

Genetic Variation at the MC1R Locus and the Time since Loss of Human Body Hair¹

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The melanocortin 1 receptor (MC1R) locus makes a protein that affects the color of skin and hair. At this locus, amino-acid differences are entirely absent among African humans, abundant among non-Africans (especially Europeans), and abundant in chimpanzee/human comparisons (Rana et al. 1999, Harding et al. 2000). Previous studies have found no evidence of either directional or diversifying selection, so the pattern in these data has been attributed to tight selective constraint within Africa—a defense against the strong sunlight there—and relaxed constraint in Eurasia (Harding et al. 2000). This interpretation implies that genetic differences within Eurasia have an ancient history and suggests the likelihood of admixture between Neandertals and anatomically modern humans. We reanalyze these data here and interpret them differently. We suggest that adaptive evolution for sun-resistant MC1R alleles ensued when humans first became hairless savannah-dwellers. The level of neutral MC1R variation among African humans provides a lower bound for the time since this event.

Although there are no amino-acid differences at the MC1R locus among African humans, there are ten between the human last common ancestor and the chimpanzee (Harding et al. 2000). This suggests that selective constraint may have been weaker in the distant past. Furthermore, many of these differences are nonsynonymous (cause changes in the protein). This is surprising because, in functional genes, most nonsynonymous mutations are detrimental and are quickly removed by selection. Consequently, nonsynonymous differences tend to be rare. Between chimpanzee and the human last com-

mon ancestor, the number of synonymous differences per silent site is $K_s = 6/261 = 0.0230$ and the number of nonsynonymous differences per nonsilent site is $K_a = 10/693 = 0.0144$ (Harding et al. 2000:1352). Thus, $K_a/K_s = 0.63$, an unusually large number for a functional protein (Li 1997:180–81).

One view attributes this high nonsynonymous substitution rate to weak selective constraint (Harding et al. 2000). This requires that selective constraint be weak in the distant past (to account for chimpanzee/human differences) but strong in the recent past (to account for the absence of amino-acid variation among African humans). But if the African sun causes selective constraint now, why would this constraint have been weak in the past?

There are at least two obvious answers: selective constraint may have been weak in ancient hominids because they lived in forests or because their bodies were covered with hair. Several lines of evidence suggest that hominids were making extensive use of the savannah by 1.7 million years ago (Klein 1999:248–53). Some argue that hair was lost at this time, but this is controversial (see below). Whatever the timing, at some point in the past hominid bodies began confronting the African sun without the protection of forest or fur. It seems likely that this would have triggered selection for MC1R alleles that provide protection from sun. The resulting adaptive evolution may account for the high K_a/K_s ratio seen in comparisons between modern humans and chimpanzees.

To make this hypothesis credible, we need also to account for the pattern of variation in Eurasian MC1R data. In Eurasia (and especially in Europe) the majority of nucleotide differences are nonsynonymous. Indeed, K_a/K_s is about the same in comparisons among Eurasians as in the chimpanzee/human comparisons just discussed. Because of this similarity, the McDonald-Kreitman test provides no evidence for selection (Harding et al. 2000:1352). Yet if the nonsynonymous fraction is inflated by selection in the chimpanzee/human comparison, then selection is also needed to explain its value in Eurasians. The movement into northern climates may have favored fair skin because of the increased need to synthesize vitamin D or to protect against folate deficiency (Jablonski and Chaplin 2000). If so, selection would have favored any mutant MC1R allele that did not produce dark sun-resistant skin. This hypothesis accounts not only for the high Eurasian gene diversity but also for the large fraction of nonsynonymous Eurasian mutants. In addition, it accounts for the fact that the Eurasian gene genealogy is nearly star-shaped (Harding et al. 2000: fig. 2). Such genealogies are consistent with diversifying selection but not with a long history of neutral evolution in a population of constant size.

This hypothesis does not, however, explain the result of another statistical test, which also failed to show evidence of selection. The HKA test (Hudson, Kreitman,

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TABLE 1
Data Used in Pairwise HKA Tests

Locus	m	n	S	D	χ^2	p
MC1R	954	443	13	17.35	—	—
Xq13.3	10,000	47	16	5.02	5.68	0.003
ZhaoNC22	9,901	88	44	133.80	1.20	0.288

NOTE: m , the number of nucleotide sites used in estimating S and D ; n , haploid size of human sample; S , number of polymorphic nucleotide sites within human sample; D , mean difference between chimpanzee and humans; χ^2 , HKA goodness-of-fit statistic; p , significance of HKA test with MC1R estimated from 10,000 simulated data sets.

SOURCES: MC1R, Harding et al. (2000); Xq13.3, Kaessmann et al. (1999); ZhaoNC22, Zhao et al. (2000).

and Aguadé 1987) compares ratios of between-species to within-species differences at different loci. Absent selection, these ratios should be similar, and this is exactly what was found in a comparison between MC1R and beta-globin (Harding et al. 2000). We can suggest several reasons this analysis might have failed to detect selection even if selection were really present. First, we have suggested that selection on MC1R inflated differences both within and between these species. If so, it may have had little effect on the ratio of between-species to within-species differences. Second, the HKA test assumes that population size has been constant and may yield misleading results in a species with a complex demographic history (Hudson, Kreitman, and Aguadé 1987). Finally, beta-globin and MC1R both produce protein, so the two ratios may be similar because selection has affected the two loci in similar ways.

To investigate this last possibility, we performed two additional HKA tests (shown in table 1) using loci that do not produce protein and are outside of any known gene. One of these gave strong evidence ($p = 0.003$) for selection at MC1R, but the other result was not significant ($p = 0.288$). In aggregate, these tests provide qualified support for the view that selection has affected MC1R. They certainly provide no contrary evidence. A recent analysis by C. Huff (personal communication) provides additional evidence of selection at MC1R.

Where does this leave us? The hypothesis of relaxed selective constraint is difficult to reconcile with the star-shaped Eurasian gene genealogy, the relatively high K_a/K_s ratios, and the significant HKA result. The hypothesis of positive selection explains all this and is also consistent with the general weakness of statistical support for selection. We feel that, on balance, the evidence favors the positive-selection hypothesis. Although this case is not yet compelling, it seems worth asking how our interpretations of human history would change should the positive-selection hypothesis turn out to be correct.

The first casualty would be the inference that European alleles for red or blonde hair were derived from admixture with Neanderthals. That inference is based on the conclusion that the root of the European gene genealogy is several hundred thousand years old, a con-

clusion that was reached using a neutral model of evolution (Harding et al. 2000). If the European gene genealogy was shaped by diversifying selection, then the observed level of gene diversity could have been reached much more quickly.

But even if MC1R does not inform us about Neanderthal admixture, it may have a different story to tell. The hypothesis of positive selection implies that neutral variation at MC1R contains information about when human skin was first regularly exposed to strong sunlight. After this time, we suppose that some newly favorable allele swept to fixation under the influence of natural selection. There may have been several such sweeps, and (as discussed below) we assume that each sweep reduced gene diversity (π) to zero. After the most recent sweep, there would have been no further change in amino-acid sequence, but π would have increased gradually toward its equilibrium value, $\theta = 4Nu$, because of synonymous mutations. Here, N is diploid effective size of the African population and u is the rate of synonymous mutations per generation.

This process is illustrated in figure 1, which shows the trajectory of π under three assumptions about N . Consider first the hypothesis that African gene diversity is at mutation-drift equilibrium—that $\pi = \theta$. Since the observed gene diversity is $\hat{\pi} = 0.67$,² the equilibrium hypothesis

2. Harding et al. (2000) report that gene diversity is 0.0007 per nucleotide site within Africa, that the synonymous substitution rate is 2.3×10^{-9} per site per year, and that 261 of the 954 nucleotide

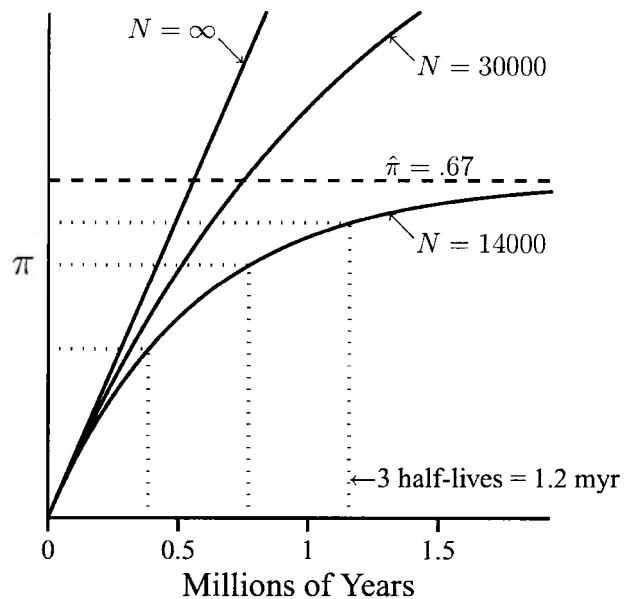


FIG. 1. Trajectories of π following a selective sweep under different assumptions about N , assuming that $\pi = 0$ just after the sweep. Dotted lines, half-lives of the process when $N = 14,000$; dashed line, $\hat{\pi}$, the observed value of π .

implies that $N \approx 14,000$. We cannot calculate the time since the selective sweep, because we cannot know how long the system has been at equilibrium. But we can calculate the time required to approach the neighborhood of equilibrium, and this will provide a minimum bound on the time since the sweep. The half-life is the time required for π to converge from any starting value halfway to θ (fig. 1). It equals $2N \ln 2$ generations (Rogers and Jorde 1995), or roughly $28N$ years, and π will reach the neighborhood of equilibrium in about three half-lives, or $84N$ years. With $N = 14,000$, this equals roughly 1.2 million years. Thus, the hypothesis of equilibrium implies that we have been hairless savannah-dwellers for at least 1 million years.

Perhaps, however, N was some larger value and African gene diversity is still below equilibrium. For any given N and observed π , we can calculate t , the time since the selective sweep.³ Figure 1 shows that larger values of N imply smaller values of t . For example, $t \approx 750,000$ years when $N = 30,000$. But if we allow N to increase without limit, t will converge toward a limit of about 560,000 years.⁴ No matter how large we imagine the African population to have been, we will not conclude that the most recent selective sweep occurred less than 560,000 years ago.

Finally, one might propose that N was much smaller than 14,000. Then the observed π would be larger than its expected value θ . This would imply that the population had recently suffered some catastrophe, such as a decline or a bottleneck in population size, that had reduced gene diversity. To make sense of the observed gene diversity, it would be necessary to assume that the predecline (or prebottleneck) population size was at least 14,000, and the arguments of the preceding two paragraphs would then apply to that population.

In summary, the lower bound on time since the most recent selective sweep is somewhere between 560,000 and 1.2 million years. The lower figure is unreasonable because it assumes that the African population was infinitely large. The upper figure is more plausible, since it rests on an assumption (that $N \approx 14,000$) that is consistent with estimates from other loci (Harding et al. 2000, Zhao et al. 2000). Thus it seems likely that humans

have been hairless savannah-dwellers for at least 1.2 million years.

These results bear on a variety of published hypotheses. Some authors argue that hairlessness was either a precondition for (Newman 1970) or a response to (Wheeler 1992) the evolution of bipedal locomotion. Others argue that it was a precondition for the evolution of larger brains (Jablonski and Chaplin 2000). These views are all consistent with the present results, since bipedal locomotion evolved at least 4 million years ago and brains began to increase in size about 2 million years ago (Klein 1999). Others see hairlessness as an adaptation that dissipates the heat generated by running after prey (Montagu 1964, Carrier 1984). Humans have been hunting for at least 400,000 and perhaps 2.5 million years. Under this hypothesis, the present results would imply that hunting appeared early. Finally, some argue that hairlessness evolved in response to clothing (Glass 1966, Kushlan 1985). The most recent variant of this argument (Pagel and Bodmer 2003) holds that hairlessness evolved to reduce parasite load, an adaptation that was made feasible by clothing and control of fire. There is no evidence of tailored clothing before about 20,000 years ago (Klein 1999:536) or even of hide scraping before 300,000 years ago (Toth and Schick 1993:161). Thus, the present results indicate that humans were naked before they were clothed.

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sites are silent. With generations of 20 years, these values imply that observed gene diversity is $\hat{\pi} = 0.67$ per sequence and that the synonymous mutation rate is $u = 1.2 \times 10^{-5}$ per sequence per generation ($\hat{\pi} = 0.0007 \times 954 = 0.67$, and $u = [2.3 \times 10^{-9}] \times 261 \times 20 = 1.2 \times 10^{-5}$).

3. We assume that $\pi = 0$ just after a selective sweep. This is a simplification, since some gene diversity can survive a sweep unless the selectively favored nucleotide is initially at full linkage disequilibrium with each polymorphic silent site. Nonetheless, the assumption seems reasonable, since linkage disequilibrium is likely to be high in a locus of only 954 nucleotides. We further assume that mating is random and that mutation obeys the model of infinite sites. These assumptions imply that $\pi(t) = 4Nu(1 - e^{-t/2N})$, where t is the time in generations since the selective sweep and N is the effective size of the African population (Li 1977: equation 6). For any given N and $\pi(t) < \theta$, this equation can be solved for t .

4. In the limit as $N \rightarrow \infty$, the equation in n. 3 becomes $\pi = 2ut$, a straight line as shown in figure 1. Setting π equal to its observed value and solving for t now gives $t = \hat{\pi}/2u = 27,811$ generations. If generations last 20 years, this is $t = 556,222$ years.

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Proximate Factors of Different Types of Grooming Hand-Clasp in Mahale Chimpanzees: Implications for Chimpanzee Social Customs¹

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Whether one would call it culture (e.g., Nishida 1987) or not (e.g., Tomasello, Kruger, and Ratner 1993), it has become clear from the accumulated data of long-term field

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studies of wild chimpanzees (*Pan troglodytes*) that they show quite a wide range of behavioral diversity that cannot simply be explained in terms of ecological differences (Whiten et al. 1999). Although de Waal (1999) has celebrated the maturity of "cultural primatology," studies of culture in nonhuman primates still seem to have a long way to go.

Laboratory studies have supplied us useful information, for example, whether particular kinds of social learning occur in nonhuman animals (see review by Tomasello and Call 1997). These studies are important because culture is usually regarded as being transmitted through some kind of social means and the details of such processes are often difficult to see in the wild. However, the settings of such studies are often too restricted, unnatural, or unusual for animals to show their potentials in the wild. Wrangham and others (1994) have pointed to the importance of recording and describing behavioral diversity in wild chimpanzees and likened it to ethnography (the term used earlier by McGrew [1992]). Many researchers have compiled and reviewed data on chimpanzee behavioral diversity (e.g., Nishida 1987, Sugiyama 1997, McGrew 1998, Boesch and Tomasello 1998, Whiten et al. 2001, Humle and Matsuzawa 2001). However, commenting on a paper on cetacean culture employing similar "ethnographic" methodology, Ingold (2001) has criticized such lists of behaviors as still being a million miles from the practice of ethnography by cultural anthropologists or sociologists. His critique is too demanding in its insistence that culture requires intentions, purposes, and values. Such concepts in anthropology are usually obtained by fully language-based interviews, and even so it is hard to know another's true intentions, purposes, and values because people sometimes do not or cannot say what they really think or intend. Nevertheless, his critique is partly justified in that such lists of traits tend to leave behind the stuff of everyday life (Fox and King 2002), and to understand their "culture" we still need more detailed descriptions of what chimpanzees do in the wild.

Among the so-called cultural behaviors of chimpanzees, various types of tool use have been relatively well described (e.g., McGrew 1992), but social behaviors or social customs have received less attention (see review by Nakamura 2002). The grooming hand-clasp is the first case of social behavior documented as custom in the chimpanzees of K-group in the Mahale Mountains of western Tanzania (McGrew and Tutin 1978). It is also observed in Mahale M-group, Kibale (both Kanyawara and Ngogo), Kalinzu, Lópe, and Taï (performed only habitually) but never in Gombe, Budongo, or Bossou (see Nakamura 2002). It has also appeared in at least one captive chimpanzee colony (de Waal and Seres 1997). McGrew and others (2001) have reported that there are two different types of grooming hand-clasp: palm-to-palm and non-palm-to-palm. In the former type, the two chimpanzees truly clasp each other's hands with mutual palmar contact (fig. 1, A), while in the latter only one or neither hand clasps the other (fig. 1, B-D) and usually the hands are flexed with one limb resting on the other

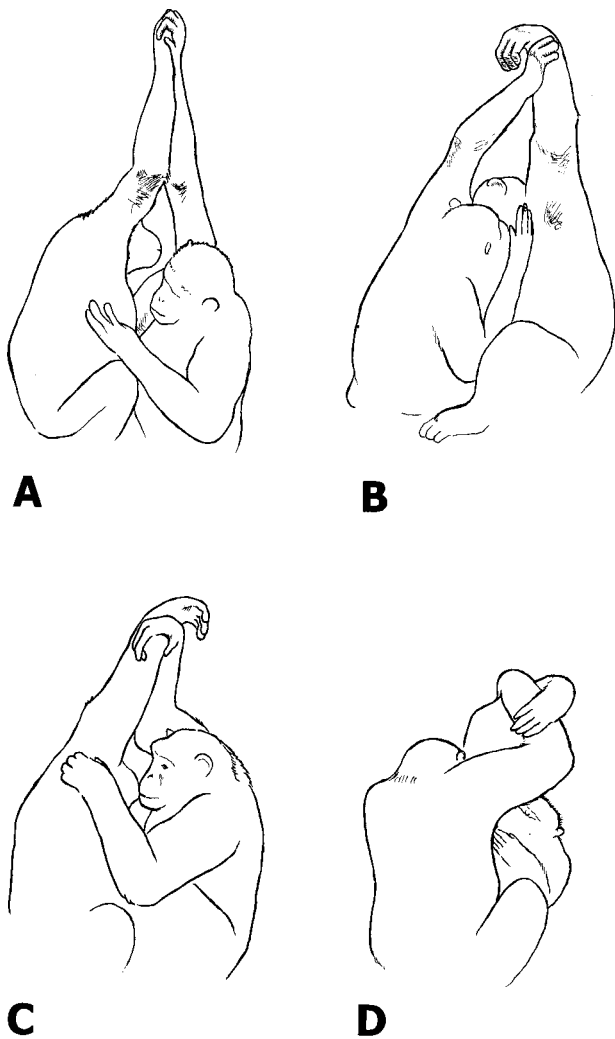


FIG. 1. Examples of various types of grooming hand-clasp observed in Mahale M-group. A, typical palm-to-palm, in which elbows and wrists of both parties are straight; B, both elbows straight but not palm-to-palm; C, elbow of one party straight and the other's flexed; D, a very flexed type not observed in K-group. (Drawn from video footage by Nakamura.)

(as in fig. 1, C). In their retrospective analysis of photographs and videos, they argue that the palm-to-palm hand-clasp dominated in K-group and was not observed in M-group. Although these observations may seem minor, their implications are important because there are so many subtle behavioral variations in human gestural communication (see, e.g., Morris 1994). A detailed study of these minute differences would be important for understanding the origin of the behavioral variations among cultures.

Unfortunately, McGrew and colleagues' analysis is based on a rather small number of samples (9 photos from K-group and 6 from M-group), and the identities of the

K-group individuals are not presented. Thus we cannot rule out the possibility that some individual(s) contributed a large proportion of the samples. The objective of this paper is to test McGrew and colleagues' idea that the palm-to-palm hand-clasp is a custom of K-group and not of M-group with a larger data set. In addition, we would like to investigate the proximate factors that likely produce the different types of grooming hand-clasp, considering whether consistent patterns are observed only at an individual level or also at the level of the group.

Perhaps because McGrew and colleagues strictly define only palm-to-palm (i.e., mutual palmar contact), with non-palm-to-palm being treated as a complementary set of palm-to-palm, the non-palm-to-palm pattern includes several types that grade into each other. Some grooming hand-clasps (e.g., fig. 1, B) are regarded as non-palm-to-palm even though their arms are both stretched as in the typical palm-to-palm. However, in other types of non-palm-to-palm, the hands are much more flexed (fig. 1, D). Thus, we made additional analyses on the angles of the wrist and the elbow rather than using palm-contact as a single measure.

METHODS

We analyzed photographs and videotapes of the grooming hand-clasp performed by the chimpanzees of K (Kajabala)-group and M (Mimikire)-group. These two groups have been habituated and studied for decades (Nishida 1990, Nishida, Uehara, and Kawanaka 2002). K-group was the initial focus of detailed studies after habituation in 1965 (Nishida 1968), but it had become almost extinct by 1983, and some females subsequently transferred to neighboring M-group (Nishida et al. 1985). K-group continued to exist for more than four years as a bisexual group, but by 1987 only a lone male was left, and he was observed sporadically until at least 1992 (Uehara et al. 1994). M-group has been continuously studied since 1968 (Nishida and Kawanaka 1972).

We analyzed 24 photographs of the grooming hand-clasp in K-group taken between 1973 and 1978 and 20 photographs and 56 still images from videotapes of the grooming hand-clasp in M-group taken between 1994 and 2000. We used only photographs in which both participants were identifiable. When we took a still image from a video, we chose the frame in which the clasped hands reached the highest point.

For individual analyses, we used only data on those who showed the grooming hand-clasp with at least three different partners to see whether they showed a consistent tendency regardless of the partner. Table 1 shows the profiles of individuals who met this condition. Of these individuals, GW and MA, who immigrated from K-group to M-group, are especially interesting. GW was observed to perform the grooming hand-clasp in both groups, but MA did not perform it when he was in K-group, perhaps because of his youth. For each individual,

TABLE 1
Profiles of Individuals Used in the Analysis

Names	Abbreviations	Observation Group ^a	Natal Group	Year of Birth	Year of Immigration		Remarks
					To K	To M	
Males							
Kamemanfu	KM	K	K?	Unknown	–	–	–
Sobongo	SB	K	K?	1958?	–	–	–
Kalunde	DE	M	M?	1963?	–	–	–
Masudi	MA	M	K	1977	–	1982 ^b	–
Fanana	FN	M	M?	1978?	–	–	–
Dogura	DG	M	M?	1981?	–	–	–
Carter	CT	M	M	1985	–	–	–
Pimu	PM	M	M	1988	–	–	Son of <i>FT</i>
Primus	PR	M	M	1991	–	–	Son of <i>PI</i>
Females							
Wantangwa	<i>WT</i>	K	Other?	Unknown	Unknown	–	–
Chausiku	<i>CH</i>	K	K	1958	–	1979	–
Wakusi	<i>WX</i>	M	Other?	1961?	–	Unknown	–
Gwekulo	<i>GW</i>	K, M	Other?	1962?	1972	1979	–
Fatuma	<i>FT</i>	M	Other?	1963?	–	Unknown	Mother of PM
Pinky	<i>PI</i>	M	Other	1972?	–	1983	Mother of PR
Christina	<i>XT</i>	M	Other	1975?	–	1987	–
Miya	<i>MJ</i>	M	Other	1980?	–	1991	–

NOTE: Question marks represent estimations.

^aThe group for which photographs of the grooming hand-clasp were available.

^bImmigrated with his mother (see Takahata and Takahata 1989).

the two researchers independently judged the following three variables: angle of the wrist, angle of the elbow, and palm contact. The angles of the wrist and the elbow were roughly categorized as straight (180°–150°), middle (150°–120°), and flexed (120°–). Any finer estimation would have been unreliable because of the different conditions of the photographs and/or the different angles of the individuals shown in them. We also judged whether the individual's palm made contact with the other's hand, wrist, or arm. The results of these analyses by the two researchers were combined, and we used data for statistical analysis only when the judgments of the two agreed.

RESULTS

Palm-to-palm and non-palm-to-palm. Palm-to-palm hand-clasps were observed in M-group. The proportion of palm-to-palm hand-clasps was significantly higher in K-group (41.7%, 10/24) than in M-group (5.3%, 4/76) (Fisher's exact probability test, $p < .001$, two-tailed). However, in contrast to McGrew and colleagues' results, it was not dominant over non-palm-to-palm even in K-group. It is notable that all four cases of palm-to-palm in M-group included *GW* as one of the participants. In each case, *GW* performed palm-to-palm with different partners (namely, PR, *WX*, *XT*, and *NK*) and also performed the non-palm-to-palm pattern with these individuals.

Angle of the wrist. Table 2 shows the results for angle of the wrist. Most cases were judged as either straight or flexed, and in most cases (91%) the judgments of the

two researchers agreed. *KM* and *GW* (when in M-group) were significantly biased straight, while *SB*, *DE*, *DG*, *CT*, *PM*, and *PI* were significantly biased flexed. Although others did not show significant bias (perhaps because of smaller sample sizes), they also seemed to have a tendency to be biased either straight or flexed.

At the group level, M-group members were significantly biased flexed (Wilcoxon signed rank test, $n = 11$, $T = 10.5$, $p < .05$), while no such tendencies were found in K-group members. Both groups included individuals representing straight and flexed types, but the only individual who consistently showed the straight type in M-group was *GW*. When *GW* was in K-group, she also showed the straight type. Although her samples in K-group were too few for a statistical test, she showed the straight type in three of the four cases and the remaining case was judged straight by one researcher and as middle by the other. In brief, *GW* almost always showed the straight type, whether in K-group in the 1970s or in M-group between 1994 and 2000. Among males, who usually experience only a single group (except for *MA* [see table 1]), *KM* and *SB* of K-group showed opposite tendencies, whereas all the males with enough samples in M-group were significantly biased flexed (those with fewer samples also seemed to show the same tendency) except for *PR*, who showed a mixture of the two types.

Angle of the elbow. Table 3 shows the results for the angle of the elbow. These angles were more often judged middle than the angles of the wrist, and the agreement between the two evaluators was only 64%, much less than for the wrist angles. This does not mean, however, that the elbow angles are difficult to estimate (see dis-

TABLE 2
Angle of the Wrist in the Grooming Hand-Clasp

Individual ^a	S/S	S/M	M/M	M/F	F/F	?	Total	<i>p</i> (S/S vs. F/F) ^c
K-group								
KM	8	2	—	—	—	2	12	< .01
SB	—	—	2	—	13	—	15	< .001
WT	—	—	—	—	5	—	5	—
CH	1	—	—	—	1	2	4	—
GW ^b	3	1	—	—	—	—	4	—
Total	12	3	2	0	19	4	40	
M-group								
DE	1	—	—	—	15	—	16	< .001
MA	—	—	2	—	4	—	6	—
FN	—	—	—	—	5	—	5	—
DG	—	—	1	—	10	—	11	< .01
CT	—	—	—	—	9	—	9	< .01
PM	—	—	—	—	8	—	8	< .01
PR	5	—	—	1	5	3	14	n.s.
WX	2	2	—	—	2	—	6	—
GW ^b	15	—	2	—	—	1	18	< .01
FT	1	—	2	—	5	—	8	n.s.
PI	1	—	—	—	16	—	17	< .001
XT	1	—	—	—	6	1	8	n.s.
MJ	1	—	—	—	6	1	8	n.s.
Total	27	2	7	1	91	6	134	

NOTE: S, straight; M, middle; F, flexed; ?, not visible or uncertain. S/S means that the judgments of the two researchers were both straight, S/M means that one researcher judged the angle straight and the other middle, and so forth.

^aSee table 1.

^bData on GW are available in both groups.

^cBinomial test.

TABLE 3
Angle of the Elbow in the Grooming Hand-Clasp

Individual ^a	S/S	S/M	M/M	M/F	F/F	?	Total	<i>p</i> (S/S vs. F/F) ^c
K-group								
KM	8	3	—	—	—	1	12	< .01
SB	9	5	1	—	—	—	15	< .01
WT	4	—	1	—	—	—	5	—
CH	1	1	—	—	—	2	4	—
GW ^b	3	—	—	1	—	—	4	—
Total	25	9	2	1	0	3	40	
M-group								
DE	2	4	3	3	4	—	16	n.s.
MA	3	1	1	—	1	—	6	—
FN	1	2	1	1	—	—	5	—
DG	1	4	2	1	3	—	11	—
CT	1	2	2	2	2	—	9	—
PM	1	3	2	1	1	—	8	—
PR	8	1	5	—	—	—	14	< .01
WX	3	3	—	—	—	—	6	—
GW ^b	9	4	2	—	3	—	18	n.s.
FT	2	3	1	2	—	—	8	—
PI	4	2	3	4	4	—	17	n.s.
XT	5	1	1	—	1	—	8	n.s.
MJ	3	1	1	2	1	—	8	—
Total	43	31	24	16	20	0	134	

NOTE: S, straight; M, middle; F, flexed; ?, not visible or uncertain. S/S means that the judgments of the two researchers were both straight, S/M means that one researcher judged the angle straight and the other middle, and so forth.

^aSee table 1.

^bData on GW are available in both groups.

^cBinomial test.

cussion). At the individual level, two K-group males (KM and SB) and one M-group male (PR) were significantly biased straight. No individuals were judged significantly biased flexed.

At the group level, we cannot conduct a statistical test on K-group because of the small number of samples ($n = 5$), but it is notable that straight judgments by both judges were most frequent for all of these five individuals and no one was ever judged flexed by both judges. There was no significant difference between straight and flexed in M-group members (Wilcoxon, $n = 11$, $T = 11.5$, n.s.), and many individuals performed the flexed type of hand-clasp as often as the straight type. Interestingly, *GW*, who also never showed the flexed type when she was in K-group, performed the flexed type in three instances in M-group.

Palm contact. Table 4 shows the results for palm contact. The agreement of the two judges was 81%. There were no clear individual tendencies, but *KM* and *GW*, who showed straight wrists, tended to show palm contact more often. However, *PM* and *PI*, who showed flexed wrists, also consistently contacted palms. There was no individual whose palm was consistently without contact.

DISCUSSION

Is palm-to-palm a custom of K-group? In a strict sense, our results have disproved McGrew and others' (2001) claim that the palm-to-palm hand-clasp is a custom only of K-group because palm-to-palm was observed in M-group as well. This does not, however, mean that their hypothesis is invalid, because all of the observations of palm-to-palm in M-group included *GW*, who had transferred from K-group. It is therefore possible that palm-to-palm is a custom only of K-group, where *GW* had acquired it. The occurrences of the palm-to-palm hand-clasp in M-group do not mean that *GW* had successfully transmitted the pattern to M-group, because it was much less frequent than in K-group and no M-group individual performed it without her. It is also noted that a very flexed type of grooming hand-clasp (see fig. 1, *D*) was observed only in M-group. This is not likely a chronological difference because we have one photograph of M-group chimpanzees (perhaps two adult males) taken in 1973 showing a very flexed type of hand-clasp.

Proximate factors of the grooming hand-clasp. In the palm-to-palm hand-clasp described by McGrew and others (2001), the wrists of the two performers stretch and palms are truly clasped. It occurs when both of the participants individually employ the straight type of hand-clasp in their wrists and elbows and the contact type in their palms. When one participant straightens its wrist, its palm will likely contact the other's hand or arm. Since non-palm-to-palm is defined as a complementary set of palm-to-palm, it includes various types of grooming hand-clasp. Non-palm-to-palm hand-clasps occur when one or both of the participants flex wrists and make no palm contact. Different types of non-palm-to-palm occur when one party straightens (fig. 1, *B*) or flexes (fig. 1, *D*)

TABLE 4
Palm Contact in Grooming Hand-Clasp

Individual ^a	+/+	+/-	-/-	?	Total	p [+/+ vs. -/-] ^c
K-group						
KM	12	-	-	-	12	< .001
SB	5	8	2	-	15	n.s.
WT	4	1	-	-	5	-
CH	2	-	-	2	4	-
GW ^b	4	-	-	-	4	-
Total	27	9	2	2	40	
M-group						
DE	4	4	4	4	16	n.s.
MA	4	2	-	-	6	-
FN	1	1	3	-	5	-
DG	5	2	4	-	11	n.s.
CT	4	-	4	1	9	n.s.
PM	6	1	-	1	8	< .05
PR	7	1	4	2	14	n.s.
WX	1	-	5	-	6	n.s.
GW ^b	18	-	-	-	18	< .001
FT	6	-	2	-	8	n.s.
PI	13	2	-	2	17	< .001
XT	3	2	3	-	8	n.s.
MJ	4	1	2	1	8	n.s.
Total	76	16	31	11	134	

NOTE: +, contact; -, no contact; ?, not visible or uncertain. +/+ means that the judgments by both researchers were contact, +/- means that one researcher judged contact and the other no contact, and so forth.

^aSee table 1.

^bData on *GW* are available in both groups.

^cBinomial test.

the wrist, and the degree of flexion also creates variations.

Our data showed that individuals had consistent tendencies for wrist angles but not for elbow angles. In wrist angles, few cases were judged middle and the two evaluators' judgments mostly agreed. This means that individuals' wrist angles are usually either completely flexed or completely straight. For the elbow angles, however, a judgment of middle was more common, and disagreement between the two evaluators' judgments may have occurred in the case of angles on the boundary between two grades. For instance, when one's elbow is about 150°, it may be judged as straight or middle, while there may not be such fluctuations of judgment when the angle is closer to 180° or 90°.

Only two individuals, one in each group, consistently showed straight wrists. Again, the one in M-group was *GW*. If palm-to-palm is a custom of K-group, there should be more individuals showing the straight wrist type, but the other male in K-group (*SB*) consistently flexed his wrist. Therefore we assume that making the wrist straight may not have been a custom of K-group. The flexed wrist may, however, be a custom of M-group, especially for males. Straight elbows seem to be the norm in K-group but not in M-group.

Figure 2 summarizes our hypothesis for proximate factors of the grooming hand-clasp. In K-group, the wrist may be straight or flexed, depending on the individual,

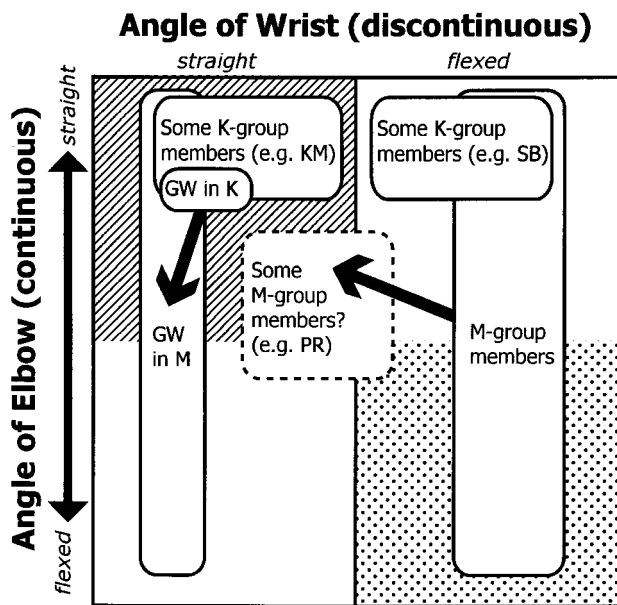


FIG. 2. Hypothetical schema of proximate factors of different grooming hand-clasps. When two individuals in the shaded part perform the grooming hand-clasp with each other, it becomes palm-to-palm, and when two individuals in the dotted part do so it becomes very flexed, as in figure 1, D. Arrows indicate possible effects of GW's immigration to M-group.

but everyone's elbow should be straight. In M-group, the wrist should be flexed, but the elbow can be anything from straight to flexed, even in the same individual. The grooming hand-clasp becomes palm-to-palm when two individuals in the shaded square in figure 2 perform it with each other and therefore probably occurs among some members of K-group. In M-group, because wrists are usually flexed, palm-to-palm is not expected to occur frequently. However, in accordance with GW's consistently straight wrist, some M-group members seem to have given way so that some palm-to-palm contact occurred with her. However, GW also seems to have changed her K-group style somewhat in accordance with the norm of M-group members, often flexing her elbow.

Interestingly, one adolescent male, PR, showed a rather extraordinary style among M-group males: he often made his wrist straight and consistently made his elbow straight. (His mother, PI, showed the typical M-group style [flexed wrist and continuous elbow].) One possibility is that this was because of his small body size: he was in early adolescence in 2000 and smaller than adult conspecifics. If an individual with a shorter hand performed the grooming hand-clasp with an adult, he would have to straighten his arm to reach the same height. However, another explanation is possible: PR's mother was closely associated with GW during his childhood and very often groomed with her in 1996–97 (Nakamura, unpublished data). Because PR stayed close to

PI, he often joined in grooming with GW. Thus, it is possible that, when he was sensitive to learning the grooming hand-clasp (at four to five years), he spent a long time with GW's nonstandard style and learned it socially. It will be interesting to see how his pattern develops as he becomes an adult.

Changes in the custom in relation to group transfer. Although our findings call for some corrections of the ideas of McGrew and others, we have confirmed that there was a subtle but concrete difference between the two neighboring groups. Because chimpanzee females usually transfer between groups (Nishida and Kawanaka 1972), they have to cope with such differences. McGrew and others predict that females will change their customs when they move to a different group, but our data do not support this idea: GW persisted in her old style 21 years after her immigration to M-group, despite its being different from the M-group norm. There are some reports of females' showing idiosyncratic feeding habits (Matsuzawa 1994, Sakamaki 1998), implying that they retained the customs of their former groups. However, our results are much more complicated than the cases of feeding in that GW not only retained parts of her old style but also modified some of them. Another M-group female, NK, had also immigrated from K-group, but we did not have enough data to judge whether she showed a similar pattern. There was no evidence that MA, a K-group-born M-group male, showed any K-group-like styles, perhaps because he was very young when he transferred to M-group (Takahata and Takahata 1989).

It is impossible to know now what really happened when GW, with her heterogeneous pattern, immigrated into M-group. However, her current pattern implies that no sanction-like responses occurred. Given that she partly changed her ways and some members of M-group adopted some of her patterns, it can be said that they did not wholly reject or compromise with the unfamiliar pattern but somehow coped with it through repeated interactions in their daily life.

In detailed studies of chimpanzee tool use, stress is often placed on the way in which "transmissible particles of information" (Ingold 2001) are transferred from one individual to another or functionally shaped. However, as our study has shown, what chimpanzees are doing in social customs does not seem to be a simple transfer of such information and is questionable whether it is useful to look for the functions of these patterns. If we regard "culture" as properties emerging through social interaction, without emphasizing its intellectual or functional aspects, studying the way in which chimpanzees shape their social customs may help us to understand the generation of culture.

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A Direct AMS Radiocarbon Date on the Barma Grande 6 Upper Paleolithic Skeleton¹

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Barma Grande is a large, high, deep cavity in the complex of caves and rock shelters located at the westernmost end of the Ligurian coast near the village of Grimaldi. Beginning in the second half of the nineteenth century, the site of Grimaldi, also known as the "Balzi Rossi" because of the reddish colour of the rocks, yielded abundant archaeological remains including important Upper Paleolithic mobiliary and parietal art and single and multiple burials (Rivière 1887, de Villeneuve et al. 1906–19, Vicino and Simone 1972, Bisson and Bolduc 1994). Because of the early discovery of the archaeological importance of the caves and the intensity of the subsequent amateur activity, the stratigraphy of most of the deposits is poorly known and records of the excavations are scanty. This lack of knowledge is particularly severe for Barma Grande, whose extraordinarily rich Upper Paleolithic layers were completely excavated unsystematically towards the end of the nineteenth century. Among the results of this activity, which became particularly intense between 1884 and 1894, were the discoveries of three single burials and a spectacular triple burial (Verneau 1906, 1908).

The first burial was found by Louis Jullien, a French antiquities dealer, who discovered the skeleton of an

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adult male (Barma Grande 1, hereafter BG 1) buried close to the entrance of the cave 8.40 m beneath the original floor of the cave. In addition, the deposits removed by Jullien yielded two or possibly more "Venus" figurines, including the "yellow steatite figurine" and the "woman with goitre." The history of these figurines, as well as of others probably found in the nearby Grotte du Prince (Grotta del Principe), is obscured by personal rivalries and by the scepticism of this period about the existence of Upper Paleolithic art. Suffice it to say that information about the discovery of these art objects is very vague and is essentially drawn from a letter written by Jullien about 20 years later (Breuil 1928). By contrast, more precise and reliable records exist about the position and depth of the burial found by Jullien and of those found a few years later by the owner of the cave, Giuseppe Abbo.

The excavations carried out by Abbo led to the discovery of three additional burials. The first burial was found approximately in the middle of the cave at a depth of about 8 m and included an adult male and two adolescents. The three specimens are indicated as Barma Grande 2, 3, and 4 (BG 2, BG 3, and BG 4) according to their distance from the entrance of the cave. Two additional single burials (Barma Grande 5 and 6) (BG 5 and BG 6) came to light in the rear of the cave, one after the other, at 6.40 m depth (fig. 1).

All the Barma Grande burials, like most of the Grimaldi skeletons (i.e., Barma del Caviglione 1, Bausu da Ture 1, 2, and 3, Grotte des Enfants 4, 5, and 6) are attributed to Würm III, between 30,000 and 20,000 years B.P. (Palma di Cesnola 1976, Mussi 2001a), on various grounds. As far as the Barma Grande skeletons are concerned this attribution is inferred basically from distinctive grave goods and ornaments and their similarities with those associated with burials from nearby sites that have a firm stratigraphic position. Among these the most significant is the burial of "Il Principe" from Arene Candide Cave (Finale Ligure, Savona), located on the Ligurian coast about 100 km east of Grimaldi. Soon after the discovery of "Il Principe," Cardini (1942) noticed important

parallels in its grave goods and ornaments with some of the Barma Grande burials and striking similarities in particular with those found in the triple burial. These include, among others, the singular incised "plano-convex bone pendants" and the extraordinarily long flint blades held by "Il Principe" and by BG 2 and BG 3 (Verneau 1906, 1908). Interestingly, the blades are made on flint deriving from a common source in the Vaucluse, in southern France (Negrino and Starnini 2003).

The typological approach followed by Cardini and subsequently by Mussi (1986) was the only means available to "date" the burials until the mid-1980s. At this time, developments in absolute dating techniques and in particular the possibility of obtaining direct AMS radiocarbon dates from human bones with little loss of material changed the situation significantly. In the early 1990s an AMS radiocarbon measurement was performed on a rib fragment from the adult male of the triple burial (BG 2). The resulting uncalibrated age of $14,990 \pm 80$ B.P. (Beta 63510, CAMS 7641) was more recent than expected on the basis of the reported similarities with the Arene Candide burial. This latter skeleton has been directly dated to $23,440 \pm 190$ B.P. (OxA-10700) (Pettitt et al. 2003), which is in agreement with the existing ^{14}C dates from charcoals from the overlying and underlying layers (Bietti and Molari 1994).

While further tests were planned to check the result, dates obtained from animal bones found by Jullien in Barma Grande and rediscovered in Canada, where he emigrated (Bisson, Tisnerat, and White 1996), seemed to confirm the unexpectedly recent date of the BG 2 skeleton. The specimens used by Bisson and coworkers include an ungulate long bone fragment found at an unknown depth, a rodent femur found at about 6 m depth, and a red deer antler labelled as found at 8 m depth, that is, at the base of the Upper Paleolithic deposits. The resulting dates were $14,110 \pm 150$ B.P., $17,200 \pm 180$ B.P., and $19,280 \pm 220$ B.P., respectively. According to Bisson, Tisnerat, and White (1996) these dates indicate the absence of a Gravettian occupation of the cave and

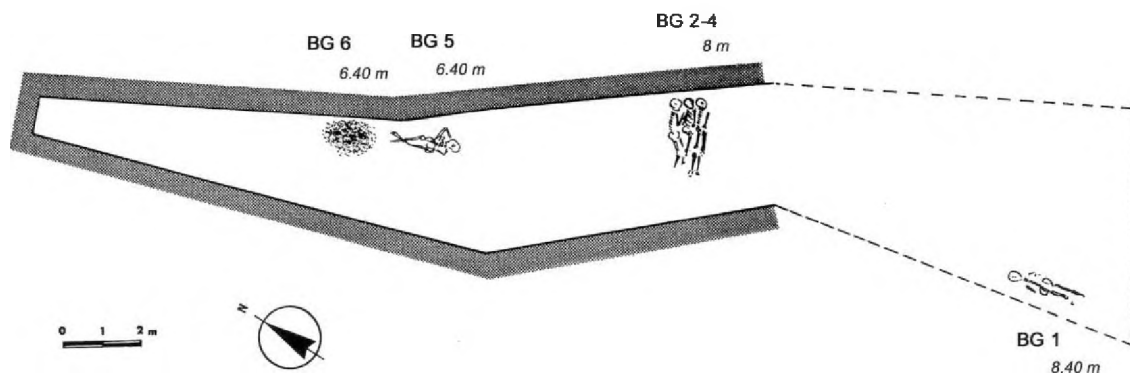


FIG. 1. Schematic reconstruction of positions and depths of the Barma Grande burials (from Mussi 1986). The part of the cave within the broken line has been destroyed by quarrying activities.

point to an Epigravettian age for both the burials and the "Venus figurines." In a recent paper dealing with Middle and Early Upper Paleolithic (i.e., Aurignacian and Gravettian) burials (Riel-Salvatore and Clark 2001), the Barma Grande skeletons are explicitly excluded from the analysis. The suggested chronology, however, has been strongly criticized (Mussi 2001b), and we agree with these criticisms for the following reasons: (1) The result provided by the first specimen, found at an unknown depth, and the date obtained from a very small and potentially stratigraphically mobile rodent are irrelevant from a chronostratigraphic perspective. (2) A clear stratigraphic relationship with the burials cannot be demonstrated for any of the three specimens dated. (3) The result of ca. 19,000 B.P. from a sample apparently deriving from the lowest Upper Paleolithic strata of Barma Grande is in clear contradiction with the presence of diagnostic Aurignacian and Gravettian tools in the cave (de Villeneuve et al. 1906–19, Cardini 1930–31, Bolduc, Cinq-Mars, and Mussi 1996) and with the widespread evidence of occupation of the Grimaldi site during this time period (e.g., Grotte des Enfants, Barma del Caviglione, Riparo Mochi, Riparo Bombrini) (Rivière 1887, Palma di Cesnola 1976, Onoratini and Da Silva 1978, Vicino 1986, Kuhn and Stiner 1998, Alhaique et al. 2000).

As far as Barma Grande is concerned, Bisson, Tisnerat, and White (1996) stress the potential bias affecting old collections due to selection of specific tools by early excavators and warn against the risks of the typological approach, claiming that both Aurignacian and Gravettian artefacts can be part of Epigravettian assemblages. This point is well taken, although Bolduc, Cinq-Mars, and Mussi (1996) document tools such as carinated end-scrapers and large La Gravette points that are not part of the Italian Late Epigravettian inventory. However, the stratigraphy of Barma Grande has been irreparably lost, and the only reliable source of information is that provided by the burials and their known location and depth in the deposit. Thus, in planning a programme of direct AMS ^{14}C dating of Upper Paleolithic skeletons from Liguria, one of the most important goals was to verify the existing BG 2 date and to test the skeletons from the two additional single burials found by Abbo. Bone samples were drilled from a femur of BG 2 and from the humerus of BG 5, while for BG 6 a whole metatarsal bone was used. Although not completely successful, the programme provided important results. In particular, while tests from BG 2 and BG 5 failed because of the very low level of collagen preservation in the samples, a direct AMS data was obtained from the complete metatarsal bone of BG 6. The sample was pretreated and measured using the standard Oxford methods (table 1).

The results are as follows: OxA-10093, Barma Grande 6, bone, *Homo sapiens*, $\delta^{13}\text{C} = -19.7$, $\delta^{15}\text{N} = 12.9$ per mil, C/N ratio = 3.8, uncalibrated ^{14}C years = 24,800 \pm 800 B.P. At two sigma, the result indicates that the burial was emplaced between 26,400 and 23,200 B.P., which brings it squarely in line chronologically with other mid-Upper Paleolithic Gravettian burials as well as Gravettian sites all over Europe (Roebroeks et al.

TABLE 1
Laboratory Pretreatment for Barma Grande 2, 5, and 6

Sample	Weight	Collagen Yield	Amount Burnt	Carbon Yield
BG 2	360	3.3	2.0	0.09
BG 5	360	17.7	6.0	0.1
BG 6	1,050	1.8	1.8	0.7

NOTE: All measurements in milligrams.

2000). The Gravettian lasts, in some areas, until ca. 20,000 B.P. and is then followed in Italy by the Early Epigravettian (Foucher et al. 2001, Mussi 2001a).

BG 6 is an incomplete skeleton including fragmentary hip and lower limb bones. Found atop the remains of an ancient hearth, the specimen was labelled as "burnt" (Verneau 1906, 1908), but macroscopic and microscopic bone analyses show no evidence of burning (Formicola 1989). The skeleton is that of an adult male with the robust body build and tall stature (Massari 1958) characteristic of the Grimaldi Gravettian sample (Formicola and Giannechini 1999). According to Verneau (1906, 1908) its lower limb bones were in a flexed position. While this pattern of inhumation differs from that exhibited by the other skeletons from the cave, it is not unusual among Gravettian remains from Grimaldi (e.g., Barma del Caviglione 1 and the "Negroids" from the double burial of Grotte des Enfants). Finally, a few perforated *Cyclope neritea* shells were collected in the soil around the bones (Verneau 1899, 1908). This relatively low degree of ornamentation compared with that exhibited by other skeletons from the same cave and by the Grimaldi remains in general is perhaps not surprising given the loss of the upper part of the body, which is usually the most ornamented.

Before discussing the implications of the BG 6 date, it is important to note that the low amount of collagen found in BG 2 suggests that modern contamination could be responsible for the relatively young date previously obtained from a fragment of rib of the same specimen. Similar effects of residual modern contamination have been documented at Abri Pataud (Mellars et al. 1987). Regarding the BG 6 date, the result fits well within the known chronological framework for mid-Upper Paleolithic European burials (e.g. Paglicci, Ostuni, Dolní Věstoniče, Paviland, Brno, Sunghir, Lagar Velho, Cro-Magnon, Arene Candide), which date between the twenty-seventh and the early twenty-fourth millennium (uncalibrated) B.P. (Mezzena and Palma di Cesnola 1989–90, Vacca and Coppola 1993, Svoboda 1995, Aldhouse-Green and Pettitt 1998, Pettitt and Trinkaus 2000, Pettitt and Bader 2000, Pettitt et al. 2002, Henry-Gambier 2002, Pettitt et al. 2003) and indicates a funerary use of Barma Grande during this time period. By extension this result implies that a Gravettian age for the "Venus figurines" found by Jullien in the cave can no longer be excluded.

Of further importance are the chrono-cultural relationships between BG 6 and the other burials from the

same cave. BG 6 was found in the innermost part of the cave at 6.40 m depth, at a distance of 0.80 m from and at the same level as BG 5, while the triple burial (comprising BG 2, 3, and 4) was found at 8 m in the middle of the cave and the single burial, discovered by Jullien close to the entrance (BG 1), was even deeper, at 8.40 m. Obviously differences in depth are not necessarily directly correlated with the antiquity of the burials. It is, however, unlikely that the slight slope of the deposit (Verneau 1908:180) or the digging of the graves fully accounts for differences of about 1.60 m (triple burial) and about 2 m (BG 1). On the basis of the similarity of grave goods and the proximity of BG 6 to BG 5, Mussi (1986) has suggested that all the burials are contemporary and belong to the Gravettian. We concur with this point of view. In addition, we also feel that BG 6 is probably one of the last examples of the funerary use of Barma Grande during this time period.

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Quantifying the Colonized/ Colonist Relationship: Suicide as a Comparative Measure of Stress in Gibraltar¹

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Twentieth-century work in colonial theory emphatically rejected the nineteenth-century linear model of colonialism as a process in which societies were subjected to a “civilizing” influence by the “superior” European culture. The first replacement models arose with decolonization and were often driven by the experiences of the colonized themselves (for example, Memmi 1969, Cabral 1979, Fanon 1985 [1952], and, for an overview, Young 2001). These models characterized colonialism as a bipolar relationship rooted in inequities of power and racism and imposing European ideology and epistemology. Spurred by the work of Foucault, studies using these models postulated that a group’s position in the colonial spectrum dictated its experience of disease and ill health, and some suggested that the imposition of imperial policies impinged on the stasis achieved before the coming of the colonizers (Vaughan 1991, Lyons 1985, Keller 2001). A second set of replacement models builds on the previous ones but suggests that power did not rest solely with the colonists and structures the colonial relationship as an interdigitation of colonist and colonized characterized by “tensions of empire” (Stoler 1989, Cooper and Stoler 1989, Thomas 1994, Arnold 1993). These tensions are seen as including aggression and resistance, the stress of being in a coercive position, differing ideologies among the colonizers, the threat of assimilation by the colonized, and the strain of maintaining white male supremacy (Cooper and Stoler 1989).

To date, these research models have rested almost entirely upon discourse, and for many reasons no one has

sought to test them empirically.² While the colonial powers of the nineteenth century amassed statistics on troops stationed at home and abroad, their primary emphasis was on troop efficiency associated with manpower. It was only under rare circumstances such as a devastating epidemic that colonial authorities became directly interested in the health of the local host population (see, for example, Sutherland 1867). Contemporary scholars interested in the retrospective study of colonial health face the daunting task of locating a site in which high-quality data of sufficient temporal depth exist for both colonized and colonizer groups. Further, there is the issue of the unusual demographic structure of the military communities that formed the backbone of colonial societies, which precludes simple comparisons (see figs. 1 and 2); for example, in the nineteenth-century Gibraltar garrison adult males outnumbered their female counterparts ten to one, and infants and children made up less than 2% of the community at any point in time (Padiak 2003). There is also the possibility that colonists have an inherent advantage because they have been selected for better health by meeting or exceeding minimum standards for height, weight, chest girth, and absence of defects and are free of any apparent afflictions (the “healthy warrior effect” [Haley 1998]). Finally, there is the issue of the questionable merit of comparisons of mortality/morbidity rates of two populations whose immunological histories radically differ because of their experiences in distinct ecological settings. Comparing a transplanted group with no history of exposure to a novel-pathogen-loaded environment with an indigenous group that has had undergone generations of adaptation to that particular niche raises other substantive issues underlying the process and by-products of colonization.

The present study addresses and/or circumvents these problems. The confluence of geography, history, human agency, and scientific opportunism has made Gibraltar an unusually rich venue for the study of colonialism (Sawchuk, Burke, and Padiak 2002). First, as a British colony since 1704, Gibraltar has developed two distinct identities: as a home for some 20,000 Gibraltarians and as a strategically situated naval port and garrison town for members of the British forces. Second, the colonial authorities developed and maintained an excellent system for the registration of vital events for both civilian and military communities from 1869 on (see Sawchuk 2000 for details). Third, Gibraltar is large enough to provide the researcher with sufficient numbers for meaningful statistical analysis and yet small enough to be manageable in terms of time and resources. Further, its limited size precludes health differentials due to differences in local ecology. Fourth, as part of southern Europe Gibraltar did not confront the British colonizer with a radically different ecological and pathogen environment

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2. Philip D. Curtin (1989) has sought to measure the effect of empire building on French and British troops sent abroad to maintain the outposts of their respective empires, but he focuses on the “cost of relocation,” using differences between the standardized mortality rates of home populations and their counterparts among men in garrisons abroad.

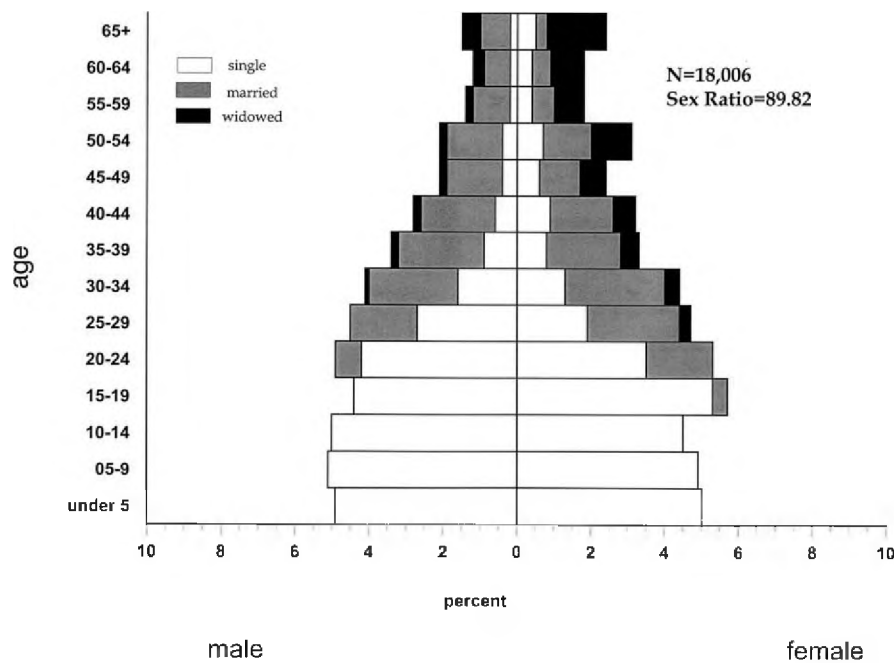


FIG. 1. Structure of the civilian community of Gibraltar in 1878.

as did colonies in Africa or the Far East. Finally, to avoid the potential confounding influence of selection for physical health, we employed a proxy measure of psychosocial well-being. Nineteenth- and early-twentieth-century troops were examined only for physical qualities and not for psychosocial ones. Reasoning that colonialism juxtaposes two or more populations and that causes of mortality indicative of stress on the individual would test the models of colonialism, we chose to assess the rates of suicide in the two populations over time.

GIBRALTAR'S TWO SOLITUDES

During the study period, the Rock had two distinct communities separated by language, religion, place, and worldview—the civilians and the military. The civilians shared a biological and cultural heritage dating back to 1704, when the territory fell under British control. Their heritage reflects a fusion of Mediterranean, North African, and European influences, coupled with long-term experience of living in a military garrison and colonial outpost.³ Fiercely loyal to the British flag and politically sensitive to their northern Spanish neighbours, Gibraltarians are neither British nor Spanish in character. Their distinctive ethos derives in part from life on a small, largely uninhabitable mass of limestone that offers little

in the way of comfort. Owing to the fact that the greater part of the Rock is impossible to cultivate, the inhabitants of Gibraltar have depended on provisions imported from the Spanish mainland, the Barbary coast (Morocco), or abroad.⁴ Until recently, the little land suitable for building was occupied by naval or military works, forcing the civilian population into a limited space.

At the beginning of the study, in 1878, there were about 18,000 Gibraltarians (approximately 85% Roman Catholics, 7% Protestants, and 8% Jews). Despite religious differences, Gibraltarians were a highly cohesive group, living in a small-scale community in which face-to-face meetings were a daily occurrence. For the vast majority of Gibraltarians life was shaped by long-term communal residence in multifamily dwelling units known as "patios." A patio was typically a three- or four-storey building surrounding a central courtyard that was the focus of much of everyday life. The sharing of vital resources (such as potable water, a privy, the laundry area) brought people of various backgrounds into close proximity, cutting across religious and class differences. Patio membership entitled an individual or a family to be part of a support network for coping with sickness, unemployment, and other forms of stress.

The native Gibraltarians had to share their tiny piece of land with a very large and dominant presence: the British military. Gibraltar was the second-largest colonial garrison, with some 4,000–6,000 men at any one

3. Gibraltar remains one of ten U.K.-held territories that is recognized by the United Nations Special Committee on Decolonization. The others include Anguilla, Bermuda, British Virgin Islands, Cayman Islands, Falkland Islands (Malvinas), Montserrat, Pitcairn, St. Helena, Turks, and Caicos Islands (Aldrich and Connell 1998:160).

4. Gibraltar was unlike other British colonies that were rich in natural resources and required a native population for their exploitation.

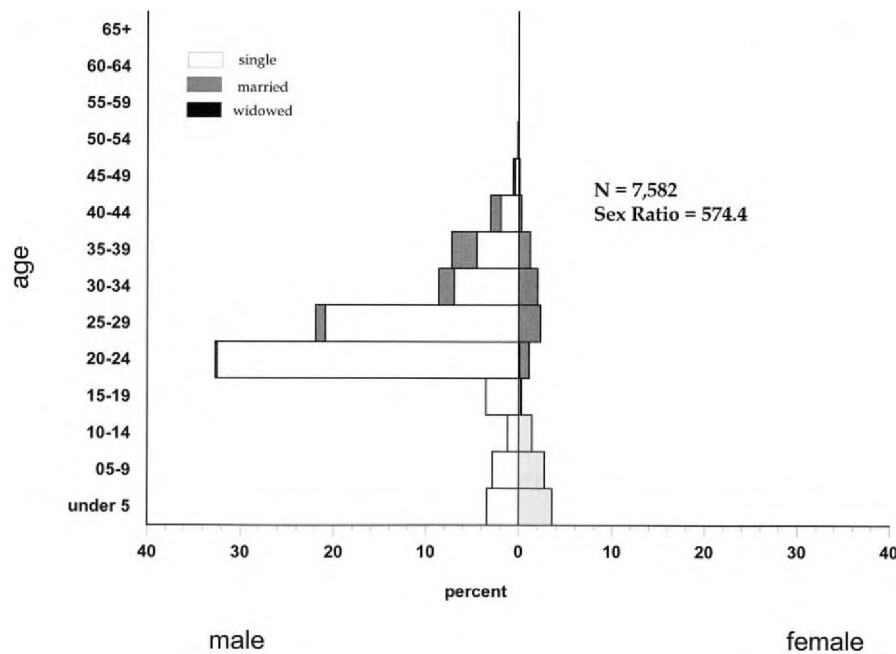


FIG. 2. Structure of the military community of Gibraltar in 1878.

time.⁵ In contrast to the civilian community, the military segment of Gibraltar was a highly transient group. Gibraltar was an outpost where fresh recruits were stationed while they adjusted to a warmer climate before going on to Egypt, India, or Jamaica. The military was composed of men from 20 to 30 years of age, generally drawn from the unskilled classes of urban Britain. Almost all of them were unmarried, as permission to marry was given to few rank-and-file men and then only after six years' service. The men of the military were torn away from their immediate and extended families, and the regiment was the soldier's "family" and support when stationed away from home.

SUICIDE

Just over a century ago, Emile Durkheim published his seminal work on suicide (1951 [1897]), which hypothesized that the frequency of suicide in populations varied with economic circumstances, demographic profile, and social capital. Since then, generations of social scientists have labored to establish correlations of marital status, economic conditions, job status, religious commitment, age, sex, and social support with suicide rates (Stack 2000, Gibbs 2000). Broadly speaking, when demographic variables such as age and gender are controlled, a rising level of suicide indicates a declining sense of well-being

(Tausig and Fenwick 1999, Naroll 1969, Kraus and Tesser 1971). There are two significant precedents for using suicide to assess stress in a population. Durkheim himself developed the "coefficient of aggravation" and the "coefficient of preservation" as comparative population (or subpopulation) indicators. Both coefficients were the ratio of suicides in one group relative to another, standardized to unity (Durkheim 1951 [1897]:132–35). A ratio of 2.0 meant that the tendency to suicide for the numerator group was 2 and that of the denominator group was 1. He termed this the "coefficient of preservation" for the numerator group. If the coefficient was less than unity, then the numerator group was suffering a greater tendency to suicide, and he termed this the "coefficient of aggravation." Despite the abiding influence of Durkheim's work, contemporary researchers have not carried this index forward. Raoul Naroll (1969) also recognized the value of suicide as a measure of the "sickness" of a society through the frustration of individuals' desires and rights and considered it the only statistically dependable measure of this sickness. Kraus and Tesser (1971:227) built upon Naroll's work and suggested that suicide levels in a society might be predicted from thwarting disorientation traits in that society.

Our research design employs suicide rates to test different experiences of colonization from 1878 to 1945 in Gibraltar. From our knowledge of conditions in Victorian Gibraltar, we knew that certain aspects of the colonial model were in place. There was a visible ethnic difference between the Gibraltarians and the British colonizers. Politically, the Gibraltarians were powerless; decision making was vested in the governor, a military man

5. Malta was the largest, with slightly more troops than Gibraltar, but their barracks were spread over a wider geographical area. Some 55,000–70,000 men were stationed in India but were scattered amongst many garrisons (Army Medical Reports, *Parliamentary Papers*, Public Record Office, London).

TABLE 1
Intercommunity Comparisons of Suicide Rates in Gibraltar, 1878–1945

Time Period	Military		Civilian		Suicide Rate/100,000		Z	p
	N Suicides	Person-Years	N Suicides	Person-Years	Military	Civilian		
1878–85	9	29,712	1	14,216	30.29	7.03	1.51	0.06
1886–95	4	45,220	1	18,150	8.84	5.51	0.43	n.s.
1896–1905	14	44,410	2	20,380	31.52	9.81	1.63	0.05
1906–15	11	38,370	1	17,840	28.67	5.61	1.74	0.04
1916–25	8	19,260	5	15,950	41.63	31.35	0.50	n.s.
1926–35	9	20,800	2	14,720	43.29	13.59	1.57	0.05
1936–45	19	38,370	4	26,630	49.51	15.02	2.30	0.01
Total	74	236,142	16	127,886	31.34	12.51	3.45	<0.01

NOTE: Suicide rates are expressed as per 100,000 unmarried men aged 15–45.

appointed in London. No elected assembly existed in Gibraltar until 1922, when a city council was formed. Throughout colonial times there was a wide array of restrictive laws designed to put the needs of Gibraltar as a fortress for 5,000 men ahead of those of Gibraltar as a home for 20,000 people. Accounts of experiences of the Gibraltarian people under colonial rule (Preston 1946; Finlayson 1991; Sawchuk 1992, 1993, 1996, 2000) have emphasized the binary model of power and powerlessness. As the former governor Sir W. Jackson remarked, “Such is the divide between the military and civilian community—a fault common in most British colonial societies of the nineteenth century—that Gibraltarians, no matter how eminent, were not made welcome” (Jackson 1990:228–29). Further, the British garrison had preferential access to scarce resources such as housing, plentiful water, and ample fresh and frozen meat. It also had access to free and up-to-date medical care in its own hospital. The troops lived in barracks with sanitary facilities superior to those of many Gibraltarians; barracks had been subject to steady sanitary improvements beginning in the 1870s (Sawchuk, Burke, and Padiak 2002). In contrast, most Gibraltarian dwellings did not have running water until after World War II.

This brief sketch fits the model of the powerless indigenous peoples suffering imperial domination. If only the colonized suffered under colonialism, then one would predict higher suicide levels among the civilians. If, alternatively, the colonists, too, suffered the “tensions of empire,” there might be higher levels of suicide among the troops.

DATA AND ANALYSIS

Our data were drawn from death registrations and set against census counts covering 50 years. Comparing suicide rates in different populations is often problematic because of the potential for differential reporting. Although these two populations had separate locations for death registration, the registrar was the same individual at any one time. This singular system eliminated the problems typically associated with interpopulation com-

parison (Diekstra 1993, Stack 2000). The death records used the term “suicide” from the beginning of the study period for cases in which the intent was clear, although often the fact of suicide was recorded under the secondary or tertiary cause of death, with the mode, such as gunshot wound, hanging, or cut throat, being the primary cause. There is, however, the potential for underreporting of suicide because of unknown intent (Farberow 1975). Because Van Poppel and Day (1996), examining nineteenth-century data, found that rates of suicide were low but rates of death from external causes relatively high and suggested that some suicides were falsified as “sudden deaths,” we examined every sudden death due to noninfectious disease. With Gibraltar’s unique topography, these causes of death were usually fracture of the skull (associated with a fall) and drowning. Sudden deaths such as these occurred in the two Gibraltar populations in roughly equal proportions but at relatively low levels. We concluded that there was no evidence of masking and that the number of violent deaths deemed not suicidal in error would be small.

A number of constraints were imposed in the construction of suicide rates in the two communities. First, because suicide is typically positively correlated with age and the military population is almost devoid of aged individuals, our analysis was confined to those below 45. Second, because there were so few military wives, males only were considered. Third, because suicide is negatively correlated with marriage, the analysis was limited to single men. The resultant age-adjusted suicide rates per 100,000 single men were constructed around a series of decennial censuses, with the first period having a duration of only eight years, from 1878 until 1885, and the remaining six being decennial periods running from 1886 to 1895, 1896 to 1905, and so on until 1945 (table 1, fig. 3). In order to compare a rare event such as suicide in the two communities, we took advantage of the properties of the Poisson distribution (Beck and Tolnay 1995) and the Z-score test (M. Evans, personal communication): $Z = D/S$, where $D = (x_1/n_1) - (x_2/n_2)$, $S = (x_1 + x_2)/[(n_1 * n_2)]$, x_1 and x_2 are the respective suicide counts, and n_1 and n_2 are the respective person-years as estimated

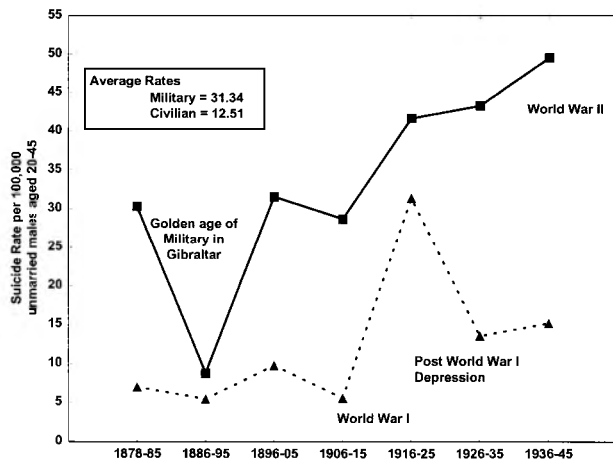


FIG. 3. *Suicide rates in Gibraltar, 1878–1945.*

from the census and the number of years in the study period. A two-sided Z score tested the hypothesis that the rates in the military population were distributed the same as in the civilian population, and these are the p values based on a 95% confidence rate or better.

Over the entire study period, suicides totaled 16 among civilians and 74 among the military population, giving average suicide rates of 13.38 and 28.36 respectively per 100,000 single males aged 15–45. Table 1 shows the suicides by decade and compares the coeval rates in the two communities. Average rates for the two communities over the entire study period proved to be significantly different, with the military community showing a lower measure of well-being ($Z = 3.45, p < 0.01$). There was some variability in the nature and scope of community differentials over time. Three time periods (1878–85, 1896–1905, 1926–35) showed differences in suicide rates that were substantial but of borderline significance. Significant differences between the two communities were observed for 1906–15 and for 1936–45.

Two of these time periods showed no significant difference. During the period 1886–95, suicide rates fell in the military as its community went through its “golden age” in Gibraltar ($Z = 0.43, p = \text{n.s.}$). Twenty years of improvements to garrison life had resulted in acceptable accommodations for the men, with suitable pastimes to break the monotony of duty on the Rock. On the international front, the British were not involved in any of the small wars so common during Victorian times, and the large ones were yet to come. The garrison was the healthiest it had been for the entire century; mortality and hospital admissions for all causes were low (Padiak 2003).

The period 1916–25 captured Gibraltar’s great postwar depression and marked a significant rise in the civilian suicide rate ($Z = 1.77, p = 0.042$). The depression struck Gibraltarians particularly hard because it followed a period of relative prosperity attributable to its importance as a coaling station for both the Royal Navy and the

merchant marine. It was a period of high community stress, with a downturn in mercantile trade, high unemployment, long breadlines, and a currency crisis (Stewart 1967). It was also a time of considerable worker unrest, with demonstrations and strikes (in 1917, 1918, and 1919) over the high price of food and low wages. One indicator of the hardship faced by the civilian population during this period is the dramatic rise in the price of bread, the staple food of Gibraltarians (see fig. 4).

The results of the intracommunity comparisons confirm that the forces driving the lack of difference in the suicide rates in these two periods lie in changes within each community (table 2). When adjacent temporal periods are compared, it is clear that, in the military community, it is the drop in the late 1880s and early 1890s that is the significant change from the consistently high rates. Similarly, in the civilian community, it is the rise in rates in the late 1910s and early 1920s that changes the pattern.

As to the impact of war on suicide rates, the two communities differed in their response to a period of what could be conceived as an interval of protracted stress. For the civilians, the rates showed modest increases but ones that were not statistically higher than in the preceding nonwar periods. For the military, temporal trends were mixed. While suicide rates during World War I increased from 26.1 to 44.6, the values were not significantly different from those of the preceding period ($Z = 1.006, \text{n.s.}$). The pattern during World War II was markedly different, with a dramatic and significant rise in the suicide rate from 30.4 (1926–39) to 73.8 (1940–45) ($Z = 2.67, p < 0.01$). During the war years Gibraltar assumed the role of a military fortress, and most of the civilians

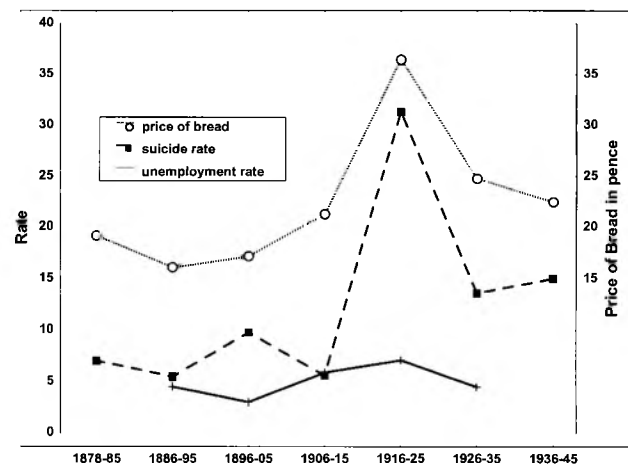


FIG. 4. *Civilian suicide rate and indicators of stress, 1878–1945.*

TABLE 2
Intracommunity Comparisons of Suicide Rates in Gibraltar, 1878–1945

Time Period	Military			Civilian		
	Rate Difference	Z	p	Rate Difference	Z	p
1878–85 vs. 1886–95	–21.45	2.18	0.02	–1.52	0.17	n.s.
1886–95 vs. 1896–1905	+22.68	2.40	0.01	+4.3	0.48	n.s.
1896–1905 vs. 1906–15	–2.85	0.24	n.s.	–4.2	0.46	n.s.
1906–15 vs. 1916–25	+12.96	0.80	n.s.	+25.74	1.77	0.04
1916–25 vs. 1926–35	+1.66	0.08	n.s.	–17.76	1.03	n.s.
1926–35 vs. 1936–45	+6.22	0.33	n.s.	+1.43	0.12	n.s.
1906–13 vs. 1914–18	+18.5	1.01	n.s.	+5.0	0.38	n.s.
1926–39 vs. 1940–45	+43.4	2.67	0.01	+18.83	1.29	n.s.

NOTE: Suicide rates are expressed as per 100,000 unmarried men aged 15–45. Z scores are computed from raw values in table 1.

were forcibly evacuated.⁶ Life in the fortress became increasingly guarded, with the entire territory on a war footing. Movement in and out of the town was strictly regulated; the town gates closed in the evening, and there was an 11 P.M. curfew. Rationing and price controls were imposed. Recreation facilities (a racecourse, football and cricket pitches) disappeared to make way for an airfield. With little real wartime action, isolation, boredom, and monotony set in among the soldiers, and Gibraltar became literally a military prison full of pubs. Drinking was hard, fights were commonplace, and the escalating tensions between the military and civilians resulted in high crime rates and violence. These conditions along with easy access to weapons contributed to 17 suicides among the military during World War II, 13 of them the result of self-inflicted gunshots to the head or body.

CONCLUSION

This study addresses psychosocial parameters in a historical milieu and reasons that suicide is a suitable comparable indicator of well-being in a colonial population. But just as risk patterns of ill health can vary over time, any study that addresses an issue such as colonialism must be wary of presenting broad generalizations that are indifferent to local contexts or to the potential confounding effects of age and sex. Previous work in Gibraltar (Sawchuk, Burke, and Padiak 2002) demonstrated this heterogeneity, showing infant survivorship significantly higher among the military while maternal mortality rates were substantially the same in the two communities during the latter part of the nineteenth century. Clearly, then, suicide is but one of a potential battery of parameters that can be employed to characterize inter- and intracommunity differences in health.

6. A total of 16,700 inhabitants were evacuated. Some 12,500 women and children as well as men not engaged in essential services were sent to the United Kingdom and 3,272 to Madeira and Jamaica. The remainder made their own arrangements and settled in Tangier and Spain. While some civilians began to return as early as 1944, repatriation was not complete until 1951 because of a serious shortage of housing.

In the case of adult males, the results of this study show that, on average, the military population suffered higher suicide rates than the civilian Gibraltarians, although at times the two populations' rates converged. The two populations experienced life on the Rock differently. The military men were stationed there temporarily, for a period averaging between two and three years, while the Gibraltarians were in their home environment. Despite the privileges garnered by the military at the civilians' expense, it is likely that the strong societal, familial, and religious supports of the Gibraltarian community enabled them to cope very well with the second-class status they had to endure. The people of Gibraltar had long been accustomed to their role as the colonized and had developed reciprocal support systems based on local networks and religious affiliation (Sawchuk 1996, 2000). Even the single men would have been surrounded and supported by their extended families. Their cradle-to-grave society, supported by strong community identification, stabilized their lives and allowed them to develop a blueprint for surviving in the small space under the control of the colonial government, despite the funnelling of scarce resources away from the patrimonial community. The Gibraltarians' ethos showed the value of social structure for the preservation of individuals' and hence the society's sense of well-being.

Considering the difficult circumstances under which the civilian Gibraltarians lived, it is remarkable that they were able to maintain the stability indicated by their low suicide rates. During Victorian times, despite their status as a colonized people and their deplorable living conditions, they clearly did not experience the depths of despair as did their privileged occupiers. Only during times of economic strain such as the early 1920s did the population exhibit stress.

At the same time and in the same place, the military men enjoyed better housing, better nutrition, better water resources, and better medical attention relative to the civilians. These same men had already been selected for better physical health and strength and were embraced

by their regiment and offered the camaraderie of their fellow men at arms. Yet these well-supplied men suffered a rate of suicide more than double that of the native Gibraltarians. In contrast, several recent studies have reported higher suicide rates for civilians (Sentell et al. 1997, Marttunen et al. 1997). We suggest that discipline, boredom, and isolation from the native community exacerbated the soldiers' sense of familial separation, while language differences further contributed to a sense of marginalization. The military men were suffering from the position they found themselves in, acting as the bulwark of power for the monarchs of the empire. We suggest that this supports the "tensions of empire" model of colonization and that the position of colonist was stressful and took its toll on well-being.

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