. L. Kroeber, *Handbook of the Indians of California* (California Book Company, Berkeley, 1953), pp.

48. J. Ewers, C, *The Horse in Blackfoot Indian Culture: With Comparative Material from Other Western Tribes* (Smthsonian Institution Press, Washington, D.C., 1955), pp.

49. F. B. Livingstone, in *War: The anthropology of armed conflict and aggression* M. H. Fried, R. Murphy, Eds. (Doubleday, New York, 1968) pp. 3-15.

50. A. L. Kroeber, in *Festschrift, publication d'hommage offerte au P. W. Schmidt* H. W. Koppers, Ed. (St. Gabriel-Modling, 1965) pp. 394-400.

51. L. L. Cavalli-Sforza, P. Menozzi, A. Piazza, *The History and Geography of Human Genes* (Princeton University Press, Princeton, 1994), pp. 541.

52. S. J. Walsh, R. John Mitchell, Natalie Watson, and John S. Buckleton, *Journal of Human Genetics* **52**, 712 (2007).

53. P. Verdu, Frederic Austerlitz, Arnaud Estoup, Renaud Vitalis, MyriamGeorges, Sylvain Thery, Alain Froment, Sylvie Le Bomin, Antoine Gessain, Jean-Marie Hombert, Lolke Van der Veen, Lluis Quintana-Murci, Serge Bahuchet, and Evelyne Heyer, *Current Biology* **19**, 1 (2009).

54. S. Bowles, *Science* **314**, 1569 (2006).

55. L. Jost, *Molecular Ecology* **17**, 4015 (2008).

56. P. Hedrick, *Evolution* **59**, 1633 (2005).

57. M. Sanetra, R. Crozier, *Molecular Ecology* **12**, 2281 (2003).

58. N. G. White, in *Arachaeology and lingusitics: Aboriginal Australians in global perspective* P. McConvell, N. Evans, Eds. (Oxford University Press, Oxford, 1997) pp. 45-81.