

# POPULATION MOVEMENT IN SWEDEN FROM A GENETIC-STATISTICAL POINT OF VIEW

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It was shown in a preliminary report that the frequency of first-cousin marriages was low in former times in Sweden (*Alström*, 1958). Before 1680, marriages between first cousins were forbidden; thereafter, they were permitted by dispensation from the King in Council, although in practice this was seldom taken advantage of until 1750. The costs of such a dispensation were high, and for a long time were an effective barrier against marriages of this kind. Moreover, there was a tradition of strong opposition by the Church dating from the Middle Ages. The necessity of a dispensation was not removed until 1844. It was concluded from the aforementioned investigation that the frequency of first-cousin marriages—which at the time in question differed in various parts of Sweden—probably reflected social attitudes, and not possible isolating factors.

In the social isolate consisting of the Swedish nobility, a strikingly high first-cousin marriage rate could be noted as early as 1750 onwards. It could, however, be shown that this high frequency was more than counterbalanced by appreciable migration. Actually, because of this immigration, the existence of a strong heterosis effect could be expected in this social group, despite the coincident high degree of inbreeding (*Alström*, 1958).

In the aforementioned preliminary report, the marriage pattern was investigated in four small subpopulations (parishes) in the southern and central parts of Sweden. This investigation has subsequently been extended, in collaboration with *Lindelius*, and the results will be published in a second report.

The chief isolating factor is that by distance, and is best studied by a method devised by *S. Wright*, 1951. This extended investigation seems to confirm my earlier view—based on the preliminary study in 1958—that for the greater part of Sweden's population (90 per cent), living in the southern and central parts of the country, no true genetic differentiation could be anticipated in the period in question (1800–1850).

The “effective population size” of the “neighbourhoods” investigated usually exceeds 1,000 individuals, and the population in this part of Sweden seems to have had an approximately continuous, areal distribution. Existing differences in density, and other deviations from the ideal model, e. g. regions exhibiting a reticular pattern, do not seem by any means to be so pronounced as to ham-

per the approximations made. Less than 10 per cent of the married population lived in towns of small size, apart from the capital, Stockholm, which contained about 80 thousand of the total 2.5 million inhabitants of Sweden. Consequently, it appears at any rate reasonable to apply *Wright's* formula for areal distribution to 90 per cent of the total population of Sweden, and to assume genetic conditions that are equivalent to panmixia.

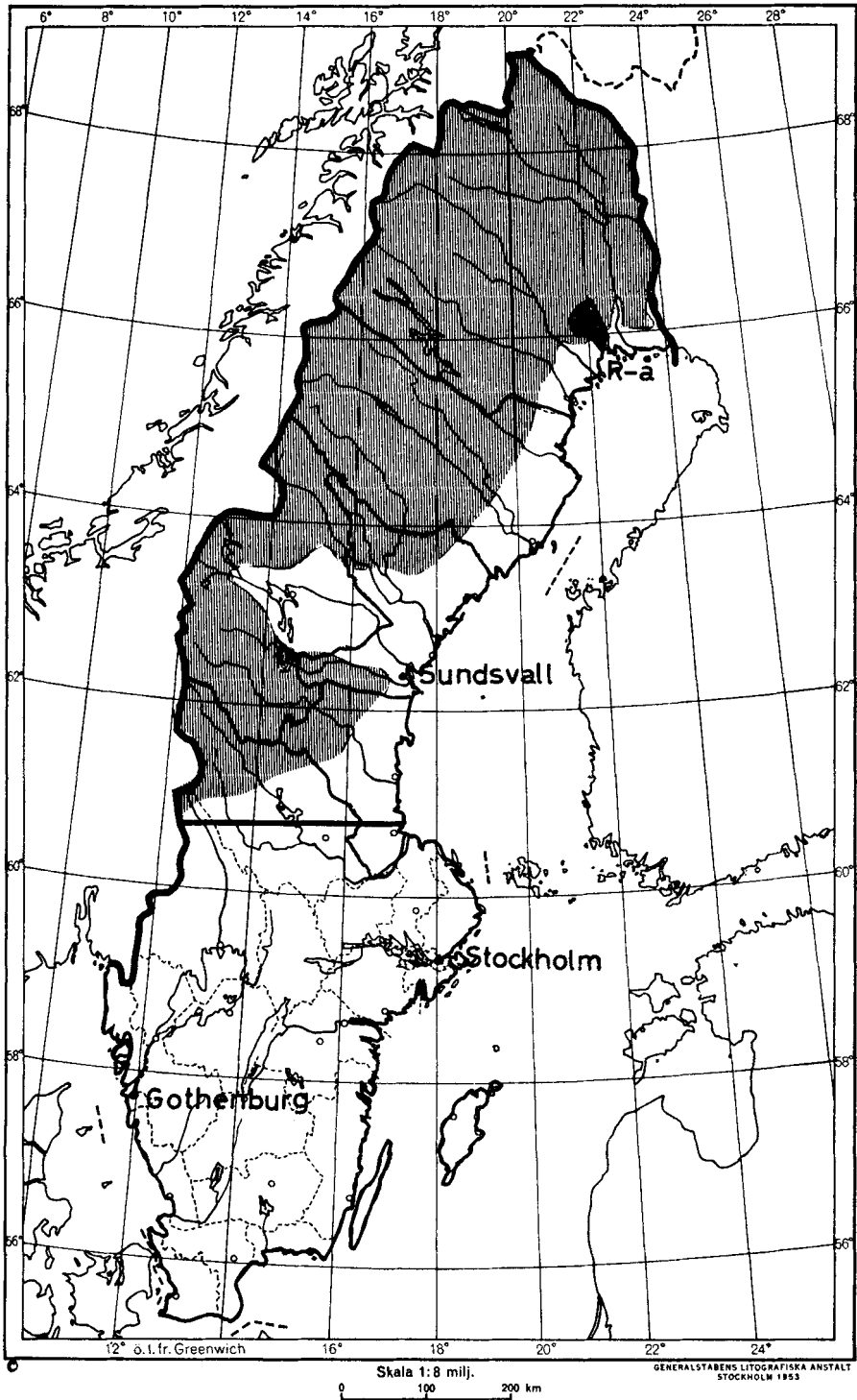
The situation is not the same in the northern part of Sweden. The population is domiciled in a belt along the coast, with marked branchings inland, along the river valleys and lake systems. Although these branchings largely form reticular patterns, blind pockets are also found. The parish R-å formed such a "pocket" during the period studied. A more detailed study has been made of this subpopulation, and will be published in the second report. The results will, however, be discussed briefly in the following.

The position of R-å in the county of Norrbotten, as well as of the other counties in Norrland, is evident from the map in *Fig. 1*. Although the north of Sweden comprised almost 60 per cent of the total area of the country, only about 10 per cent of the married population resided there. At that time, the whole land area of Sweden was approximately 410 thousand km<sup>2</sup>, and in 1815 its married population amounted to about 874 thousand persons.

Today, 17 per cent of the married population of Sweden is resident in Norrland, to which there has been considerable migration from other parts of the country, chiefly in the present century. This immigration has been most intense in the two northernmost counties, Norrbotten and Västerbotten. Here it has, however, presumably been concentrated essentially to certain regions, i.e., mining and industrial districts, lying partly in the inner, previously unpopulated parts of the counties. These northernmost counties have nevertheless retained to a great extent—even into the present century—their earlier, marked reticular pattern of population distribution. This is in the form of a broad populated zone along the coast, where the majority of the inhabitants have resided, together with blind pockets along the valleys towards the inland. These pockets, with their base directed on the whole towards the south-east, have merged with the more densely populated coast zone.

It is also essential to note that—as far as the residential areas are concerned—the whole population of Norrland is continuous with the rest of the population via a zone in the east, running along the coast through the county of Gävleborg. In the West, on the other hand, it is separated from the rest of the population by a large, barren, extremely sparsely populated region of mountains and woods. This region, represented by the shaded area in *Fig. 1*, occupies large parts of the counties of Jämtland and Kopparberg. At this level there is, in fact, an hourglass-like constriction between the northern and southern regions, the former smaller and the latter larger from the point of view of population density.

The objection might now be raised that these circumstances could be worth



studying if it were a matter of investigating, for instance, the distribution and population-genetic conditions in *Drosophila* (apart from these insects not being native to Sweden). Human beings can, however, be expected to have marriage patterns that do not, in any respect, coincide with these conditions of residence or localization of birthplaces. They do, in fact, have entirely different possibilities of moving freely over large distances.

Actually, the human migration fields in Sweden had, at any rate during the period investigated, a structure with conditions analogous to those found in wild animal populations in *S. Wright's* schema. Thus, there was an overwhelming preponderance of short-distance migrants—measured in distance parent-offspring birthplaces—as compared to long-distance migrants. The topographical circumstances determine whether we have a largely areal, continuous distribution—the approximative condition mentioned above—which applied to the majority of the population. They also determine the other alternative, i.e., a strong incidence of reticular or even purely linear distribution, which seems to exist in the minority of the population domiciled in the north of the country. These divergent structures imply divergent population-genetic situations in the northern and southern parts of the country, with divergent possibilities of inbreeding and potential genetic differentiation.

The effective breeding size of a human population is practically equivalent to that part which marries and has offspring which, in turn, reach mature age. From the point of view of population genetics, childless marriages, or offspring who die before they have the possibility of reproducing, lack any interest. On practical grounds, liaisons with illegitimate children have been excluded from the calculations. When calculating the effective breeding size, it is also necessary to take into account the variance for the number of children in each sibship, and the average number of children. We now envisage a large human population divided into a number of subgroups, in which the mating partners—in ideal cases half of each sex—can be regarded to mate approximately at random.

The effective breeding size,  $N$ , of a population—in the present case the parish R-å—can be calculated either according to the “island” model (*Dahlberg*, 1929, *Wahlund*, 1928), or according to the “neighbourhood” model of *S. Wright*, which is based on the distances parent-offspring birthplaces.  $N$  for R-å is of approximately the same order of magnitude in both cases, i.e.,  $N_{isl} = 737$  and  $N_N = 599$  with pseudoexact figures. The migration frequency into R-å was  $m = 0.25$ , which gives the following frequency of inbreeding,  $F$  (see *S. Wright*, 1951, p. 331; *Li*, 1955, p. 305):

$$F = (1 - m)^2 / [2N - (2N - 1)(1 - m)^2] \sim 0.001$$

This does not give any differentiation in gene frequency with respect to the total population.

Calculated as a neighbourhood according to *S. Wright*,  $N_N = 599 \sim 10^{2.8}$  and

—assuming an areal, continuous distribution for the whole country—the effective size of the total population can be denoted as  $\tilde{N}_T$ , which gives  $\tilde{N}_T/\tilde{N}_N = 1,167$ . Nor does this plausibly imply any differentiation in gene frequency with respect to the total population (see *S. Wright*, 1951, p. 332, Fig. 7).

However, we consider only the northernmost tenth of the population, and assume it to be distributed along a linear range. Under such conditions, a “marked differentiation occurs with relatively large neighbourhoods” (*S. Wright*, 1951, p. 334 and Fig. 8, p. 333). Then, in our case,  $\tilde{N}_T/_{10(1815)} / \tilde{N}_N = 117 \sim 10^{2.07}$  and  $F \sim 0.10$  with respect to the northern part of the population and, obviously, is still greater with respect to the whole country. This would imply a marked differentiation. However, the population in Norrland is not linear, but has a predominantly reticular structure. This would result in a population-genetic situation halfway between the two extremes estimated above. It is nevertheless entirely reasonable to presume that, even *within* the northernmost part of the country, there was a not negligible random genetic differentiation in several different localities. It seems quite clear that a differentiation could exist in relation to the larger, southern part of the country’s total population. This population structure with respect to residential areas, as well as this marriage pattern, seem on broad lines to have been retained into the present century. Only during the past two generations has a process come into action which breaks down the former isolate conditions at an accelerated rate.

The genetic structure of the population of Sweden discussed above is intended to explain certain circumstances.

*Torsten Sjögren*—a master of human genetic research—found in his classical work on juvenile amaurotic idiocy that during the period covered by his investigation up to 1930, this disease was manifested in the southern part of Sweden only up to the unbroken line in *Fig. 1*. This level does, in fact, divide the population into exactly the two parts discussed in this paper.

In his subsequent brilliant publications, *Torsten Sjögren* has studied and elucidated a series of genetic disorders in the northernmost part of Sweden. These have manifested themselves in different population pockets. It is presumably not fortuitous that these recessive diseases have become manifest precisely in this part of the country. Relatively limited foci of rare dominant traits as well, such as tremor essentialis—also studied by *Sjögren*—occur in this region. Figuratively speaking, this northern part of Sweden can be regarded as a gold mine from the human genetic point of view.

Many of *Torsten Sjögren*’s disciples have followed the paths he has charted through this territory which, however, now seems to be rapidly changing in nature.

## SUMMARY

1. A study has been made of the population conditions in Sweden in 1800–1850. The country was then divided into two parts, differing with respect to population-genetic structure. The southern part, comprising 40 per cent of the total land area, contained 90 per cent of the married population. The 10 per cent minority was distributed over the northern part, amounting to 60 per cent of the total land area.

2. These population regions were joined by an hourglass-like constriction at the level of the unbroken line on the map of Sweden (*Fig. 1*).

3. In the southern part, there was an areal, approximately continuous distribution of the population. The neighbourhoods calculated according to *S. Wright* imply panmictic conditions for this part of Sweden.

4. The northern part of the population was distributed in an eastern zone along the coast, with reticular branchings in the west towards the inland, as well as blind pockets. It is reasonable to presume that a not negligible random genetic differentiation existed even *within* this northern part of the population.

5. It seems quite clear that such a genetic differentiation might occur in the northern part in relation to the southern, main part of the total population.

6. These population-genetic isolating mechanisms were presumably in existence up to the present time, but now seem to be in the process of being eliminated at a rapid rate.

7. It is pointed out that the reasonableness of these theories is reflected in an interesting way by the factual conditions observed by *Torsten Sjögren*, in his long series of brilliant genetic investigations.

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