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Twinning Rate in Scandinavia, Germany and the Netherlands During Years of Privation

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Abstract. Twinning rates were studied in Swedes, Åland Islanders, Finns, Germans, and Dutch during years of starvation when death rates were two to three times higher than average. In contrast to the situation among some animals, this study suggests that nutrition above a certain threshold is unimportant for human reproduction, including twinning. The twinning rates for these different populations display marked temporal differences, but low values in the twinning rate are not consistently associated with periods of epidemics, famine, or similar nutritional stress. After years of privation and/or separation of spouses, a rapid "catch-up effect" can often be seen in the twinning rates, as well as marriage and birth rates. Psychoendocrine factors and interparental immunological conditions that may be involved in this phenomenon are discussed.

Key words: Twinning rate, Privation, Starvation, Epidemiology, Åland Islanders, Finns, Swedes, Germans, Dutchmen

INTRODUCTION

Cyclical variation in population size in response to favourable and adverse environmental conditions has long aroused scientific interest. There are many examples of periodic outbursts of generative energy. Probably the best known example of cyclical abundance is the lemming of the Nordic countries. Another example is

the Canadian rabbit, which in bad years produces only one brood of about three young, while in good years it produces 2 to 3 broods with 8 or 10 young in each brood, ie, up to 10 times more than in bad years [33,51].

Domestic animals also show variation in reproductive output that result from environmental conditions. Aristotle commented on the increased fertility of sheep in favourable environments and Charles Darwin stated that "the amount of food affects the fertility of the same individual; thus sheep which on mountains never produce more than one lamb at birth, when brought down to lowland pastures frequently bear twins" [20]. Ewes can be artificially stimulated ("flushing") by giving them special food at the approach of the mating season (estrus). It has been shown that flushing leads to a higher ovulation rate in sheep, and in some cases the number of lambs in the flushed flocks was nearly 200% greater than in non-flushed groups [17,57,82]. It has been suggested that efficient food for flushing may contain gonadotrophic hormones [30].

The majority of domestic animals breed more often and produce larger litters of young than wild animals belonging to the same species. Birds, eg, the common fowl, provide even better evidence of increased fertility resulting from domestication [20]. Certain species of wild animals, however, rarely breed in captivity. Apes and monkeys are particularly liable to be infertile in captivity. It has been shown that the lack of certain exteroceptive factors (length of daylight) as well as changed nutrition have something to do with the failure to breed. The explanation that has been suggested is that in some cases, for example in elephants and birds in the wild state, the regular seasonal migrations for the purpose of breeding are connected with the seeking out of special food substances suitable for reproduction. The conclusion from the fertility literature [for reviews and references see 31,35,51] is that improved nutrition increases fecundity in certain species, including humans. On the other hand, it is well known that wild animals, including primates, when removed from their natural conditions and brought into captivity, often become partly or completely sterile while maintaining a healthy condition with "optimal" nutrition.

Many authors studying twinning have been inclined to assume that nutrition may be an important factor even in the manifestation of human multiple maternities [15,16,38]. There is, however, no consensus concerning the effects of food shortage on the twinning rates. Cristalli [19] drew attention to the surprising increase in the rate of multiple maternities in Naples during and after the First World War and regarded the food privation during the war as one of the causes. Other studies have shown that there is no increase in the rate of twin maternities during periods of nutritional privation. For example, Balard (1924) did not find any significant increase in the twinning rate during World War I in the city of Bordeaux [8]. It has also been suggested that malnutrition may play a role in the high frequency of twinning in East-Nigerian Blacks [18]. Nylander [58], however, suggested that some substance in the diet (eg, yams, a staple) may act like a fertility pill in the Yoruba tribe of western Nigeria causing high serum levels of follicle-stimulating hormone which may trigger the release of more than one ovum and thus an increased tendency to have dizygotic (DZ) twin maternities.

A decreased DZ twinning rate during World War II has been reported for countries where food was in short supply, viz, for Norway [79], France and Holland, but not where populations were comparatively well nourished, Sweden and Denmark [15]. The monozygotic (MZ) twinning rate, however, remained constant during this period in these areas. Bulmer [15] suggested that the decrease in the DZ twinning rate was due to a decreased tendency of the ovary to produce double ovulations. He pointed out that diminished secretion of gonadotrophin by the pituitary is known to follow prolonged underfeeding in animals.

Eriksson [23] studied secular changes of the rate of multiple maternities (including years of privation) during the last 200-300 years in Sweden, the Åland Islands and Finland. The preliminary findings gave no evidence that during periods with severe crop failures, epidemics or war, the twinning rate deviated markedly from the rates for any of the adjacent periods. The twinning rates displayed appreciably high fluctuations, but these did not show any consistent, clear correlations with periods of famine.

Disagreement in the literature concerning the importance of nutritional status on the effect of twinning was an impetus for this study. The effects of periods of food shortage and famine, poor conditions and other socioeconomic factors, must have been more noticeable in twin maternities in earlier times, particularly in northern latitudes where heavy frosts caused crop failures. These, in combination with isolation and the difficulties of transporting food during severe winters, could bring on famines. Also, the noted decrease in DZ twinning rate in the Netherlands during the food shortage in the war winter 1944-45 [15] suggested that more detailed analyses of the areas of greatest privation, especially the larger cities in the west of the country, were warranted.

MATERIALS AND METHODS

Sweden and Finland have the oldest continuous population statistics in the world for a whole nation. In the 17th century the Lutheran state church began to keep population records, giving the numbers of persons christened, married and buried in each parish. The whole population was also divided by households and village communities. This record keeping was officially prescribed in the Ecclesiastical Law of 1686, and in 1748 a Royal Decree reminded the clergy of its obligations to carefully keep the records. In 1749, the so-called Statistical Tables (in Swedish "Tabellverket") came in force. Included in these tables was a noting of the number of women who had had twins or other multiple maternities. For Åland, we have used the parish registers: records of births and baptisms but also records of deaths and burials in order to catch perinatal deaths [for further details and references see 23].

For the other parts of Finland and for Sweden, Germany and the Netherlands we have used the national data on multiple maternities from official annual reports on vital statistics. For the 1860s in Finland unpublished ruridecanal records (dean-

ery level population change tables, in Swedish "prosteritabeller") have been used. In this way, local differences in rates of maternities, twinning, and mortality could be studied.

In the official statistics of Sweden there are for the period 1751-75 only quinquennial twinning rates available [78]. To get better idea of the yearly variation in the twinning rate, we have compiled numbers from the so-called "Wargentin's tables". Some years are partly defect, probably due to missing information of twin and other maternities from one or several parishes.

Eighteenth and nineteenth century Swedish and Finnish population data are considered reliable. The ministers who kept the parish records and made the statistical compilations were often personally acquainted with most of their parishioners. In addition, the different records kept in each parish, as well as the tax-rolls and estate inventory proceedings, allow crosschecking among different sources. Nonetheless, there are certain things which should be kept in mind when the older Swedish and Finnish population sources are used. Perinatal deaths for example, were sometimes omitted from the records of births [63]. However, often they were registered in the records of deaths. Consequently, in our studies on twinning in Åland we have also used the death records. Certain local studies, though, have shown that sometimes a considerable portion of stillbirths and infants who died before being baptized was omitted both from the records of births and from the records of deaths [63]. Because in the past the stillbirth rate for twins was 3 to 4 times as high as for singletons [23] the significance of this source of error cannot be overlooked, especially when regional comparisons are made or individual parishes are studied. At the provincial or deanery level, however, the parish records and the population statistics provide a reasonably accurate source of information for studying temporal, short-term variation in twinning.

According to Eilert Sundt's law, the size of populations fluctuates periodically, with peaks occurring about every generation (30-35 years) [78]. These population waves may give rise to periodic fluctuations in the twinning rate. When a population wave has reached the age most prone for DZ twinning (30-40 years) there may be a peak in the rate of twin maternities. Such fluctuations were eliminated as far as possible by calculating moving averages of the twinning rate in Åland for the period 1653-1959. The twinning rates were worked out for 33 successive years, and the average obtained was taken as the value for the median or 17th year. Thus, every individual year was included 33 times in the calculations of the average twinning rates. Of course, for the first and last 16 years of the period investigated, no values were obtained.

RESULTS

Moving Averages of the Frequencies of Twin Maternities in Åland

Detailed retrospective studies on the twin maternities were made on the Åland Islands, Finland. This material is the oldest continuous longitudinal series of

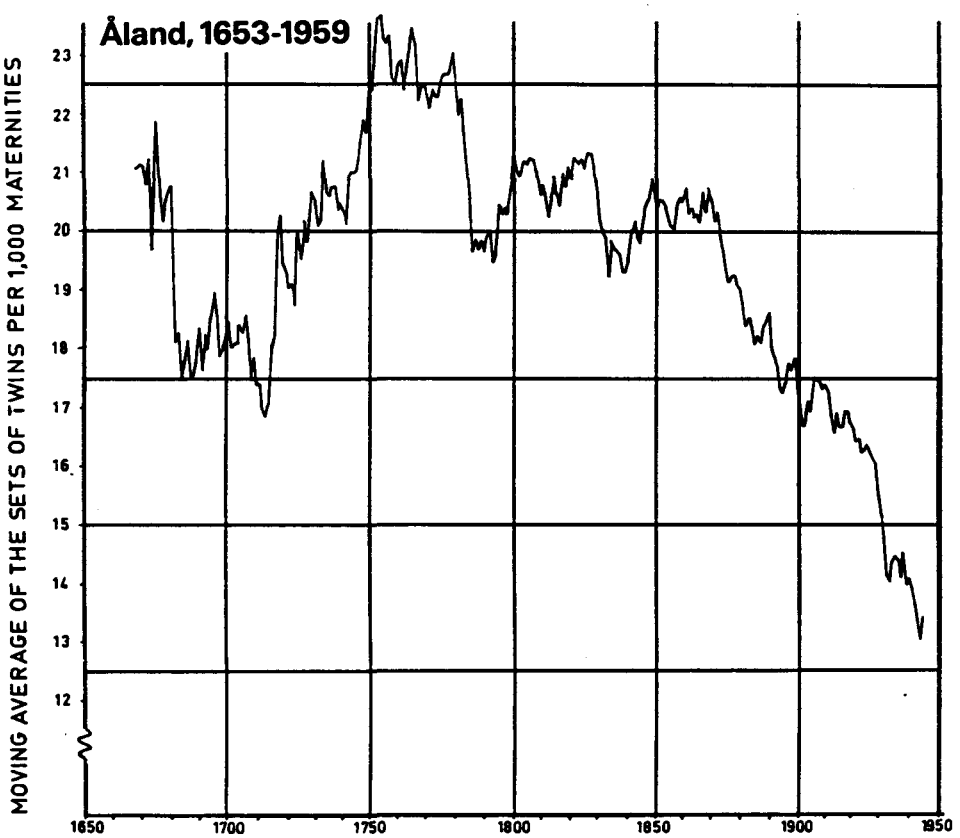

Fig. 1. Moving average of the frequencies of twin maternities in the Åland Islands (Finland), 1653-1959.

multiple maternities on record for any population. Figure 1 depicts the moving averages of the twinning rates in Åland and shows that from the beginning of the 1680s to 1720 there is a deep depression in the twinning rate, reaching its minimum in 1714 (16.9/1000). The historical consensus is that the famine of the 1690s and the period of the Great Northern War had a devastating effect on the population of Åland. In 1695-1697 the mortality caused by hunger and epidemics was very high in Finland. Dendroclimatological studies indicate two consecutive very cold summers in Finland in 1695 and 1696. The year 1696 constitutes the lowest chip in the growth curve of pine (*Pinus silvestris*) within past centuries [27]. The disaster of the 1696-97 famine in Finland has been called one of the most dreadful in the history of Europe: a quarter or perhaps even a third of the country's population perished [47]. Also, during periods of the Great Northern War (1700-21), and particularly during the flight to Sweden, there must have been a shortage of food or other privations among the Åland Islanders. Åland was totally devastated by the war [48], but after the war (1722-49) it had one of the

highest noted population growth rates in the Nordic countries (64% according to Jutikkala [47] and 57% according to Pitkänen [63]. There is no direct evidence that incompleteness of registration affected twin maternities in particular, apart from the fact that incomplete registration of perinatal deaths may have affected the number of twin maternities to a greater extent.

After the Great Northern War (during the years with high birth rates on the Åland Islands) the twinning rate rose steadily and peaked in 1754 at 23.7/1000. During the period 1736-1743 there were periodic epidemics and crop failures in Åland but in the twinning rates no significant deviations can be observed. From 1750 to 1780 the twinning rates in Åland were among the highest noted (around 23/1000) for white populations. A decline commenced in the 1780s. This downward trend was slight at first, displaying fluctuations, but from about 1870 it was unmistakable. Standardisation of the twinning rate for maternal age shows that up to the 1920s the decline in the twinning rate in Åland was mainly due to a decrease in mean maternal age [23].

Table 1 - Twinning rates in Kökar, 1720-1799

	Total maternities	Twin maternities		Deaths
		No.	‰	No.
1720-1729	129	1	7.5	72
1730-1739	198	6	30.3	151
1740-1749	167	1	6.0	141
1750-1759	228	6	26.3	153
1760-1769	180	8	44.4	159
1770-1779	194	2	10.3	163
1780-1789	204	2	9.8	188
1790-1799	183	8	43.7	151
1720-1799	1487	34	22.9	1178

Twinning During Hunger Years in the Isolate of Kökar

During 1753-68 the Baltic herring vanished from the waters of the fishing parish, Kökar (the southernmost parish of Åland archipelago). This fish shortage, coupled with dire poverty and general famine, was so serious that the tax inspectors were astonished that the Kökar islanders had been able to survive at all, and they were granted considerable relief from taxes [2]. During this time period there was no decrease in the twinning rate. In fact, during the disaster decades 1750-69 the twinning rate was high, 34.3 ± 9.1/1000 (Table 1).

Twinning Rates in Sweden

We have examined the rates of multiple maternities in both Sweden and Finland during periods of severe crop failure and famine (Table 2). The famine of 1771-1773 in Sweden was the worst known in that country. Mortality rates reached

extremely high levels in most of the counties, and as a result of crop failures, prices escalated to extraordinarily high levels [45]. There appears to be a clear and firm relationship between harvests and mortality levels during these years of severe crop failure. However, epidemic diseases (dysentery, smallpox, typhoid fever) played an important role in the mortality increase [29]. Between 1750 and 1774 the twinning rate for total Sweden is known only for 5 years periods (Fig. 2). For the main part of Sweden we have compiled numbers from the "Wargentin's tables". During the years 1767-73 the yearly twinning rates were relatively low, 14.5-15.5/1000.

Table 2 - Total, twin and triplet maternities, number of deaths and size of population in Finland, Sweden and the Netherlands around years of privation. (H = hunger areas; R = rest of the country)

	Maternities						Deaths		Average size of population	
	Total		Twin		Triplet					
	H	R	H	R	H	R	H	R	H	R
Finland										
1864	10696	61419	133	941	3	18	40975		1812201	
1865	9784	56402	122	871	0	14	45743		1835113	
1866	9532	51833	113	765	2	6	61894		1840376	
1867	9086	51970	106	782	2	8	69774		1830852	
1868	5073	40578	74	598	1	2	137720		1775686	
1869	9782	49364	130	812	3	12	43675		1733549	
1870	9963	54676	121	835	1	6	31841		1754164	
1871	10672	59856	127	857	3	7	31958		1786307	
1872	10567	56667	126	765	4	9	35889		1819228	
1873	11143	58314	137	829	1	13	435225		1847294	
Sweden										
1866	11247	128462	157	1784	2	25	7608	75058	300351	3837058
1867	10419	120864	129	1677	1	21	7722	74350	305429	3872751
1868	10269	106872	155	1518	0	19	8679	79113	301637	3882743
1869	10175	109653	167	1573	2	21	7965	84810	298802	3867117
1870	9821	112149	135	1687	0	26	7787	74662	302509	3861132
Netherlands										
1940	38575	148570	427	1967	7	25	22420	65303	2223804	6654807
1941	37419	146296	395	1770	2	14	22571	67145	2239040	6726444
1942	36976	154490	358	1858	7	12	22558	63452	2245740	6796246
1943	42010	168660	414	2176	4	22	23151	68287	2194762	6907748
1944	45340	176062	485	2180	3	9	23971	84116	2157954	7016478
1945	37360	174029	339	1944	0	19	43618	97780	2173898	7088400
1946	68575	218182	714	2755	14	33	17951	62200	2241343	7182137
1947	60863	208556	710	2646	5	21	17909	59737	2326681	7302594
1948	53876	195634	639	2483	9	24	17124	55335	2377038	7423115
1949	49369	188219	655	2520	6	26	19420	61657	2412355	7543239
1950	47407	183575	538	2306	3	24	18049	57531	2443333	7670194

The year 1773 which was preceded by failure of crops in 1771 and 1772, involved a catastrophically high mortality rate in Sweden that never has been surpassed.

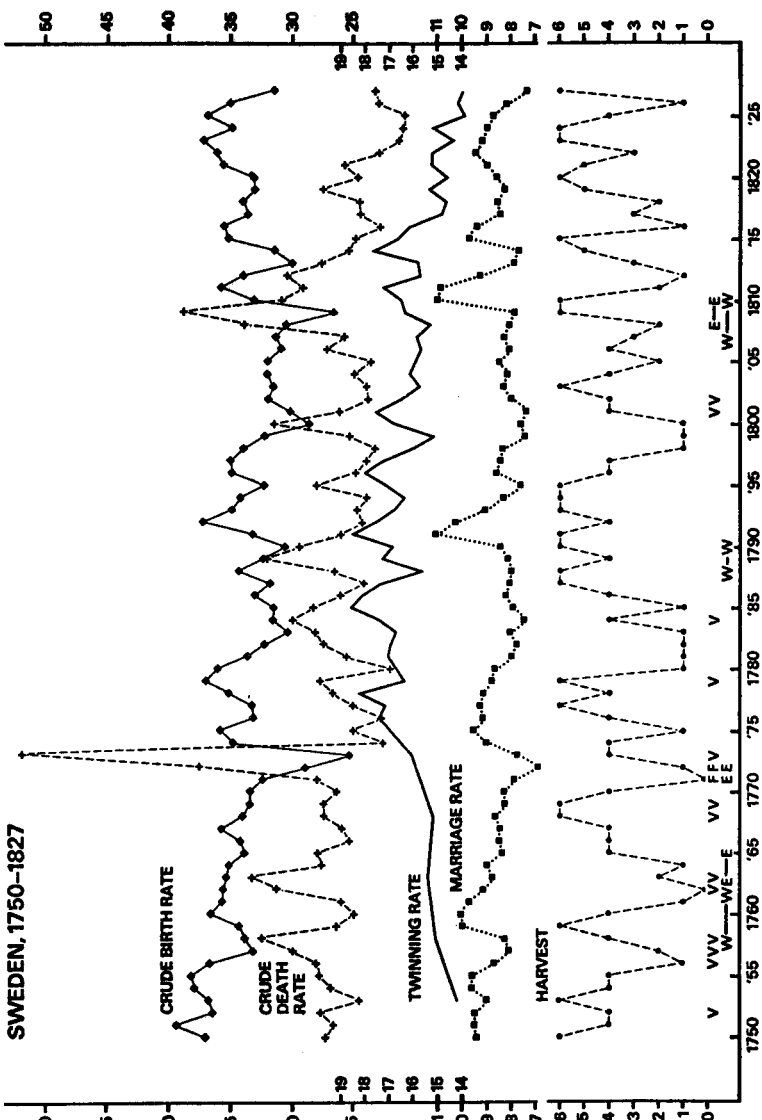

Fig. 2. Twinning rates in Sweden (1750-1827) in relation to crude birth rates (only live births), crude death rates (stillbirths included), marriage rates, official estimates of harvests (0 = minimum, real failure of crops), epidemics and wars.

Note: The twinning rates in Sweden for 1751-75 are available in the official statistics only as averages for five-year periods (eg, 1751-1755). From 1776 the twinning rate values are given for each year. The letters at the bottom indicate epidemics (E), famines (F) and wars (W). E indicates different epidemic diseases, mainly typhus, typhoid and dysentery (in Swedish "rödsot"), V indicates smallpox (variola). For details see [81].

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After the severe crisis years 1771-73 there is a strong catch-up effect in the twinning rate: 18.3 ± 0.6 for 1774 and 18.1 ± 0.5 for 1775, which are among the highest noted for Sweden. Similar catch-up peaks in the twinning rate are also noted after the successive bad harvests during 1780-1783 and 1798-1800.

Before 1774 the twinning rate in Sweden was relatively low. It is unknown to what degree this was influenced by underregistration of stillbirths and neonatal deaths, which both are much higher among twins than among singletons [23]. Quensel [67] suggests that the reported number of births and the reported number of the deceased under one year of age was too low in the 18th century (similar observations have been made also for Finnish parishes by Pitkänen [3]). Until 1774, when new population registration forms were introduced, baptisms and burials were registered instead of births and deaths. An indication of the more efficient registration of perinatal deaths is that the stillbirth rate in Sweden rose from 24.8/1000 in 1751-60 to 28.3/1000 in 1790-1800. However, during 1801-30 it dropped to values around 25/1000 and rose to values above 32/1000 again during the subsistence crisis in 1851-70.

From about 1775 to 1800 the average twinning rate in Sweden was above 17/1000, ie, the highest noted for a whole nation [23]. At the same time some economic recovery took place after the generally poor conditions that prevailed in the 1760s and early 1770s [see also 71]. The increase in the twinning rates, however, reversed during the first part of the 19th century. Values ranging from 16 to 18/1000 declined steadily and reached rates below 14/1000. In 1836-1855 the twinning rate was only 13.61 ± 0.08/1000. The triplet rate also decreased from quinquennial values between 0.23-0.32 in 1751-1820 to values below 0.20/1000. After the depression in the twinning rates there was a slight upward trend. After the 1930s a marked decrease in the twinning rates took place in Sweden. In the 1970s the rate was only about 50% of what it had been 200 years earlier. A corresponding fall to about 30% occurred in triplet and quadruplet maternities [23].

The decline in twinning during the first part of the 19th century is surprising. Firstly, after 1810 economic conditions in Sweden improved considerably. Prices for corn and other commodities decreased [45]. An increase in the average height of soldiers indicates a clear improvement in the average nutritional status of the population [71]. This development was probably influenced by the spread of potato cultivation. At the same time mortality declined to a lower level. It has often been stated that, among other things (vaccination against smallpox, medical improvements, more favourable climate, peace after 1814 [cf 81]), improvement in nutrition also contributed to this development. Heckscher [36,37] has especially stressed the importance of food supplies. Secondly, the age pattern of fertility was relatively stable from 1750 to 1815, but from 1820 to 1850 there was a decrease in fertility, especially among women in the less twinning-prone ages below 30 (caused by later marriages). On the other hand, after 1810 there was an increase in fertility among women in the most twinning-prone ages, ie, above 35 years of age [39]. In terms of these changes, one would expect increasing — not declining — twinning rates.

The stabilization and slight reversal in twinning rates occurs at the same time

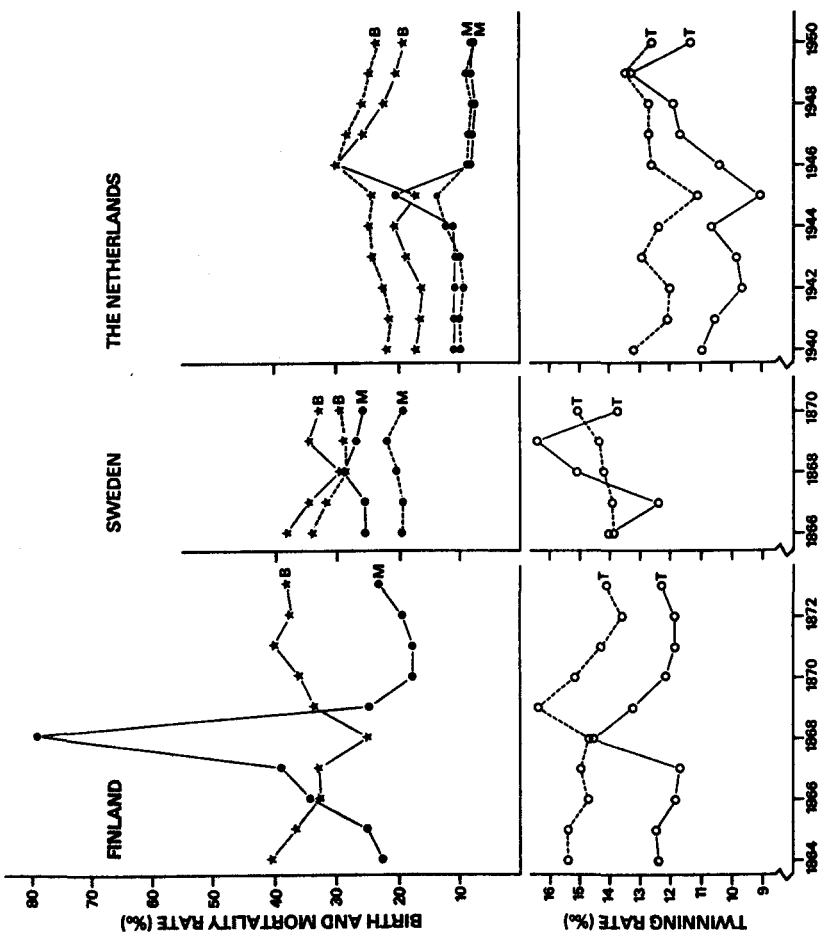

Fig. 3. The birth rates (B), mortality rates (M) and twinning (T, sets of twins per 1000 maternities) in hunger areas and the rest of the countries (Finland, Sweden, The Netherlands) around years of privation. For Finland birth rates are given for the whole of the country.

——— = hunger areas
- - - - - - - - - = rest of the country

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as Sweden experiences a mild subsistence crisis [71]. Between 1750 and 1850 the population of Sweden doubled (from 1.78 to 3.48 million). The increase in population was particularly rapid after 1810; during 1801-1850 the annual population increase was 8.1/1000 of the population, ie, the highest recorded for Sweden [39]. The rapid increase in population, particularly on the number of landless (crofters, borders, etc.) led to a subsequent proletarianization [83].

An indication of difficult reproductive conditions is that the stillbirth rate in Sweden reached the highest recorded values between 1831-1880, average above 31/1000, ie, almost ten times higher than the rate of late fetal death in the 1980s. During the same period the long-term decline in child mortality reversed. In addition, although mortality rates show a downward trend, there were occasional setbacks during several epidemics of cholera, measles, scarlatina, whooping-cough and dysentery in the 1850s and during the famine years of the 1860s (Table 2 and Fig. 3). In the "hunger-areas" (ie, regions with the highest mortality in 1867 such as the northernmost provinces of Norrbotten and Västerbotten, and the city of Stockholm) there is a postprivation catch-up peak in the twinning rates, particularly in 1869.

Twinning Rates in Finland

In the 1860s there were many years of crop failure and famine in Finland. The years 1862, 1865, and 1867 were particularly severe. In 1868, when starvation was rampant, almost 80/1000 of the whole population of Finland died [21,80] and the number of children born was about 30% less than the average for 1861-70 (Table 2, Fig. 3). Neither for Finland as a whole, nor for the "hunger areas" of Ylä-Vaasa, Ylä-Karjala, Tyrvää and Hattula, with mortality varying between 143-232/1000 [73], was any significant decrease in the twinning rate noted during any of the years from 1866 to 1869. On the contrary, there is an unexpected peak in 1868.

The triplet rate, however, was very low in the severe famine year of 1868, only 0.07/1000, the lowest observed until the 1930s [23]. It is also noteworthy that in 1869 there is a peak in the twinning rate for the rest of Finland, in spite of the fact that 1868, the year in which the majority of these twins were conceived, was a severe famine year particularly for poor people, at least until the harvest was finished at the end of August. In August and September, mortality, particularly due to typhoid fever, was still high [73,80]. During the last World War neither in total, age-standardized, nor in DZ twinning rates in Finland was there any significant decrease noted during or after the years with relatively low caloric intake of food, particularly in urban areas [23].

Twinning in Germany

At the end of World War I, and for the following couple of years (about 1916-20) there was — as a consequence of blockade and inflation — starvation in Germany

with no less than one million civilian casualties [34]. During these years of privation there is no indication of a decrease in twinning rates. In spite of the poor nutritional situation and a severe epidemic of Spanish flue in Germany after World War I, the total twinning rate, DZ twinning rate, and triplet rate for the year 1919 are the highest noted in Germany for the 20th century [see also 72 and 66].

Table 3 - Total, twin and triplet maternities in Germany, 1915-1925

Year	Maternities				
	Total	Twin		Triplet	
		No.	‰	No.	‰
1915	1407648	17578	12.49	179	0.127
1916	1048339	13659	13.03	143	0.136
1917	928059	11611	12.51	128	0.138
1918	944256	11770	12.46	111	0.118
1919	1281881	17144	13.37	188	0.147
1920	1630110	21028	12.90	217	0.133
1921	1612767	19573	12.14	231	0.143
1922	1454799	17055	11.72	161	0.111
1923	1346206	15426	11.46	152	0.113
1924	1318916	14961	11.34	161	0.122
1925	1339604	15741	11.75	149	0.111

Twinning Rate in The Netherlands During the Famine Winter, 1944-45

In September 1944 the allied forces in the west launched operation "Market Garden". Despite heroic efforts by the British and American paratroopers [70], the battle of Arnhem ended in tragic defeat, and the Dutch population north of the great rivers was to enter its grimmest winter in several centuries. Famine was especially severe in the large cities in the western Netherlands ("Randstad"), as can be judged from the peak in the mortality rate of 1945 (Figure 3).

The situation was further aggravated by the unusual cold of that winter, and by the fact that the coal mines of Limburg, on which the Dutch were dependent for heating, were now on the other side of the front line. A detailed historical study of this period is provided by de Jong [44]. The effects of maternal undernutrition upon the newborn infant have been studied by Smith [74,75]. The causal relations of the Dutch hunger winter to fertility and fecundity have been studied by Stein and Susser [77]. In order to study the effect of the hardships upon the twinning rate, we provide some temporal and spatial comparisons. As for variation in time, it should be appreciated, of course, that the effect of the famine winter (1944-45) on the twinning rate, if any, should be reflected by the twinning rate 8 to 9 months later, or during the second half of 1945. We compared the twinning rates over the following periods: 1941-1944 (Nazi occupation, but no famine), 1945 (effect of famine winter on the twinning rate), and 1946-1950 (postwar era).

We compared the five large cities in the western Netherlands (Amsterdam, Rotterdam, The Hague, Utrecht, Haarlem) with the rest of the country, where

famine was less severe. It is quite clear, given the size of the Dutch population, that all but the smallest fluctuations in the rates compared would be "significant". Therefore, the data were interpreted with a view to estimation rather than to significance testing. Results are summarized in Figure 3 and, in more detail, in Table 2.

The data show a marked decrease in the twinning rate in 1945, as also reported by Bulmer [15], followed by a steady increase during the postwar years 1946-1949. Remarkably, however, there is a consistent difference between twinning rates in the large cities and the rest of the country, not only in 1945 but during the whole period observed. Similar results with higher twinning rates in rural than in urban areas have been noted during this century for Finland and Sweden [23,26].

Remarkably, this decline in the twinning rate in 1945 is almost as striking in the rest of the Netherlands as in the hunger areas of the large cities, not only in 1945 but during the whole period observed (1940-1950) although birth and mortality rates confirm that privation was much more severe in the large cities. In 1946 a peak in birth rates occurred, followed by a slow but steady decline which was more pronounced in the large cities than in the rest of the country. During this period the increase in the twinning rate was greater in the large cities, with these cities almost catching up with the rest of the country in 1949.

DISCUSSION

Epidemics and Twinning

In 1771-72 Sweden experienced a general harvest failure followed by famine and epidemics. According to official statistics for 1773, no less than 53% of all deaths were caused by three epidemic diseases alone: smallpox, typhus, and dysentery. In 1779 some 60% of all deaths in Sweden in ages under 10 were caused by smallpox alone (vaccination started in 1801, but was not made compulsory for all children until 1816) [39]. Typhus, meaning haze or mist, seems to have been applied to different forms of epidemics raging in the Nordic countries. These included relapsing fever (Typhus recurrens) caused by Borelia recurrentis spirochaeta, typhoid fever (Typhus abdominalis, incl. also paratyphoids) due to the Salmonella typhi bacillus and exanthematic typhus caused by Rickettsia prowazeki [10,13,62,73,80].

When analysing the rates of multiple maternities during years of privation, starvation is only one, even if a very primary and central one, of the many factors that may influence reproductive performance, including twinning. The rise in mortality during years of privation was often caused by typhus fever which is caused by Rickettsia prowazeki which is transmitted by body lice. In pregnant women exanthematic typhus very often causes spontaneous abortion [10]. Thus typhus may be one of the factors contributing to the noted decrease in birth rate around years of epidemics. According to our results, hardships borne by women during famine, typhus epidemics, and other epidemics seem not to have any convincingly stronger selective effect on twin gestations than on singleton pregnancies.

Harvests, Wages and Reproduction

In the 18th and in the beginning of the 19th centuries the area under cultivation was much smaller and harvests in the Nordic countries were only about 10% per hectare of what they are today. The size of the population, however, was about 25% of what it is today. There were many reasons for the bad crops: ineffective agricultural implements, swampy ground, deficient manuring, bad seed for sowing, acreage of arable land divided up into small portions, and deficiency of manpower, particularly due to periods of prolonged war [39]. Therefore, there were few stocks of grain and the great majority of the population, particularly the poor, lived at near-subsistence levels. For the poor people a crop failure was always a catastrophe [37].

Furthermore, the crisis years in the beginning of the 1770s were connected with a severe privation period for the whole of northwestern Europe with increasing prices of grain, and a shortage of money [1].

According to Heckscher [37], marriage, fertility and mortality were determined by the harvests, particularly in societies where the population tended to increase faster than the food supply. However, this Heckscher-Malthusian idea of the strong connection between harvest and mortality in short-term population development in Sweden has been criticized.

According to Utterström's studies in Sweden [81], the lack of food seldom was the sole cause of increases in mortality and rarely the principal cause. Epidemics, whether or not connected with wars and famine, also played a large role. The climate, the standard of housing and hygiene were all important. Recent studies by Bengtsson and Ohlsson [9], using cross-spectral analysis, showed that the fluctuations of the demographic variables investigated (crude birth rate, infant mortality, crude death rate in Sweden 1749-1914) were closely associated in time with fluctuations in real wages and in harvest yields. They observed "marked variations in the birth rate, which clearly points to some forms of birth control within existing marriage".

Because of a strong association between fluctuations in birth rate and real wages, Bengtsson and Ohlsson [9] stated that "involuntary birth control (brought about by hunger, low caloric intake, etc, negatively influencing fecundity and increasing the incidence of spontaneous abortions) was an important factor behind the fertility variations observable during the latter half of the 18th century."

There are some abvious differences between the effects of famine and those of epidemics [60]. During crises caused by famine, the situation usually changes slowly. Shortage of food makes its first appearance in the demographic statistics as a decrease in the birth figures gradually followed by increased mortality due to diseases typical of famine such as typhoid fever and typhus. Mainly the rural population is severely stricken. In contrast to famines, epidemics break out suddenly and may, depending upon the specific disease, strike the poorer part of heavily populated towns more than the general population [7,55].

If the urban areas suffered more from starvation, one would expect the twinning rate (if affected by famine conditions) to be more pronounced in rural popula-

tions. However, both in Sweden and Finland there are in the 1860s no appreciable differences between the twinning rates in rural and urban areas [23,26].

Postprivation Twinning Peaks: Twinning Rate in Relation to Estimates of Crops, Mortality Rates and Wars

During years following poor harvests there are peaks in the mortality rates (Fig. 2). One or two years after periods of privation with high mortality there are peaks not only in the birth rate but also in the twinning rate. According to the "Wargentin's tables" the yearly twinning rates in Sweden during 1754-70 varied between 13.4 and 15.9/1000. Only the postprivation year of 1766 was exceptionally high, 16.9/1000. During the crisis years 1771-73 there was no downward trend in the twinning rate, 14.7, 15.5 and 15.4/1000 for respective years. After the severe crisis year of 1773 the twinning rate jumped up to 18.3/1000 in 1774, 18.1/1000 in 1775, and remained relatively high (above 15/1000) until 1817. This same trend is seen after the repeated crop failures of 1780-83 and 1785, and during the Swedish-Russian war of 1788-90 and 1808-09. After these wars the marriage rate was very high (around 11/1000). Notwithstanding, relatively many young couples married and started to get children after periods of privation, the twinning rate does not show any clear downward trend during the years after the peaks in the marriage rate. During the three successive years 1798-1800 with bad harvests there was a drop in the twinning rate in 1799 (15.5/1000) but for 1800-01 it was above 17/1000. After four successive years of bad harvests, 1780-83, the twinning rate for 1785 peaked by 18.6/1000. Also, the twinning rate peak in 1791 (18.5/1000) and 1811 (17.7/1000) appear after years of wars with high mortality.

For some years the peak in the twinning rate appears one year earlier than the peak in the birth rate, eg, for the years 1778 (18.3/1000), and 1791 (18.5/1000). A similar prerunning peak in the twinning rate was noted in the USA after World War II [4,5,43]. Also for Italy a sudden increase of DZ twinning rate was noted in 1919 before the general birth peak in 1920 [61]. After World War I we have noted peaks in the twinning rate for the Netherlands in 1918 and in Germany in 1919. These figures are quite unexpected, because one would expect that the many young couples marrying after the war would have lowered twinning rates. Without knowledge about maternal age distribution, parity and the age standardized twinning rates, these high postprivation peaks in the twinning rate remain unexplained. One of the interpretations of the postprivation peaks in twinning rates is that mothers with high fecundability (shorter waiting time to conception) also are more prone to produce DZ twins (for further discussion see 4,5,23,26,61].

Effect of Famine on Reproduction

Reproduction requires energy. A singleton pregnancy requires about 50,000 calories above normal metabolic requirements. Lactation, in premodern times an essential part of reproduction, requires for singletons about 1,000 calories a day [for references see Frisch, 32].

In famine and starvation both fecundity and fertility are reduced. Amenorrhea is often reported and, in severe starvation, gonads atrophy.

Bongaarts [12] is of the opinion that breast-feeding (suckling stimulus) is the principal regulator of the lengths of the birth interval. Frisch [31,32] stresses the importance also of the nutritional state to the length of lactational amenorrhea.

During a famine the frequency of intercourse is likely to decline for a variety of reasons. Well documented studies from both World Wars and during the 1974-1975 famine in Bangladesh have established noticeable loss of libido among males as well as female and, under conditions of starvation, reduction of the production of sperm by males [12,50,56,77]. Furthermore, when food shortage is common, it may become customary for the men to migrate in search of work or to beg for food, thus reducing the frequency of intercourse.

It is reasonable to assume that during famines less fecund couples would be affected first, namely those of higher age and higher parity, thus groups with a relatively high twinning rate. Stein and Susser [77] stated that during the Dutch famine winter in 1944-1945 the infertility selectively affected women in the older age groups and those of higher parities, thus the most twin-prone groups. However, this cannot fully explain the reduction in the rate of DZ twinning in the Netherlands as a consequence of the hunger winter since it can still be demonstrated after standardization by maternal age [15].

In spite of a considerably increased standard of living with more than sufficient intake of calories, the twinning rates exhibited during the last two generations decline for both Sweden and Finland. This decrease cannot be explained by a decrease in maternal age or lower parity [26 see also reviews by James, 40,41].

One of the main lessons to be learned from our longitudinal analysis is that the twinning rates do not necessarily reflect the average nutritional status of the population. Above a specific, yet undetermined, threshold, nutrition seems to be unimportant for reproduction in general and also for twinning [see also 12,56,77].

Twinning After Privation and Unintentional Separation of Couples

During privations, such as wars and famines, couples may be involuntarily separated for long periods. After such privation years peaks in the twinning rate have often been noted in Sweden and Finland (Fig. 2 and 3) and during the difficult hunger years after World War I in Germany (Table 3).

In the Scandinavian countries and in the Netherlands there are peaks in the twinning rate after World War II. Jeanneret and MacMahon [43] noted that after the massive military discharges in 1945 a striking peak in twin maternities occurred in 1946 in the USA that could not be explained by any difference in maternal age or parity. This phenomenon has been explained by the fact that women who conceive more promptly are apparently more likely to produce twins than when they happen to conceive late [3]. Another possibility is that certain women, after unintentional sexual abstinence, are more likely to experience a twin pregnancy. Mothers of twins may comprise an elite group from the standpoint of reproductive capacity.

They may be more apt after privations or separation to become pregnant because of having fewer anovulatory cycles and a higher polyovulation rate and may have better physical capacities to carry through a multiple pregnancy [22].

Males could contribute to the variation in twinning rates not only in the fertilizing capacity of their semen but also in the prenatal survival of their offspring. Bishop [11] stated that a high rate of embryonic death is a characteristic of reproduction in all mammals and suggested that an unsuspectedly large part of embryonic death is attributed to genetic causes due to the transmission of lethal genes also by the male. This could contribute to the high prenatal selection of twin zygotes: the likelihood of the presence of lethal genes with prenatal selection is greater in two zygotes than one [22].

The hypothesis that some women with irregular opportunities for intercourse may conceive more easily and be more twin-prone than others is supported by the relatively high twinning rates noted in early marital conceptions [16] and in the first year of marriage [65,68]. High DZ twinning rates (standardized both for age and parity) have also been observed in extramarital maternities [4,5,24,25,59].

Among wives of boatmen, who in the 18th and 19th centuries served in the Swedish admirality and used to be away from home for much of their time, a high rate of multiple maternities, including recurrent twinning, was noted [23].

We have no evidence for coitus-induced ovulation in humans, as in rabbits. However, individual differences in erotic potential and in psychoendocrine response to sexual arousal cannot be excluded. After reunion with their husbands some women may be predisposed to conceive more promptly and to be more twin-prone. Differences in the polyovulation rate can be divided into two main components: 1) activity of circulating follicle stimulating hormone (FSH) and, 2) sensitivity of the ovary to FSH. So far little is known about interindividual differences of these polyovulation components, but it has been shown that erotic stimulation causes a prompt and substantial increase in women's gonadotrophin levels [for references and details see James, 42].

There is little experimental support for postprivation catch-up peaks in the twinning rate. Loeb [51] who studied the effects of nutrition on the production of ripe follicles in guinea pigs, found that pronounced underfeeding prevents maturation in all cases and causes atrophy before the follicles have reached medium size. This leads, at least, to temporary sterility. The results are more marked in the ovaries of young animals, just as the general effect is greater. In extreme cases he states that "hypotypical" ovaries may be produced in which the connective tissue between the follicles is affected resulting in a union of follicles and a consequent polyovular condition. It is unknown whether the effect of starvation in humans may cause the development of follicles containing more than one egg and thus higher possibilities for DZ twinning.

Interparental Immunological Conditions

Recent reports have clearly implicated an isoimmune response against spermatozoa as a causative factor of infertility. Women with circulating antisperm antibodies

have a lower probability of conception than women without such an immune reaction, and the probabilities decrease with increasing titres [69]. Serum derived isoantibodies have also been shown to inhibit sperm-binding to the zona pellucida, as well as sperm penetration across the zona [49].

If immunization of a woman through the reproductive tract against the components of semen of a given male is a common phenomenon, it should be less effective after a period of separation, and thus increase fecundity, including the probability of pregnancies with multiple embryos. The frequency of an interparental immunization might be associated with hereditary factors. This would reconcile the conflicting views regarding the importance of the father's genotype in DZ twinning and throw new light on why we have high frequencies of twinning in some isolates.

Population Structure and Twinning

Analyses of the secular twinning data on the Åland Islands and its surroundings have shown [26] that a considerable portion of the decrease in twinning seems to be related to the general decline in maternal age, particularly over the last century (Fig. 1). Changes in the matrimonial migration patterns also seem to have an effect on the twinning rate. The increase in the rate of multiple maternities during the 18th century presumably reflects, in part, the increasing endogamy made possible by demographic increases after the bottleneck in the population size after the crisis years during the Great Northern War (1700-21).

The higher rates of multiple maternities in insular isolates in southwestern Finland (Åland and Åboland) may well reflect the effect of inbreeding in these isolated populations descended from a relatively small founder group. The decline in the twinning rates is also matched by the changing pattern of regional endogamy on the Åland Islands and other Nordic populations.

Studies in progress on the demographic patterns [54] genealogical linking and socioeconomic conditions of the Åland Islands will be used to provide insight into the possible genetic and nutritional basis for twinning. Using more detailed material one can compute the coefficient of kinship among parents of twins – and among parents of mothers of twins – relative to the random kinship in a population. This procedure will answer questions not suitably treated by contemporary cross-sectional national samples. Our ongoing studies in Åland on multiple recurrent twinning within sibships and the twinning rate in sibships with triplets indicate that some mothers have a strong constitutional tendency for multiple maternities even during severe socioeconomic conditions, such as hunger years and similar privations.

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