Prehistoric Migration in Europe: Strontium Isotope Analysis of Early Neolithic Skeletal Remains

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The term Linearbandkeramik (LBK) is traditionally used to describe the first farmers of central Europe and the pottery they introduced approximately 7,500 years ago. Radiocarbon dates for the LBK suggest a rapid spread into central Europe from its origin on the Hungarian Plain. The geographical homogeneity of LBK artifacts and architecture, along with domesticated plants and animals with origins in southwestern Asia, seems to be reflective of a “wave” of colonization by migrating farmers, who may also have brought Indo-European languages and genes (Childe 1929, Quitta 1964, Ammerman and Cavalli-Sforza 1984, Bogucki 1988, Lüning, Kloos, and Albert 1989, Kreuz 1990, Price, Gebauer, and Keeley 1995, Price 2000, Troy et al. 2001).

An alternative view is that the LBK spread through the adoption of agriculture by the indigenous hunter-gatherers (Tillmann 1993, Whittle 1996) or a combination of colonization and indigenous adoption (Gronenborn 1999, Zvelebil and Lillie 2000). Indigenous people along and west of the Rhine River may have made “La Hoguette” pottery before the LBK era (Jeunesse 1987, Lüning, Kloos, and Albert 1989). In western Germany, flint tools from the earliest LBK exhibit continuity with preceding Mesolithic forms, and many are made of flint quarried from areas populated only by Mesolithic groups at that time (Mauvilly 1997, Gronenborn 1999). Mitochondrial DNA (mtDNA) studies support the case for indigenous adoption (Richards et al. 1996, 2000), although such evidence is indirect because the mtDNA has come from modern Europeans.

The two views have been difficult to resolve through architecture or artifacts because ideas or trade items can spread without people’s migrating. To examine human mobility directly, we measured strontium isotopes in human skeletons from three LBK cemeteries in southwestern Germany. Strontium substitutes for calcium in the hydroxyapatite mineral of skeletal tissue, and strontium isotopes in prehistoric human teeth and bones provide a geochemical signature of the place of residence. The $^{87}$Sr/$^{86}$Sr values in natural rocks vary from older granites, with $^{87}$Sr/$^{86}$Sr ratios typically above 0.710 and as high as 0.740, to younger basalts, with lower $^{87}$Sr/$^{86}$Sr ratios around 0.703 to 0.704. These differences, all in the third decimal place, are easily detected by thermal ionization mass spectrometry (TIMS), with which $^{87}$Sr/$^{86}$Sr can be measured with a typical precision of 0.00001 or better.

Because of their large atomic mass, strontium isotopes retain the same $^{87}$Sr/$^{86}$Sr ratio as they pass from weathered rocks through soils to the food chain (Hurst and Davis 1981, Beard and Johnson 2000). Even if there were some mass-dependent fractionation of strontium along biogeochemical pathways, it would be corrected for upon measurement by mass spectrometry, as strontium ratios are normalized to the constant value of $^{87}$Sr/$^{86}$Sr in natural rocks (Beard and Johnson 2000). In other words, strontium isotopic signatures faithfully make their way from local geologic materials ultimately into the human skeleton.

One can identify migrant individuals who moved between geologic regions by comparing the isotope signature in adult teeth, composed between four and twelve years of age, with that in the bones, with characteristic turnover times varying between 6 and 20 years for different bones of the body (Parfitt 1983, Ericson 1985, Price et al. 1994, Grupe et al. 1997, Grupe, Price, and Sollner...
1999). If the teeth and bones of an adult have different signatures, then that person spent his or her early and final years in different geochemical provinces (Ericson 1989, Sealy et al. 1991, Price et al. 1994, Price, Grupe, and Schröter 1994, Price, Burton, and Bentley 2001). Because bone phosphate is much more subject to postburial contamination than the hydroxyapatite of tooth enamel (Price, Burton, and Bentley 2001), it is often more reliable to compare each individual tooth value with a “local” $^{87}\text{Sr}/^{86}\text{Sr}$ range defined for the recovery site rather than with the different individual bone values. Here we define the local signature at a site as within two standard deviations of the average $^{87}\text{Sr}/^{86}\text{Sr}$ of the sample of human bones from the site. This conservative definition is unlikely to misidentify locals as immigrants (Grupe et al. 1997, Grupe, Price, and Sollner 1999, Price, Burton, and Bentley 2001). Local ranges in surrounding areas can be characterized by indicators such as the $^{87}\text{Sr}/^{86}\text{Sr}$ in streamwaters or [better] the skeletons or shells of local animals (Price, Burton, and Bentley 2001).

Our study area in southwestern Germany is geochemically appropriate for this investigation. Higher $^{87}\text{Sr}/^{86}\text{Sr}$ values (>$0.715$) are found in area uplands underlain by granites, including (fig. 1) the Odenwald [near Flomborn and Schwetzingen], the Bavarian Forest [near Dillingen], and the Vosges and Black Forest mountains [Grupe et al. 1997, Tricca et al. 1999, Probst et al. 2000, Price et al. 2001]. These uplands are isotopically distinct from most of the regional lowlands [$^{87}\text{Sr}/^{86}\text{Sr} < 0.710$]. Elsewhere, loess sediment can have higher $^{87}\text{Sr}/^{86}\text{Sr}$ values, ranging from $0.713$ to $0.716$ in Brittany and Normandy, for example [Gallet et al. 1998]. Within the study region, however, loess patches appear to be unlikely sources for the higher $^{87}\text{Sr}/^{86}\text{Sr}$ values because (1) loess in southern Germany is rich in carbonates derived from the Alps [Mahaney and Andres 1991, Schnetger 1992, Hatté et al. 1998], for which the expected $^{87}\text{Sr}/^{86}\text{Sr}$ is about 0.708–0.7095 and (2) snail and human bone samples so far analyzed from Dillingen and Flomborn, both on loess, exhibit $^{87}\text{Sr}/^{86}\text{Sr}$ below 0.710 [Bentley 2001: table 5.1].

We sampled human skeletal remains from LBK cemeteries and found a high incidence of migration at the LBK cemeteries of Flomborn and Schwetzingen, near Heidelberg, and at Dillingen, near Ulm [fig. 1, table 1] [The data are presented in the electronic edition of this issue on the journal’s web page]. We identified 7 nonlocals out of the 11 individuals (64%) sampled from Flomborn, 9 out of 36 (25%) from Schwetzingen, and 11 out of 17 (65%) from Dillingen. Four patterns have emerged from the data [fig. 2, table 2] which, taken together, suggest that nonlocals in these LBK cemeteries had social identities different from the locals. These patterns are as follows:

1. Nonlocal females are common. Of the individuals

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**Fig. 1. Simplified geologic map of southwestern Germany, showing sample sites.** Vertical stripes, Palaeozoic granite and gneiss ($^{87}\text{Sr}/^{86}\text{Sr} > 0.715$); light gray, Triassic and Jurassic sedimentary ($^{87}\text{Sr}/^{86}\text{Sr} \sim 0.708$–0.709); dark gray, loess ($^{87}\text{Sr}/^{86}\text{Sr} \sim 0.708$–0.7095); white, Pliocene and Quaternary alluvium ($^{87}\text{Sr}/^{86}\text{Sr} \sim 0.708–0.709$); horizontal stripes, Tertiary molasse and glacial moraine. Inset: the distribution of LBK settlement ca. 5300 B.C.
at Flomborn that have been identified by sex, all 4 (100%) of the females are nonlocals (fig. 2, a). At Schwetzingen, 5 of 16 females (31%) are nonlocals, all with tooth-enamel values above the local range (fig. 2, b). Three of the 16 males (19%) are nonlocals, but 2 of those have tooth values below the local range, that is, characteristic of a different geochemical zone from that of individuals above the range. Thus five of the six tooth values above the local range at Schwetzingen are from females. At Dillingen (fig. 2, c), all 5 (100%) of the females are nonlocals (all above the local range) compared with 6 out of 12 nonlocal males (5 above the local range, 1 below).

2. $^{87}\text{Sr}/^{86}\text{Sr}$ may correlate with burial orientation. At Schwetzingen, 7 (30%) of the 23 burials with head directions ranging from north to east are nonlocals, compared with two nonlocals (15%) among the 13 burials facing in other directions (fig. 2). At Flomborn, 4 (80%) of the 5 sampled west-facing burials are immigrants.

3. Many nonlocals are buried without a shoe-last adze (a characteristic artifact of the LBK). At both Flomborn and Dillingen, burials with shoe-last adzes are significantly more likely to be locals than those without (table 2). Four of the 6 (67%) Flomborn burials without a shoe-last adze have tooth values above the local range. Of the

<table>
<thead>
<tr>
<th>Site</th>
<th>Era</th>
<th>Excavated Burials</th>
<th>$n$</th>
<th>Male</th>
<th>Female</th>
<th>?</th>
<th>Total Immigrants</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flomborn</td>
<td>Early LBK</td>
<td>85</td>
<td>11</td>
<td>2/3 [67%]</td>
<td>3/4 [75%]</td>
<td>1/4</td>
<td>64%</td>
</tr>
<tr>
<td>Schwetzingen</td>
<td>Late LBK</td>
<td>202</td>
<td>36</td>
<td>3/16 [19%]</td>
<td>5/16 [31%]</td>
<td>1/4</td>
<td>25%</td>
</tr>
<tr>
<td>Dillingen</td>
<td>Middle-Late LBK</td>
<td>27</td>
<td>17</td>
<td>6/12 [50%]</td>
<td>5/5 [100%]</td>
<td>–</td>
<td>65%</td>
</tr>
</tbody>
</table>

**Note:** “Immigrant” is defined as beyond two standard deviations of the average bone value at the site.

**Fig. 2.** Strontium isotopes in tooth enamel from three LBK cemeteries: a, Flomborn, b, Schwetzingen, and c, Dillingen. Each symbol represents a different individual: circles, female; squares, male; triangles, unknown sex (due to young age at death). Filled symbols, burials with shoe-last adze; empty symbols, burials without adze. (There were no adzes in the sampled Schwetzingen burials.) The “local” $^{87}\text{Sr}/^{86}\text{Sr}$ range has been defined as two standard deviations from the average human bone value at each site (individual bone values not shown). The local range for each site is indicated by a gray bar.
TABLE 2

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Flomborn</th>
<th>Schwetzingen</th>
<th>Dillingen</th>
</tr>
</thead>
<tbody>
<tr>
<td>Females local</td>
<td>0.314</td>
<td>0.011</td>
<td>0.097</td>
</tr>
<tr>
<td>Males local</td>
<td>0.134</td>
<td>0.993</td>
<td>0.065</td>
</tr>
<tr>
<td>Without shoe-last adze local</td>
<td>0.021</td>
<td>n.d.</td>
<td>0.013</td>
</tr>
<tr>
<td>With shoe-last adze local</td>
<td>0.822</td>
<td>n.d.</td>
<td>0.461</td>
</tr>
<tr>
<td>Westerly burials local</td>
<td>0.036</td>
<td>0.482</td>
<td>0.118</td>
</tr>
<tr>
<td>Easterly burials local</td>
<td>0.693</td>
<td>0.048</td>
<td>0.026</td>
</tr>
</tbody>
</table>

Note: Low p-values (< 5% in italics) indicate that the hypothesis is probably not true, that is, that there is a significant difference between the mean tooth value of the category and the mean bone value at the site. Since there are many p-values, some “significant” values could have occurred by chance. The most convincing patterns are those that are repeated.

5 Flomborn burials with a shoe-last adze, only 1 (20%) has a tooth value above the local range (fig. 2). Among the 11 burials without a shoe-last adze at Dillingen, 9 (82%) are nonlocals, all with tooth values above the local range. Of the 6 Dillingen burials with a shoe-last adze, 2 (33%) are nonlocals, and only 1 of those is above the local range. The presence of nonlocal males without adzes confirms that the correlation is not merely between shoe-last adzes and males who happen to be locals.

4. Nonlocal 87Sr/86Sr values are mostly above the local range for their place of burial. Of the 27 immigrants from the three sites, 23 tooth values are above the local range for the site and only 4 below it.

The last pattern is suggestive of where the nonlocals obtained their diet in the younger part of their lives. The 87Sr/86Sr values for the nonlocals are not high enough, however, to be “from” the granitic uplands, where water samples are generally above 0.720 (Tricca et al. 1999, Probst et al. 2000). The best interpretation at this point may be that the higher 87Sr/86Sr values reflect a significant proportion of the diet from the regional uplands. If so, the higher 87Sr/86Sr values may reflect a larger diet catchment rather than a fixed “origin” for the nonlocals.

Optimal foraging theory predicts that a six-household LBK village in southwestern Germany would require 6 km² of agricultural land, supplemented by about 14% wild plants (Gregg 1988). At the same time, Gregg (1988) estimates the optimal diet for Mesolithic foragers as 80% wild game, 20% wild plants. A simple calculation based on these figures and the local geology shows that one-quarter of the wild foods came from the granitic uplands and all the agricultural foods were locally grown, the predicted 87Sr/86Sr would be 0.71036 for Flomborn farmers and 0.71113 for foragers (Bentley 2001:247–51).

The enamel 87Sr/86Sr values for many of the nonlocals at Flomborn and Schwetzingen are close to the value predicted for foragers. Because Early LBK sites are numerous in the Rhine Valley lowlands but scarce in the uplands, a viable hypothesis is that some of the nonlocals were foragers who may have frequented the area uplands during the early LBK (Cziesla 1994). The frequent absence of a shoe-last adze with these nonlocals also suggests that they may have been foragers. Indigenous foragers were significant agents in the spread of farming into southwestern Germany, influenced by small groups of immigrant farmers (Gronenborn 1999, Price et al. 2001). Near the western limit of the LBK at the time, nonlocals of both sexes at Flomborn may represent its initial residents, whose diet catchment had been larger before they settled. Later on in the same region, at Schwetzingen, there is less immigration overall, mostly involving females with similar “upland” strontium isotope signatures. The nonlocal females invite a comparison with models and ethnographic cases of forager women who marry into farmer or pastoral communities (Zvelebil and Rowley-Conwy 1984, Cronk 1989, Zvelebil and Lillie 2000, Thorp 2000).

An alternative interpretation for the data we have presented here is that the migration did not involve foragers at all. There are few archaeological traces of Mesolithic occupation in the uplands around Bavaria or the Upper Rhine Valley at the time of the transition to the Neolithic (Nielsen 1997, Taute 1988, Jochim 1998). However, the reason so few Terminal Mesolithic sites have been discovered is at least partly their ephemeral nature. Late dates from Late/Terminal Mesolithic sites in southern Germany and eastern France overlap with the early LBK period, indicating that foragers persisted into the LBK (Brunnacker et al. 1967, Kind 1997, Gronenborn 1999, Jochim 2000).

In any case, strontium isotope analysis of LBK skeletons suggests that many people made residential changes during the LBK of the Rhine Valley. Whether it involved foragers or farmers, the observed pattern of female migration is consistent with genetic evidence for patriality in European prehistory (Seielstad, Minch, and Cavalli-Sforza 1998). Although our evidence is not conclusive, it can be seen to support the interpretation (e.g., Gronenborn 1999, Zvelebil 2000, Price 2000) that Neolithic colonization of southeastern Europe was followed by some degree of indigenous adoption in central and northern Europe.

References Cited


Helping-at-the-Nest and Sex-Biased Parental Investment in a Hungarian Gypsy Population

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Unlike their counterparts elsewhere, Hungarian Gypsies live in small settled communities, some of which form isolated (Gypsy-only) villages while others form part of a larger urban community whose composition is mainly ethnic Hungarian. In contrast to rural Gypsies, those living in urban communities encounter opportunities for exogamy. As a result, although Gypsy communities are traditionally highly endogamous, those in Hungary exhibit varying levels of exogamy, a practice that seems both to favour differential investment in daughters and to yield high fitness returns (measured in terms of numbers of grandchildren) [Bereczkei and Dunbar 1997]. Yet despite high levels of endogamy, rural Gypsies nonetheless show a female-biased sex ratio at birth and invest more heavily in daughters much as urban Gypsies do [Bereczkei and Dunbar 1997]. That even those populations that experience fewer opportunities for endogamy should show female-biased investment seems anomalous. One possible explanation is that daughters provide a valuable service in that they are more likely than Gypsy boys or ethnic Hungarian girls to help their parents in taking care of siblings.

One of the potentially altruistic social interactions between genetic relatives is that in which older siblings help with the rearing of younger ones [Emlen 1984]. Since the production of a full sibling contributes to the individual’s reproductive success as much as the production of an offspring, a trade-off is expected to develop which allows individuals to increase their inclusive fitness. One strategy is to invest directly in one’s own reproductive effort by having more offspring of one’s own; the other is to help parents rear younger siblings [Charnov 1981, Woodroffe and Vincent 1995]. The latter is likely to be realized when (a) the offspring can provide valuable help in child care and (b) parents have opportunities for producing additional children when the older offspring begin helping [Betzig and Turke 1986, Turke 1988]. In one of the few studies carried out on humans, Turke (1988) has shown that daughters contributed to their parents’ reproductive success on Ifaluk (Micronesia); among women who had completed fertility, those who had borne a daughter first had a larger number of surviving children than those who had borne a son first.

The present study investigates the circumstances under which helping-at-the-nest might be advantageous in a Hungarian Gypsy population. Gypsy girls traditionally help with raising younger children, and their parents expect them to engage in various kinds of duties such as looking after babies, playing with children, and cooking. Gypsy families differ considerably in these respects from the ethnic Hungarians among whom they live; the ethnic Hungarians thus provide a benchmark population against which to evaluate the behaviour of the Gypsies.

The following assumptions and predictions are tested:

Assumption 1: Gypsy girls spend more time caring for their younger siblings than Gypsy boys. The difference is not expected to be significant among ethnic Hungarians.

Assumption 2: Given the assistance expected by Gypsy mothers from older girls, first-born daughters will remain at home with their parents longer than first-born sons or later-born daughters, even if they have already married.

If these assumptions hold, then the following functional consequences should follow if the helpers-at-the-nest hypothesis is true: Gypsy mothers of daughters who act as helpers should have (1) shorter inter-birth intervals and (2) longer reproductively active life spans (the period between first and last offspring) than mothers of non helpers; if (1) and (2) are both true, then it should follow that (3) mothers of helpers will have more children than those having first-born sons, whereas no such differences are expected among ethnic Hungarians.
Fig. 1. Mean lifetime fertility (completed family size) of Gypsy and non-Gypsy mothers as a function of the sex of their first-born offspring.

METHODS

The present study involved two rural populations: a Gypsy population living in Gilvanfa and a number of small villages around Gilvanfa [total number of adult female subjects aged above 45 years = 119] and a non-Gypsy (ethnic Hungarian) population living in a predominantly ethnic Hungarian village named Magyarmecské and other small nearby villages, which acted as a control group [total number of adult female subjects aged above 45 years = 137]. Gilvanfa and Magyarmecské, which are 5 km apart, are relatively poor areas of Hungary, the inhabitants of both ethnic groups all being victims of recent economic changes. They are located in the same culturally and historically homogeneous county (Baranya) and the same administrative district. There are significant differences between the two populations in education, income, and occupation. More Gypsies than ethnic Hungarians are unemployed, and they are more likely to have completed fewer than eight years of education and to have an annual income lower than the national average [see Bereczkei and Dunbar 1997].

The fieldwork lasted from August 1994 to June 1995. All 256 individuals were interviewed, using a questionnaire with 590 variables covering a full reproductive history [pregnancies, births, stillbirths, deaths, and inter-birth intervals] as well as details of the family social and educational circumstances and history. Additionally, the extent of helping behaviour was determined for a sample of 55 Gypsy girls over a total of 56 days and 42 ethnic Hungarian girls over 45 days. Observations were carried out in the subject's home for up to two hours at a time at intervals of three to four days, recording all gross behavioural acts performed by the subject. Since village houses were quite open, observation conditions were excellent. More than 12,000 behavioural acts were recorded. The subject's activity was later coded as one of eight mutually exclusive categories [changing the baby, holding babies, guarding babies and children, playing with children, cooking for children, helping in preparation for school, earning money for siblings, and a general category for all non-child-care behaviours].

Since our interest was in measures of fitness rather than fertility per se, we indexed completed family size as the number of offspring who survived to 12 months of age for females aged 45 and above. Birth-spacing data were analysed by the survival (or cumulative hazard) method [Forthofer and Lee 1995]. These data are used to examine the distribution of different lengths of time between two events and to calculate the proportion of cases for which the terminal event has occurred. The hazard function enables us to compare two sets of inter-birth intervals [for women having first-born daughters and those having first-born sons] and to estimate the probabilities of intervals' occurring at different time points.

RESULTS

The Gypsy women in this sample had had an average of $3.93 \pm 2.56$ live births, compared with $2.32 \pm 1.72$ live-born infants for the ethnic Hungarian women [Mann-Whitney $z = 6.08; N[G] = 119, N[H] = 137, P < 0.001$]. Gypsy mothers who bore daughters first had more children than those who bore sons first [fig. 1] (mean number of living offspring at the time of the study 4.44 versus 3.48 offspring, respectively; Mann-Whitney $z = 2.89$,
TABLE 1
Cumulative Probability of Having a Subsequent Birth as a Function of the Sex of the Firstborn Offspring for Gypsy Women

<table>
<thead>
<tr>
<th>Duration of Interval [months]</th>
<th>First Birth Interval After</th>
<th></th>
<th>Second Birth Interval After</th>
<th></th>
<th>Third Birth Interval After</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A Son</td>
<td>A Daughter</td>
<td>A Son</td>
<td>A Daughter</td>
<td>A Son</td>
<td>A Daughter</td>
</tr>
<tr>
<td>12</td>
<td>0.13</td>
<td>0.25</td>
<td>0.11</td>
<td>0.36</td>
<td>0.29</td>
<td>0.07</td>
</tr>
<tr>
<td>24</td>
<td>0.50</td>
<td>0.73</td>
<td>0.19</td>
<td>0.54</td>
<td>0.35</td>
<td>0.36</td>
</tr>
<tr>
<td>36</td>
<td>0.65</td>
<td>0.86</td>
<td>0.44</td>
<td>0.68</td>
<td>0.58</td>
<td>0.71</td>
</tr>
<tr>
<td>48</td>
<td>0.83</td>
<td>0.89</td>
<td>0.52</td>
<td>0.79</td>
<td>0.76</td>
<td>0.86</td>
</tr>
<tr>
<td>60</td>
<td>0.87</td>
<td>0.97</td>
<td>0.63</td>
<td>0.82</td>
<td>0.83</td>
<td>0.93</td>
</tr>
<tr>
<td>72</td>
<td>0.91</td>
<td>0.99</td>
<td>0.73</td>
<td>0.86</td>
<td>0.91</td>
<td>0.97</td>
</tr>
<tr>
<td>84</td>
<td>0.98</td>
<td>1.00</td>
<td>0.82</td>
<td>0.93</td>
<td>0.98</td>
<td>1.00</td>
</tr>
</tbody>
</table>

**Note:** Median inter-birth intervals are as follows: first, 38.4 [son], 54.0 [daughter] \( P < 0.05 \); second, 38.2 [son], 37.6 [daughter] \( P < 0.05 \); third, 40.8 [son], 37.6 [daughter] \( P > 0.05 \).

*Estimated by the hazard method of Forthofer and Lee (1995).*

\( N = 64 \text{ and } 53, \quad P = 0.002 \). Among the non-Gypsy ethnic Hungarians, the difference between these two groups was not significant [means of 2.23, \( N = 61 \text{ versus } 2.39, \quad N = 73 \), respectively; Mann-Whitney \( z = 0.102; \quad P = 0.91 \). Significant differences in birth spacing occur between Gypsy mothers having first-born daughters and those who bore sons first. Table 1 shows the cumulative probability of having a subsequent birth at different points in the birth order as a function of the sex of the first offspring when inter-birth intervals are allowed to vary between 12 and 84 months. Women having first-born daughters \( N = 64 \) typically have shorter birth intervals [irrespective of individual offspring’s sex] than those having first-born sons \( N = 53 \). Nearly three-quarters of the women in the former group gave birth to a second child within two years, compared with half of the women in the latter group. Although the difference between the two groups of mothers is not significant for the third interval, a relatively large cumulative effect can be seen over a life span [Fig. 2]. Gypsy mothers gave birth to their fourth child 8.63 years after their first-born daughter but 11.09 years after a first-born son [Long Rank Test [see Forthofer and Lee 1995] \( z = 2.11, \quad P = 0 < 0.05 \). Most

![Fig. 2. Probability of having a subsequent birth (prior to the fourth birth) as a function of sex of the first-born offspring among Gypsy women.](image-url)
of this difference can be attributed to shortened inter-birth intervals after each successive birth, not just a shorter inter-birth interval after the first-born daughter. Moreover, this difference occurs despite the fact that Gypsies breast-feed their daughters longer than they do their sons [see Bereczkei and Dunbar 1997].

Among 53 Gypsy women who had sons first, only 12 bore more than four children, whereas 29 of the 64 women having first-born daughters bore five or more surviving children. Put another way, 7.6% of the 184 children in son-first families were born as fifth or subsequent children compared with 16.3% of 286 children in daughter-first families [χ² = 51.12, P < 0.001]. In contrast, there is no difference between the equivalent two groups in the ethnic Hungarian population [χ² = 2.85, P = 0.89].

These data suggest that females who bore a daughter first continue reproducing to an older age. Indeed, for women over 45 whose first child was a daughter, the age at the birth of the last child was 37.4 compared with 34.2 for women whose first child was a son [Mann-Whitney z = 5.24, N = 64 and 53 respectively, P < 0.001].

During the interviews, 80% of both Gypsy and ethnic Hungarian mothers reported that their oldest girls participated in household duties [comparison between ethnic groups of number of subjects making such a statement: χ² = 0.795, N = 97, P < 0.85]. As far as housework [such as cleaning and cooking] is concerned, no significant differences were found between the two communities in a comparison across households for children of approximately the same age. However, striking differences were found in respect of child-care-related activities such as looking after babies, playing with children, and helping in preparation for school. In households where there was at least one younger child to be looked after, 77.9% of the 73 first- and second-born Gypsy girls older than ten years of age were regularly involved in the care of their younger sibling[s] compared with only 51.2% of 46 later-born Gypsy girls [χ² = 12.54 corrected for continuity, P < 0.01]; in contrast, 58.4% of first- and second-born and 39.2% of later-born ethnic Hungarian girls older than ten years of age engaged in these tasks [χ² = 2.16 corrected for continuity, P > 0.05]. Neither of these values is significantly different from that for later-born Gypsy girls, but both are significantly less than the equivalent figure for early-born Gypsy girls.

Table 2 shows the mean proportion of time spent in various helping activities during the observational samples by ethnic Hungarian and Gypsy daughters. First- and second-born Gypsy girls of all ages devoted a significantly higher proportion of their time to child-care activities than later-born girls, and these differences hold up even when only girls older than ten years are considered [overall mean for individual subjects for all child-care categories 39.8% versus 21.8% of activities, respectively; Mann-Whitney test, z = 3.12, P < 0.005]. The differences are highly significant for each helping category. Similar differences have been found between early-born Gypsy daughters and early-born ethnic Hungarian daughters, although they are not significant in three categories [changing the baby, guarding babies and children, helping in preparation for school].

Many of these activities continue even after the girls get married. First-born Gypsy daughters marry on average at 17.5 years of age, but they do not leave home and begin to live separately from their parents until they are on average 19.7 years old [fig. 3]. In other words, early-born Gypsy girls stay at home for almost two years after marriage or cohabitation [Mann-Whitney test comparing age at marriage and age at leaving home: z = 2.75, N = 46, P < 0.005], during which time they continue to help their parents raise their younger siblings. For Gypsy sons and ethnic Hungarian sons and daughters, the difference between the age of marriage and the age of separation from parents is reversed and, in each case, also significant [Gypsy sons, z = 4.18, P < 0.001; ethnic Hungarian daughters, z = 3.96, P < 0.001; ethnic Hungarian sons, z = 3.39, P < 0.001]. In other words, they typically leave home first and marry afterwards.

**Discussion**

We have shown that, in this rural population, [1] early-born Gypsy girls engage in substantial help in housework related to child care of their younger siblings even after their marriage; [2] this assistance both increases the length of the mother’s reproductive career and reduces inter-birth intervals for subsequent children; and [3] Gypsy women giving birth to first-born daughters have significantly more children than those giving birth to sons first.

These results raise the question of how female-biased strategies increase inclusive fitness. Natural selection may favour sex biases in parental investment if one sex of offspring enhances the reproductive success of its parents (or siblings) by providing resources [Hamilton 1967]. Offspring that provide help to their parents or siblings repay some of the costs of parental investment, and this assistance may reduce the parents’ net reproductive cost [Sieff 1990]. Although these ideas have only rarely been tested in human societies [Cronk 1989, 1991], there is evidence that offspring can contribute to parents’ reproductive costs in a number of different ways. In South Asia, for example, Kanjar females are more economically productive than males and help their brothers to marry. Among the Mundugumor of Papua New Guinea, fathers favour daughters, who are then used to obtain wives for their brothers [Cronk 1991]. On the Micronesian island of Ifaluk, daughters are more likely than sons to assist their parents in future reproduction. Women who bear a daughter first have greater reproductive success than those who bear a son first [Turke 1988]. However, there is no evidence of female-biased investment among the Ifaluk.

Our data from a rural Gypsy population seem to provide another example of the same phenomenon: having a first-born daughter reduces the mother’s costs of rearing her current infant, thus allowing her to transfer the resulting spare time and energy to producing and raising additional children. The female surplus among first-born
TABLE 2
Child Care Activities Involving Siblings by Girls Older than Ten Years as a Proportion of All Recorded Behavioural Acts

<table>
<thead>
<tr>
<th>Activity</th>
<th>Percentage of Time*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Early-Born Gypsy Daughters</td>
</tr>
<tr>
<td>Changing the baby</td>
<td>4.8</td>
</tr>
<tr>
<td>Holding babies</td>
<td>4.7</td>
</tr>
<tr>
<td>Guarding babies and children</td>
<td>7.1</td>
</tr>
<tr>
<td>Playing with children</td>
<td>8.3</td>
</tr>
<tr>
<td>Cooking for children</td>
<td>5.6</td>
</tr>
<tr>
<td>Helping in preparation for school</td>
<td>5.2</td>
</tr>
<tr>
<td>Earning money for siblings</td>
<td>4.1</td>
</tr>
</tbody>
</table>

*Overall mean of values for individual subjects.

Table 2 shows that the female-biased child-care patterns observed in this rural Gypsy population may therefore be intended to increase the number of children rather than to produce a Trivers-Willard (1973) effect (which may be a strategy more characteristic of urban Gypsy populations).

A female-biased sex ratio thus seems to be associated with two kinds of parental strategies among the Gypsies. In an urban environment, given relatively scarce and unpredictable resources and the opportunity for hypergamy into the sympatric wealthier ethnic Hungarian population, Gypsy girls, rather than sons, are favoured by their parents because, in contrast to sons, they have the opportunity of “marrying up” into the ethnic Hungarian population. In terms of breast-feeding and education, these Gypsy parents therefore invest more heavily in their daughters [Bereczkei and Dunbar 1997]. In the more endogamous rural environment, in contrast, there are no large local status and wealth differentials [Gypsies and ethnic Hungarians live in separate villages], and thus there is no real chance of marrying up. Instead, early-born Gypsy girls are expected to engage in helping activities related to child care that reduce the mother’s burden from parental duties. Among rural Gypsies, therefore, older girls enhance the resource base of their younger siblings. These results thus suggest that the

Fig. 3. Mean age of marriage and mean age of leaving home for Gypsy and non-Gypsy children.
choices that individuals make are highly contingent on circumstances.

One common counterargument against the helping-at-the-nest model is that people prefer sons and therefore produce as many children as necessary to obtain a son. Hence, having had a daughter first, they are more likely to continue reproduction for longer in order to be sure of getting a son. This argument is difficult to refute on demographic data alone. However, our results suggest that female-biased sex ratios among the Gypsies are not a by-product of a preference for sons; they genuinely prefer daughters and invest more heavily in them. Investment differentials were demonstrated in respect of higher abortion rates after daughters, longer breast-feeding, and longer periods of education for daughters in both urban and rural communities (Bereczkei and Dunbar 1997). If sons were considered more valuable, these differences in direct and indirect parental care would have shown the reverse pattern.

Daughters thus seem to be the focus of Gypsies’ fertility in both urban and rural communities. This may be one of the reasons first-born Gypsy children still frequently inherit the mother’s name rather than the father’s as is otherwise the norm in Hungary and elsewhere in Europe. The influential role that Gypsy girls and women play in family life may be reflected in the fact that Gypsies are frequently cited as a society based on a form of “matriarchy.”

Finally, it is worth emphasizing that one inevitable reason late-born Gypsy daughters engage in relatively little helping-at-the-nest is that they have less opportunity to benefit from enhancing their mothers’ fertility because their mothers are already approaching menopause. Although late-born daughters should have the same beneficial effect on the mother’s time and energy budgets by relieving her of child care for younger siblings, the fitness payoff that accrues to the mother from producing a late-born daughter relative to that for producing a late-born son is much lower because the mother has fewer future reproductive opportunities to offer. On average, the Gypsy mothers in the sample produced their third-born child at age 25.5 and their fourth-born child at age 27.5; mothers would thus be in their late 30s and already approaching the end of active reproduction by the time these offspring were old enough to help with child care [10–12 years of age]. Since these will, on average, be second-born daughters, later-born daughters are likely to be too young to have a significant impact on the mother’s reproductive output; they are therefore more likely both to resist requests to provide child care and to pursue their own interests. At the same time, mothers will have less to gain from their help and are therefore likely to be less willing to engage in conflict with their daughters.

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Hypolactasia and the Chinese Diet

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It may, at first sight, seem surprising that the Chinese, who are known to have eaten just about every creature that flies, runs, swims, or crawls, should have taken so little interest in milk, a wholesome, nutritious commodity long regarded in the West as the “perfect food.” This attitude appears to defy common sense.1 It is not that milk from lactating domestic animals was unknown to the ancient Chinese. Indeed, oracle-bone and bronze inscriptions suggest that the collecting of milk from cows and mares was not an unfamiliar art during the Shang Dynasty [ca. 1520–1030 B.C.].2 Moreover, accord-

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1. This issue was raised more than a century ago by Hahn (1896) and commented on by Lauffer (1914–15:168) and Creel (1937:80). For a detailed discussion see Simoons (1991:454–63).
2. From an analysis of Shang oracle bones and ancient bronze vessels (Yuan 1986) has proposed that the glyph which has been customarily rendered as nai (1) [a conjunctive and disjunctive particle] should be interpreted as nai (2) [milk] (see appendix, column 2). His idea is supported by Xu (1989:500), who points out that the original pictogram of the word is an excellent representation of the shape of the teats of lactating female mammals.
Hypolactasia and Lactose Absorption

The answer to the first question is in fact quite straightforward. The reason the ancient Chinese did not develop dairy farming is that the consumption of substantial amounts of milk could be hazardous to their health.

To many people in Europe or North America it may still seem incredible that milk could be harmful to anyone’s health. Yet as early as 400 B.C. Hippocrates is reported to have observed that milk was bad for patients with fever whose bellies were “distended and full of rumbling.” (Chadwick and Mann 1950:168). And in A.D. 200 Galen noted that Green 1951:210–11, cited in Sahi 1994b: 17):

With regard to milk, it should not be given to all, but only to those who digest it well and perceive no symptom in the right hypochondrium. For even if sometimes it should ever be taken without bread, it both goes through more quickly and is flatulent. — But somebody was sick all the time, no matter in what way he prepared it. And someone else, similarly trying to use the milk, had no trouble for he digested it well, and had no hyperacidity, or eructation, or gas, or weight in his hypochondrium.

It was only in the 1960s that the reason for this discrepancy became known. Cow’s milk contains about 5% lactose or milk sugar, a β-d-galactoside of glucose and the principal carbohydrate in milk. As a disaccharide, lactose has to be hydrolyzed to galactose and glucose before it can be absorbed from the small intestine. The intestinal enzyme that hydrolyzes lactose is called lactase. All infant mammals produce liberal amounts of this enzyme, but after weaning the level sharply declines, eventually becoming so low that adults are no longer able to digest lactose—a condition called hypolactasia, lactase intolerance, or lactose malabsorption. The undigested lactose creates an osmotic load and draws large amounts of water from the body fluids into the intestine. It then passes into the colon, where it is fermented by bacteria into propionic and butyric acids, methane, hydrogen, and carbon dioxide. These conditions may cause stomach cramps and diarrhea and interfere with the absorption of other nutrients. In other words, adults are lactose-intolerant (or lactase-deficient). This scenario is true for all mammals except humans, of whom a considerable proportion today are lactase-sufficient—able to continue producing lactase and utilizing lactose in the diet throughout their adult lives.

It is now known that the occurrence of hypolactasia is genetically controlled. It cannot be reversed or ameliorated by adaptation, if an individual is lacking in the lactase-persistence gene, he will lose the ability to produce lactase as an adult no matter how vigorously and for how long he continues to drink milk after weaning. Extensive population studies have shown that the prevalence of hypolactasia is highest in East and Southeast Asia (85–100%) and lowest in Northwest Europe, Australia, and New Zealand (< 10%). Intermediate values are found for Central Europe (40–40%), Southern Europe (40–70%), the Middle East (24–80%), Africa (13–90%), and India (30–80%) (Sahi 1994b). If adult hypolactasia is the norm for all mammals, our earliest prehistoric ancestors must also have been mostly lactose malabsorbers as adults. How and when did the variations in hypolactasia we see today arise? The generally accepted answer to the “how” part of the question is the cultural-historical hypothesis of Simoons (Simoons 1970a; McCracken 1971, Johnson et al. 1974; see Sahi 1994b: 75–85) 

8. The literature on hypolactasia is voluminous. For an excellent overview of the current state of the field, see Sahi 1994a, b.

9. For a summary of the evidence, see Sahi (1994a: 8–9). The long-held view that hypolactasia can be corrected by adaptation (see Bray 1984: 5) is no longer tenable.

10. The values vary widely among different population groups. In the Middle East the occurrence of hypolactasia is only 24% among nomadic Bedouins but 75–80% among the Arabs of Israel, Jordan, Lebanon, and Egypt. In Africa it may be as low as 13–17% among the cattle-raising nomads of Beja in northeastern Sudan, the Tuaregs in Niger, and the Fulani in Nigeria but as high as 70–90% in other populations. In Pakistan and northern India it is 30%, but in southern India and Sri Lanka it is 70%. Most of the field studies were carried out using a hydrogen breath test to detect the presence of hypolactasia (see Flatz, Kuhnau, and Naftali 1984).
which is based on the proposition that when milk is a significant part of the diet, lactose absorbers will have a better chance of survival and reproduction than those who are lactose-intolerant.

In any large prehistoric population there would have been a few individuals who, through mutation or inheritance, had retained the ability to digest lactose as adults. If milk was a major part of the diet, such individuals would have been able to use all the nutrients in milk without adverse effects. They would have been stronger and would have produced more offspring than their lactose-intolerant neighbors. In each generation the number of lactose absorbers would have increased, and in time, barring other dietary changes, they would have become the dominant group in the population. This is presumably what happened in Northwest Europe. If milk was not a major but still a significant part of the diet, the advantage enjoyed by the lactose absorbers would have been less compelling, and the proportion of lactose absorbers and nonabsorbers in the adult population would have been more evenly balanced. This is the situation in many parts of the world. Finally, if milk was not a significant part of the diet and lactose absorbers enjoyed no advantage over those with hypolactasia, there would have been no increase in the number of lactose absorbers in the population. This is what happened in East and Southeast Asia and in West and Central Africa (Simoons 1970b). 11

EMERGENCE OF ADULT LACTOSE ABSORBERS

If the earliest prehistoric settlers in the world were virtually all lactose nonabsorbers, how could milk ever have become a significant part of their diet so that selection in favor of lactose absorbers could get started? As far as I can see, this was possible only in a situation in which milk was so abundant that its adoption as food would have been highly beneficial not only to lactose absorbers but also to the community as a whole. Such a unique situation, I submit, existed about 7000-8000 B.C. among the prehistoric pastoral tribes of the Fertile Crescent, who would have had herds of lactating animals, such as goats, ewes, and cows (and later camels), at their disposal. 12 They probably started off their pastoral life-

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style with animal flesh as the primary food, but once they had learned the art of milking they would soon have realized that they had a rich and renewable resource on their hands. 13 They might have fed milk first to young children, who would have had no difficulty in digesting the lactose and would have grown healthy and strong. Then they would have found that a few adults could also tolerate it. These fortunate individuals would have been encouraged to drink milk because it meant that they would consume less meat, making more meat available to feed the rest of the population. This marked the point when the selection process in favor of lactose absorbers began to take off. Soon the art of milking would have been passed on to the early agricultural communities that were sprouting contemporaneously adjacent to the pasture lands that supported the lifestyle of the herders.

This process of selection, however, did not reach its logical conclusion among all the pastoral peoples of the Near East and North Africa. Some time before the selection was complete, technology intervened. It was discovered that if the milk were left to stand at above room temperature it would soon turn sour, producing a variety of soured [fermented] milk products. In fact, in the warm summers of parts of the Near East the process is almost inevitable. These secondary milk products have come to be known variously as yogurt [from cow’s or ewe’s milk], koumiss [from mare’s milk], or kefir [from camel’s milk]. Furthermore, upon churning the fats in milk or soured milk would separate to produce butter and butter oil. 14 What is pertinent for us at this point is that in the soured milk products the lactose has been disarmed—hydrolyzed into galactose and glucose and converted into lactic acid, which is well tolerated by those who cannot utilize lactose. For many years it was thought that lactose specifically enhanced the absorption of calcium (Harris 1985:40–42; Hui 1985:88). If so, lactose absorbers might still enjoy a significant advantage over nonabsorbers by drinking fresh milk rather than fermented milk. Recent work, however, has shown that there is no solid evidence in support of this hypothesis (Simoons 2001:8–12). For practical purposes, therefore,
the soured milks are as nutritious as fresh milk itself.  
Thus, with the emergence of fermented milk products the advantage enjoyed by lactose absorbers would have been greatly reduced and the selection pressure in favor of lactose-tolerant individuals virtually eliminated. When this happened, lactase-deficient individuals would have continued to exist even among descendants of herders who could trace their ancestry to the pioneering nomadic pastoralists of the Neolithic. At the same time, lactose nonabsorbers could, if conditions were favorable, suddenly adopt soured milk products as a major food resource and become successful nomadic herders. Presumably this is what happened in the steppes of Northeast Asia during the 1st millennium B.C.

Surprisingly, it is in the populations of Northwest Europe that we find the most successful process in favor of the selection of lactose absorbers. The extraordinarily low incidence of hypolactasia in Northwest Europe is, I suspect, the result of a unique set of circumstances. When agriculture and animal husbandry reached Northwest Europe during the Neolithic, it was animal husbandry, including dairy culture, that first took root. The region was damp, cloudy, and cold. The staple crops, such as wheat and barley, selected in the warm, sunny, semiarid Near East would have done poorly there until new varieties (or new crops) better adapted to the prevailing conditions were developed. At the same time, there was plenty of rich pasture available to feed herd animals, and animal flesh and milk soon became the most important sources of food. It appears that in these circumstances the overall nutritional advantages that accrue to lactose absorbers were even more compelling than those we have seen among the nomadic pastoralists of the Near East.

It has been postulated that the extraordinary selective advantage enjoyed by lactose absorbers over nonabsorbers in Northwest Europe is linked to the absorption of calcium (Flatz and Rottauwe 1973; Flatz 1987:56–59). In a climate that provided only a low level of sunshine, pelvic deformity, rickets, and osteomalacia are presumed to have been common ailments because of the lack of vitamin D and the poor absorption of calcium. Those who could not tolerate milk would have consumed less dietary calcium than those who could. As a result, lactose absorbers would have enjoyed much better health and reproduced more successfully than nonabsorbers. This calcium-absorption hypothesis has been well received among anthropologists (see, e.g., Harris 1985: 142–48; Durham 1991:254–85), but it is apparently not supported by historical, osteoarchaeological, or biomedical evidence (Simoons 2001:12–45). Be that as it may, it is possible that the cool climate may have favored lactose absorbers in another way. Under cool conditions milk would have kept longer and soured milks would not have occurred spontaneously; the art of making them would have to have been transmitted from the Near East at a later date. Consequently, in Northwest Europe the selection process was able to continue long enough to enable lactose intolerance to reach the lowest level known. For the people of Northwest Europe the integration of animal husbandry in general and dairy farming in particular with grain production thus made excellent economic as well as nutritional sense.

As to when these variations arose, we can only speculate. Calculations on the time it took for the observed variations to emerge based on various values of selection power suggest that we are dealing with time spans in the range of 3,000–5,000 years. In the Near East, the selection process presumably started shortly after humans first learned to rear herds of lactating mammals (ca. 7000–9000 B.C.) and ceased there when civilized societies with established systems of agriculture and animal husbandry made their appearance (ca. about 3000 B.C.) in Sumer and Egypt. The intervention of soured milk products probably occurred about halfway between these two events (ca. 4000 B.C.). In Northwest Europe, the selection process probably started when the practice of animal husbandry was first transmitted from the Near East (ca. 6000 B.C.) and ceased when the art of making soured milk products became a stable part of the food production system (ca. 2000 B.C.).

THE SITUATION IN CHINA

In the case of prehistoric China the situation appears to have been just the opposite of that of the Fertile Crescent and Northwest Europe. There is no indication that lactating herd animals or dairy products constituted the primary food resource for a significant portion of the population of China at any time during the Neolithic period. In the early communities of the wetlands along the Yangtze and the loess plateau carved by the Yellow

15. The free energy of glucose and galactose is 686 kcal/mole and that of lactic acid 639 kcal/mole; thus there is a loss of 47 kcal/mole or 7% of the free energy in the lactose conversion. This loss is minor. There is no loss in the value of the other constituents of milk, proteins, fats, and vitamins. On the assumption that in the Near East soured milk was discovered soon after the start of the harvesting of milk from lactating animals, Russell (1988:32) has concluded that hypolactasia has had only a minor effect on the evolution of dairy farming as a component of animal husbandry. Sherratt (1981), in contrast, argues that soured milk was not widely used until the 4th millennium B.C., in which case hypolactasia could have had a significant effect on the point at which a tribe could be persuaded to adopt dairy farming.

16. For example, among the nomadic Bedouins in Jordan, descendants of the original nomadic pastoralists of the Near East, the incidence of hypolactasia is still about 24%, considerably higher than the 4% in Denmark and 5% in Great Britain (see Sahi 1994b: 12, 15).

17. The proximity of their lifestyle to dairy farming and cattle herding may have conferred yet another advantage on the Northwest Europeans. Indications are that since antiquity common cattle have been important in spreading tuberculosis among humans. If so, the Northwest Europeans would have developed a greater resistance to tuberculosis than their eastern and southern neighbors (see Haas and Haas 1995). I thank F. J. Simoons for drawing my attention to this possibility.

18. It has been estimated that with a selection power of 5% it would require from 160 to 250 generations (3,000–5,000 years) to reach the low level of hypolactasia seen in Northwest Europe. A stronger selection power, 5–7%, would require a shorter selection period (see Flatz 1987:59–60; Sahi 1994b:11; Simoons 2001:46).
River, the environment was far less conducive to the rise of a pastoral economy than that which prevailed in the Fertile Crescent. Excavations at the Hubei Basin and Hangzhou Bay in the south ([9000–4000 B.C.] and the Peiligang and Yangshao sites in the north ([6000–4000 B.C.]) show that the earliest domesticated animals were the dog, pig, chicken, and water buffalo (Smith 1995:125, 138–139). Sheep, goat, and cattle made their appearance in small numbers only after 5000 B.C. (Chang 1986:113, 160, 217; Guo, Li, and Zheng 1999:396–97). It is not known whether these early lactating mammals were wild or domesticated. The prevailing food production system appears to have been based on agriculture, supplemented by limited animal rearing, hunting, gathering, and fishing. It is not until the Shang Dynasty (ca. 1520–1050 B.C.) that we see, through archaeological excavations in the Shang heartland in southern Henan and oracle-bone inscriptions, evidence of the occurrence of large herds of cattle or sheep (Chang 1980:143). Throughout the long prehistoric period calcium was presumably supplied by the wealth of green leafy vegetables cultivated or collected from the wild. There was always plenty of sunshine to allow the synthesis of vitamin D needed for the utilization of dietary calcium. There would have been little selection pressure for lactose absorbers against nonabsorbers even if milk had been freely available. As a result, the adult population during the Shang Dynasty was probably as firmly lactase-deficient as it had been at the dawn of the agricultural revolution 7,000–8,000 years earlier.

Animal husbandry in the sense of the rearing of cattle and sheep presumably reached its highest expression in the northern heartland of Chinese civilization during the Shang and early Zhou. Even then it was by no means the predominant component of the food production system (Chang 1980:136–49, 214–15; R. Huang 1987). Dairy farming could have been attempted, but since more than nine out of ten adults who tried to drink milk would have experienced unpleasant effects and alternative sources of food were plentiful, it would have remained an esoteric activity practiced on a limited scale. Apparently animal husbandry was also important to the livelihood of the ancestors of the Zhou people who conquered the Shang and founded the Zhou Dynasty (1030–221 B.C.). In fact, the Shiji tells us that the proto-Zhou clan had at one time pursued a pastoral lifestyle among the Rong and Di tribes to the northwest and north before they returned to the practice of agriculture in their traditional homeland along the Wei and Jing Rivers in eastern Shannxi. As indicated by numerous references in the Shiji (Book of Odes) (see Waley 1960 [1937]: nos. 110, 150, 161, 195, 199, 220, 238), an anthology of folk songs and ceremonial odes collected between 1100 and 600 B.C., cattle and sheep herding continued to be a significant part of the economy during the Western Zhou (1030–722 B.C.). Furthermore, according to the early Han Dynasty Zhoutai (The Rites of the Zhou), horses, cattle, and sheep were mentioned as the principal livestock in six of the nine provinces of Zhou China (Zhi fangzhi, pp. 344–50; see Huang 2001). But without dairy products as a renewable food resource, the herding of cattle and sheep just for their meat was an expensive strategy that could not be sustained in the face of a rising population and mounting demands of land for agriculture. According to the Erya (Literary Expositor), ca. A.D. 300, new fields were constantly being cleared for grain production. During the early Zhou years the Rong and the Di were gradually absorbed into the Chinese economic and political sphere and became farmers instead of herders. As a result, the land available for pasturage

19. In Smith’s (1995) account of the emergence of agriculture there is a striking contrast between the wealth of information on the domestication of large mammals in the Fertile Crescent and the paucity of such information in the Yangtze and Yellow River valleys in China. The former runs to 16 pages (pp. 53–67, 88–98) while the latter consists of scattered statements that take up less than a page. Furthermore, hunting and fishing remained significant sources of food until the middle of the 1st millennium B.C. (see Huang 2000: 60, 61–63).


21. Chang notes the numbers of cattle used in burial rituals: “1,000 cattle in one ritual once, 500 once, 400 once, 300 thrice, 100 nine times, and so on.” These numbers are much larger than those reportedly used on ritual occasions in Homer’s Iliad and Odyssey, but they pale into insignificance when compared with those employed by another people in Southwest Asia in the 10th century B.C. In Kings I [8:63] we read that Solomon and all Israel with him offered to the Lord 22,000 oxen and 120,000 sheep. If this statement is true, the world has probably not seen a ceremonial bloodbath of animals of this scale ever since.

22. In the absence of dairy foods, the diet was nevertheless probably low in calcium by Western standards [see, e.g., Latourette 1957: 567; Koo 1976:130]. A comprehensive nutritional survey carried out in the late 1980s showed that active healthy males in the Chinese countryside consumed only an average of 344 mg/day of calcium as compared with 1143 mg/day for the equivalent group in the United States (Chen et al. 1990:50, table 5.5). Evidently, by adapting to a smaller bone structure, height, and weight, the Chinese are able to maintain health with a lesser amount of calcium intake.
began to shrink, as did the size of herds of sheep and cattle and the amount of meat harvested from them.\textsuperscript{27} The typical Chinese style of agriculture, which stresses grain production and deemphasizes the rearing of lactating mammals, gradually established itself as the dominant mode of food production.

\textbf{The Nomadic Warriors of the East Asian Steppes}

Even as the system of intensive agriculture encroached on the land formerly available for pasture in the Zhou heartland in the first half of the 1st millennium B.C., it was expanding and achieving consolidation among the vassal states to the east and south. Its spread farther north was halted by the great Eurasian steppes, which were unsuitable for supporting an agricultural economy. In the latter part of the millennium, the local inhabitants within and along the margin of the Asian steppe, “which until this time had been neither exclusively agricultural nor exclusively pastoral, began to take up for good an unmistakable pastoral steppe nomadism”\textsuperscript{28} and soon formed a formidable national entity (Chang 1977:390–97). This new nomadic nation was distinguished from that of the Zhou Chinese in two important respects. First, its economy was based on a specialized technique of horse usage which enabled mounted warriors to move large herds of horses, cattle, and sheep rapidly in search of new pastures across the steppes. This gave the herders a degree of mobility and a geographical range of operation far beyond that enjoyed by the Rong and the Di. Secondly, its people had adopted the milk of horses, cattle, and sheep as their major food resource. Thus, the steppe nomads known to the Chinese as Xiongnu\textsuperscript{29} became virtually independent of settled farming to meet their need for food. By the start of the Han Dynasty (202 B.C.–A.D. 220) they had achieved such a high degree of economic, political, and military power that they posed a serious threat to the newly established Chinese empire.

How did the Xiongnu, in contrast to their Chinese neighbors, come to adopt milk as their primary food resource? Chinese tradition holds that they were ethni-

cally not very different from the Rong-Di or the Chinese (Lattimore 1988[1940]:56, 342).\textsuperscript{30} In fact, the Shi ji (110.2879; Watson 1961:155) states that they were descendants of the rulers of the legendary Xia Dynasty (2000–1520 B.C.) and that even “as early as the time of Emperors Yao and Shun [i.e., preceding the Xia Dynasty] and before, we hear of these people [i.e., ancestors of the Xiongnu] . . . living in the region of the northern barbarians and wandering from place to place pasturing their animals.” This means that in the 2d millennium B.C. the proto-Xiongnu tribes would have lived for generations in close proximity to the Rong and the Di. If so, could the utilization of milk as food have been transmitted from the Rong and the Di to the proto-Xiongnu? The Shi ji (Record of Rites) says that the Rong and the Di wore skins of animals and “some of them did not eat grain-food”\textsuperscript{[p. 230; Legge 1885:229, cited by Chang 1977:42]},\textsuperscript{31} which would suggest that most of them ate meat with grains as a supplement. Perhaps more informative is a passage about the food habits of the northern barbarians from the \textit{Huangdi neijing suwen} (Yellow Emperor’s Manual of Internal Medicine, Questions and Answers), a composite work that reached its present form in the 2d century B.C.: “In the North, natural resources tend to lie hidden. The terrain is mountainous and the weather marked by biting winds, frost, and ice. The people find pleasure in living in the wilderness and consume milk as their primary food [my emphasis].\textsuperscript{32} As a result coldness often descends into their organs and causes distended bellies [my emphasis].\textsuperscript{33} These illnesses are best

27. I would not, however, go so far as Eberhard (1971:155), who says that “between 400 and 100 B.C. the meat-eating Chinese reduced their meat intake greatly, gave up eating beef and mutton and changed over to pork and dog meat.” While it is likely that the Shang and early Zhou Chinese ate more beef and mutton than their descendants of the late Zhou (500–320 B.C.), they could hardly be characterized as a basically meat-eating people. Nor can it be said that they substituted pork and dog flesh for beef and mutton at that time. Pigs and dogs had been raised for meat at least since 6000 B.C. (Chang 1986:31).

28. The passage continues, “They established a sphere of activity of their own, eccentric to the sphere of civilized society in China.” This may also mean that within this sphere farmers and herders coexisted and complemented each other’s activity.

29. But called Huns by some scholars in the West [see e.g., Pulleyblank 1983:451; Cavalli-Sforza, Menozzi, and Piazza 1994:201, 224; Lubo-Lesnichenko 1989:50; “the Huns stemmed basically from the Siberian branch of the Mongoloid race”]. There is, however, no direct evidence to relate the Xiongnu of 200 B.C. in East Asia to the Huns of Europe in A.D. 400 [Thompson 1999:1].

30. Průšek (1971:209–28) also maintains that the Rong and the Di were ethnically and linguistically no different from the Zhou Chinese. Furthermore, they may well be related to the Xiongnu and other nomadic peoples that the Chinese were to encounter from 300 B.C. on in the Asian steppes.

31. “Those on the west were called Rong [Jung]. They had their hair unbound, and wore skins. \textit{Some of them did not eat grain-food} [my emphasis]. Those on the north were called Di [Ti]. They wore skins of animals and birds, and dwelt in caves. \textit{Some of them did not eat grain-food} [my emphasis]. Most scholars agree that by the start of the Spring and Autumn period (722–480 B.C.) the Rong and the Di had already become largely settled farmers [Hsu and Linduff 1988:50; Průšek 1971:217; Pulleyblank 1984:447]. We may therefore infer that these statements refer to the condition of these tribes at an earlier time, well before the founding of the Zhou Dynasty (1030 B.C.).

32. In the original, \textit{ru shi}. Literally, \textit{ru} is “milk” and \textit{shi} is “to eat” or “food” [i.e., the stuff that is eaten]. Veith translates \textit{ru shi} as “live on milk products,” but in this context it is preferably translated as “drink milk” or “use milk as a primary food.” Although the \textit{Huangdi neijing suwen} was compiled in about the 2d century B.C., much of the material could have existed at an earlier time, possibly in very early Zhou or late Shang times.

33. The original reads \textit{zang han sheng mian bing}, and Veith translates it as “The extreme cold causes many illnesses.” The commentary by Zhang Jingyue (ca. A.D. 1563–1640+), a well-known physician and commentator on the \textit{Huangdi neijing suwen}, says, “The land is cold, so is the character of milk. Therefore, coldness settles in the internal organs. Elimination is retarded and the belly becomes distended.” The illness as described fits in well with a condition of hypolactasia. Such a condition would not have occurred if the milk had been processed to remove the lactose. The statement suggests that the Zhou people knew that milk could cause ailments in the digestive system.

This passage suggests that during the late Shang and early Zhou (ca. 1200–1000 B.C.) some of the northern pastoral peoples had acquired such large herds of lactating mammals that they had begun to consume milk as a major food, but they were all lactose nonabsorbers and suffered from the typical symptoms of hypolactasia. The northern barbarians apparently included the Rong and the Di as well as the proto-Xiongnu. We presume the Rong and the Di abandoned the use of milk as food when they realized that the adverse effects they endured were due to the ingestion of milk. In time they were absorbed into the Chinese agricultural system. The Zhou Chinese were evidently aware of the fact that ingestion of substantial amounts of milk could cause stomach ailments. This awareness undoubtedly served as a deterrent to the establishment of dairy farming as a significant component of their food production system.

But what happened to the proto-Xiongnu who lived at the margin of the steppes? Their descendants became part-herders and part-farmers and remained outside the Chinese sphere of influence. They could have discontinued the use of milk as food and gone back to a diet of meat supplemented by grains. This would mean that Rong and the Di abandoned the use of milk as food when they realized that the adverse effects they endured were due to the ingestion of milk. In time they were absorbed into the Chinese agricultural system. The Zhou Chinese were evidently aware of the fact that ingestion of substantial amounts of milk could cause stomach ailments. This awareness undoubtedly served as a deterrent to the establishment of dairy farming as a significant component of their food production system.

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This, however, would have provided only about 1,000 years for the selection process, hardly adequate to allow the emergence of a Xiongnu population that was largely free from hypolactasia. Thus we are forced to conclude that at about 300–400 B.C. the people living on the steppes bordering China, who were on the verge of adopting milk as their primary food resource, were lactose nonabsorbers. This is possible only if what the Xiongnu consumed was not milk itself but fermented milk products in which lactose had been converted to lactic acid or alcohol. Indeed, we find that according to the Shiji (110:289) and the Qian Hanshu (94:3759) what the Xiongnu consumed was not milk [ru] itself but a fermented form of it, known as luo, which is a type of soured milk or yogurt.

How did the Xiongnu acquire the technology of making and utilizing fermented milk products? There are only two possibilities: either they developed it themselves or they learned it from others. The suddenness with which they appeared on the scene as nomads dependent on milk as their principal food resource suggests that they had acquired the technology by transmission. Furthermore, at about the same time they had also acquired another technology critical to the success of their lifestyle, that of mounted horsemanship. It seems likely that both technologies had been transmitted to the proto-Xiongnu in the latter part of the 1st millennium B.C. by the Scythians and Sakians, the first nomadic societies in the western sector of the great Eurasian steppes and the dominant powers of the region from the 8th to the 3rd century B.C. (Chang 1977:396; Pavlinskaya 1989). The Scythians were skilled horse riders. According to Herodotus (1983:128) they drank milk, and it is reasonable to assume that they knew the art of making fermented dairy foods.

What was true of the Xiongnu during the Han Dynasty was very probably also true of their nomadic successors, the Xianbei, the Tuoba, the Qidan, and the Mongols of later eras, who invaded China and established short-lived dynasties within the Great Wall. All these nomadic nations were lactose nonabsorbers but were able to utilize milk because they had learned to improve its digestibility by fermentation. This hypothesis is borne out by the observation that among the modern Mongols, who are direct descendants of the ancient nomads of the East Asian steppes, the prevalence of hypolactasia is as high as 88%, virtually the same as that for Chinese (Sahi 1944b, Wang et al. 1984, Zheng et al. 1988). This is not surprising, since consuming mainly fermented milk products greatly reduced the selection pressure in favor of the ability to metabolize lactose.

The above scenario is in agreement with the thesis that, in contrast to the situation in the Fertile Crescent, the emergence of these aggressive East Asian mounted nomads was a rather late historical development, probably contemporaneous with the formalization of the intensive agricultural system in northern China during the Eastern Zhou Dynasty (722–221 B.C.) (see Lattimore 1989:1940:340–65). There was neither the time nor the selection pressure for a lactase-sufficient population to evolve.

luo and not milk is the principal drink. For further discussion see Huang (2000:253).

37. The statement actually applied to the Massagetes, which may be just another name for the Scythians (Cavalli-Sforza, Menozzi, and Piazza 1994:201). There is no specific record that the Scythians made fermented milk products, but in view of their proximity to the Near East, where dairy farming originated 7,000 years earlier, this seems a reasonable assumption.

38. U.S. diplomats and Peace Corp volunteers who have recently lived in Mongolia report that the modern Mongolians consume mainly yogurt and lactic cheeses and not much fresh milk.
DAIRY FOODS AND THE CHINESE DIET

This then brings us to our second question: Why did the Chinese fail to incorporate milk and milk products into their food system? Actually, the question is itself based on a misconception. When we study the historical literature we find that milk, in the form of luō, was, in fact, significant in the diet of the ruling classes in northern China from the Han until the end of the Yuan [Mongol] Dynasty [ca. 202 B.C.–A.D. 1368] [Hu 2000: 250–53]. Indeed, the Shiming [Expositor of Names] in the early 2d century A.D. states [13:8b] that “luō is prepared from milk juice; it makes one fat.” Furthermore, there was a prefect of mare milkers at the Han court whose duty it was to collect mare’s milk and process it into a mare’s-milk wine [Qian Hanshu, 79:7a, cited in Bielenstein 1980:34].39 The making of yogurt [luō], butter [su], and soft cheeses [ganluo] from cow’s milk is described in detail in the celebrated agricultural compendium Qimin yaoshu [Important Arts for the Peoples’ Welfare] of A.D. 544. Luō and other dairy products are mentioned in the Tang Dynasty [A.D. 618–906] pharmacopoeia Xin xiu bencao [pp. 170–71] and the Song Dynasty [A.D. 960–1279] Zhenglei bencao. It is also clear, however, that although for more than a thousand years milk products were a significant component of the diet of upper-class Northern Chinese, they never became an integral part of the diet of the common people. As a result, dairy farming remained a peripheral component of the food production system. The main reason for this situation was probably economic. On good agricultural land, animal husbandry involving lactating animals, even with milk as a secondary product, could not compete with agriculture in terms of productivity.40 Thus milk, like beef and lamb, always remained an expensive commodity, affordable only occasionally if at all by the general population. A second reason was gastronomic. The flavor of soured milk is not one that everyone finds immediately appealing, it is an acquired taste that may require a considerable amount of time to develop. There is a well-known 6th-century story which relates that when the southern official Wang Hsu first arrived at the Northern Wei (Tuoba) court, he would at first drink only tea, since he could not bear the taste of yogurt as a drink [luojiang]. It was only after several years of acclimatization that he accepted it, though in time he liked it so well that he even considered it superior to tea and called tea “yogurt’s slave” [luozi] [Hu 2000:511].

After the departure of the Mongols in A.D. 1368, milk products lapsed into obscurity on the Chinese dietary scene. Nationalism has often been cited as a primary cause of this apparent decline in interest in dairy foods [Anderson 1987:66], but the main reasons may have been simply economic and gastronomic. As the population increased, dairy farming, already on a shaky economic base, became less and less cost-effective except in areas where intensive agriculture could not be maintained. Another reason is the commercialization, in the late Tang and Song Dynasties, of doufu and other processed soy foods which provided the key nutrients, such as calcium and proteins, formerly supplied by milk products. Moreover, as the center of culinary culture moved southward, writers on matters related to food also became less and less informed on the use of milk and milk products in the diet. Dairy products received little attention and did not reappear in the food literature until they were introduced again from the West in the 19th and 20th centuries.

That the main barrier to the adoption of milk and dairy products in the Chinese diet was economic is borne out by the rapid rise in the production and consumption of dairy foods in China in the past 20 years [Wilkinson 2001]. This rise is commensurate with the rise in the standard of living of the populace. In 1979 the total production of milk was 100,000 tons. In 2000 it was nearly 7 million tons, yielding a per capita consumption of nearly 6.9 kg [compared with 260–330 kg for North America and Europe], which is still only one-fifteenth of the world average. Milk is consumed in the form of fluid milk, milk powder, yogurt, and ice cream. The popularity of yogurt indicates that the gastronomic gap could be easily overcome.41

The effect of hypolactasia on the utilization of milk may also help to explain another puzzle in the history of the development of processed foods in China. Soybean has been processed into soymilk since the Eastern Han Dynasty [A.D. 25–220], and doufu has been widely made from it and used since the late Tang, yet nowhere in the Chinese literature before 1800 is there any mention of the consumption of soymilk itself. The reason is now clear. In addition to sucrose, the soybean contains two α-D-galactosides, raffinose (a trisaccharide) and stachyose (a tetrasaccharide). The human digestive system lacks enzymes that can hydrolyze either of these sugars. The effect of the ingestion of these unusual sugars would be similar to that seen after the ingestion of lactose. The Chinese no doubt soon found out that soymilk could be injurious to one’s health while the curds prepared from it were easily digestible. It was not until the late Qing Dynasty, when it was found that prolonged heating of the milk improved its digestibility, that soymilk became an accepted item of the food system [Hu 2000: 322–23]. It is now widely consumed as a breakfast food throughout China.

39. Wine from milk [zu ji] was celebrated in a poem by the famous Tang poet Du Fu [Hu 2000:248 n. 86].
40. Hsu [1991:44] compares the productivity of a piece of land used in intensive agriculture in China with that of a piece used as pasture for animal husbandry, including dairy farming, and reports that the number of calories produced in agriculture is nine times that produced in animal husbandry.
41. On a trip through northern Fujian, southeastern China, in October 2001, I found milk being served as a drink at dinner in restaurants in Fuzhou, Wuyi, Shaowu, Gutian, and Hetang, and in Shaowu, a town with a population of 130,000, some of my fellow diners ordered yogurt. Apparently, the gastronomic barrier had long been breached. The consumption level is still rather low. If this trend continues, it will be interesting to see when hypolactasia becomes noticeable.
appendix: chinese characters for words used

In the Text and Footnotes

dong luo 漵酪

ganlue 乾酪

Li ji 禮記

luojiang 酪漿

Mingyi bielu 名醫別錄

naiyou caihua 奶油菜花

Qidan 契丹

Rong 戎 and Di 狄

ru jiu 乳酒

Shiji 史記

Shiming 釋名

Tuoba 托跋

xin 新

Xiongnu (or Hsiungnu) 匈奴

zang han sheng man bing 藏寒生溼病

Zhenglei bencao 證類本草

zi 茲

Erya 爰雅

Huangdi nei jing suwen 黃帝內經素問

luo 酪

luonu 酪奴

nai (1) 乃 ; nai (2) 奶 (see footnote 2)

Qian Hanshu 前漢書

Qimin ya oshu 齊民要術

ru 乳

ru shi 乳食

Shijing 詩經

su 酢

Xianbei 鮮卑

Xinxiu bencao 新修本草

yu 醴

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