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Growth of consanguineous populations: effect of family and group size

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ABSTRACT

Objective: Although inbreeding is detrimental to the offspring, consanguineous marriages still remain very common in many countries. To better understand this sociobiological puzzle, we compared the growth of isolated consanguineous versus non− consanguineous populations of varying sizes. **Methods:** In a computer, over five generations, we simulated first cousin marriages, family size, and offspring survival to find the effect on population growth. **Results:** In large groups, the practice of first cousin marriages decreased the population size due to an excessive number of deaths among the offspring. In small groups, however, first cousin marriages increased the population size; without first cousins, there is a relative shortage of marriageable potential spouses. Marriages to first cousins produced additional unions and a surplus of viable offspring despite excessive deaths caused by inbreeding. Consequently, small consanguineously marrying groups grew faster than small non−consanguineously marrying groups. Independently, family size directly affected the number of consanguineous marriages and inbreeding in consanguineous groups. **Conclusions:** In small groups, kin marriages, despite the harms of inbreeding, result in relatively faster population growth.

1. Introduction

Consanguineous marriages are a puzzling sociobiological phenomenon. Although the offspring suffer higher mortality and morbidity, kin marriages are surprisingly popular: approximately 10% of marriages in the world are amongst relatives. In India, human consanguinity is at least 2000 years old; in the Middle East, it dates to pre−Islamic times [1]. A long period of inbreeding should decrease the size of any population. However, the depressing effect of consanguinity on human populations is not apparent. Ironically, many countries that have a long tradition of kin marriages (e.g., India, Pakistan) are densely inhabited. Clearly, the presumed

negative effect of consanguinity needs to be further elucidated and a better understanding of population dynamics is needed [1,2].

One of the characteristics of consanguineously marrying societies is that they are often segregated into small groups, e.g., tribes, subtribes, brotherhoods, castes [1,3]. India (population ~1.3 billion), with its long history of consanguinity, has over 50,000 such groups while United Arab Emirates (native population ~1 million), which also follows this practice, has over 68 tribes, subtribes and extended families [4,5]. Similarly, non−tribal populations that arrange kin marriages are invariably small, e.g., in some islands and in isolated mountainous villages [1,6,7]. The aim of this study was to examine the effects of a) size of the group and b) size of the family on growth of consanguineous verses non−consanguineous populations. Since field studies are difficult, the effects on growth were studied on populations (with and without first cousin marriages) simulated in a computer.

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2. Materials and methods

2.1. The model

The growth of any population depends on many parameters: fertility, mortality, sex ratio, polygyny, incest taboo and other social norms. In consanguineous populations, additional parameters are important, e.g., kin preference since it affects the level of inbreeding. Incorporating all these parameters into a model increases the complexity and is more likely to introduce error. The removal of many interacting factors involved, and by first studying simpler models, will make understanding of human behavior easier. A model is a simplified reality and is equivalent to a controlled experiment in which the effects of one variable is examined at the time. We designed such a model to gain an insight into why in some segregated groups, some people marry kin. In the model, the effect of initial size of population and family on the growth was compared in two settings: a population in which first cousin marriages were allowed with one in which such marriages were prohibited. Simulation of each population was run 100 times, and the results were averaged.

2.2. Study parameters

The marriages were arranged in populations of different effective sizes (N=200, 100, 40, 25). Preliminary analysis showed that N>200 does not produce qualitatively different outcomes from N=200. In the model, each member of a population carries information about its genealogy (who are the parents and, if married, who is the spouse and offspring), biology (sex and age) and genetics (recessive lethal alleles) and his/her behavior is governed by a set of sociobiological rules: what marriages are allowed, preferred age of marriage and biological relatedness of mate. At the outset, the population is composed of an equal number of males and females with a pyramidal age structure (range 0 to 60 years). In all populations, marriages are monogamous, non−incestuous and arranged between individuals 15 years of age and older; the man marries the youngest available female (unless she is more than 20 years younger or more than 5 years older). Remarriage was allowed in case of incidental death (non−specific mortality) of spouse. In the model, all events occur over five generations with time advancing in five−year steps.

2.2. First− cousin marriages and population inbreeding

Consanguineous marriages are unions between close cousins (second and closer), uncles and nieces, and less commonly between other close relatives. First cousin unions are the most prevalent type of consanguineous marriages (50%−60% of all kin marriages) with a high coefficient of inbreeding

(0.0625), and contribute 65% −70% to the mean coefficient of inbreeding in consanguineous populations[1,3,8]. First cousin marriages were selected for modeling because they have the highest prevalence with the greatest global contribution to overall inbreeding. There are four different types of first cousin marriages; they are generally defined from the groom's perspective. Thus, a man can marry the daughter of his father's brother or sister; or the daughter of his mother's brother or sister. All the four types of possible first cousin marriages have the same coefficient of inbreeding for autosomal alleles. However, in the model, marriages are arranged between first cousins in the traditional Arab way[3]; this was done to provide an additional way of verification of proper marriage arrangements. Here, the man always marries his father's brother's daughter (FBD union) if such a cousin is available, otherwise he marries any of the three different types of first cousins. If a first cousin is unavailable, the man marries a biologically unrelated woman or, if he could not find such a partner, he stays unmarried. On the other hand, if a woman has a male first cousin of marriageable age, who is her father's brother's son (their pairing would create FBD union), she will marry only after this first cousin is married. In Arab world this always produces more FBD type unions than other types of first cousin marriages and was consistently reproduced in the model. In general, the inbreeding coefficient exponentially decreases as the relationship between married relatives becomes more distant; in addition, the prevalence of such unions is less than that of first cousin marriages in most consanguineous populations. Therefore, the unions of more distant kin contribute significantly less than that of first cousins to the overall inbreeding in population. Consequently, in the model, marriages between first cousins once removed were neither preferentially arranged nor were they banned. In the model, uncle−niece and aunt−nephew unions were not allowed [1,3]. The mean coefficient of inbreeding in a population is calculated as a sum of the coefficients of inbreeding of all marriages (0.0625 for first cousin unions and assumed 0 for all other unions) divided with the total number of marriages.

2.3. Other parameters

The factors that affect marriage arrangement in the populations with and without first cousin marriages (and the number of their offspring) were controlled in order to make valid comparisons and permit evaluation of the effect of the parameter of interest, the group and family size. Migration is not incorporated in the model. In human consanguineous groups (e.g., tribes and castes), inter−group marriages are rare; they are often banned and when established (for other than political reasons) are frequently dissolved.

In the model, after marriage, couples have offspring with a (five−year) probability that varied in relation to woman's

age: 0.8 for age 15 to 19, 0.9 for age 20 to 29, 0.6 for age 30 to 39 and 0.2 for age 40 to 50 years [9]. Fertility difference between the consanguineous and non−consanguineous unions is a contentious issue, and in the model was assumed to be the same [10]. Sex of a newly born is randomly determined and the offspring inherits from its parents recessive lethal alleles on the autosomal chromosomes as per Mendelian rules of inheritance. At the time of the foundation of the population, lethal mutations are randomly seeded to provide an average 1.4 recessive lethal alleles per individual [11]. This was verified to cause the same numbers of excess deaths (which are proportional to the coefficient of inbreeding) in simulated populations as in real populations (see Results). The survival of the offspring is determined by likelihood of homozygosity of recessive lethals. Therefore, the distribution and the frequency of these alleles at the outset of simulation were set to be the same. As lethal alleles are lost at a higher rate in more inbred (first cousin marrying) population and their frequency effect offspring survival in inbred families more than that of outbred families, the frequency of recessive lethal alleles was a controlled variable and was kept constant; lost allele was replaced by random insertion into the genome of the randomly chosen newly born in the same population thus mimicking mutation. Similarly, compensatory pregnancies that may increase the number of offspring in first cousin marrying population were excluded to keep the experiment conservative. In the experiment, the population was exposed to non−specific mortality, which was controlled. The effective population size comprises individuals with ages 15 to 55 years; family size is defined as an average number of living children of the same mothers ages 30 to 55 years.

3. Results

3.1. Validation of the model

i) In the model, the highest fraction of first cousin marriages obtained was 0.5 of all marriages, similar to those in many societies with high rates of consanguinity and to the highest rates (0.6) reported in consanguineously marrying populations [1,8]. ii) The proportions of FBD marriages in the study were always higher than the proportions of each of the other three types of first cousin unions. In the Arab world, this is consistently found in consanguineously marrying populations and was replicated in the model [1,3,12]. iii) The highest mean coefficients of inbreeding obtained in the simulated and real human populations were 0.039 and 0.045, respectively [8]. iv) In consanguineous populations, excess of deaths among offspring is related to homozygosis of recessive lethal alleles, is linearly related to the mean coefficient of inbreeding (F) and equals 0.7 X F [11]. In the model, more inbred first cousin marrying populations have more deaths than less inbred populations

without first cousin marriages and correlation between the expected and observed excess of deaths in modeled populations with different F was high (Figure 1).
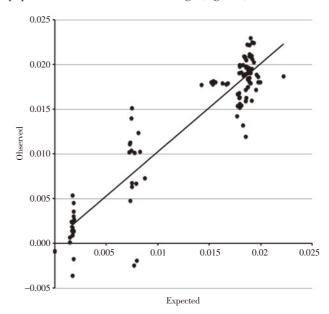

Figure 1. Correlation between observed and expected excesses of deaths in simulated populations with different mean coefficients of inbreeding.

3.2. Effect of population size on the rate of marriages and growth

Mortality in non−first cousin marrying population (control group) was adjusted so that the size of population (N= 200, 100, 40 and 25) is kept constant throughout mating cycles of five generations. In first cousin marrying populations (experimental group), the values of simulation parameters were kept the same as in control group. In larger populations (N=200 and 100), allowing first cousin marriages predictably increases inbreeding and decreases relative growth of population. In smaller populations (N=40 and 25), allowing first cousin marriages increases relative growth of population (despite increased number of deaths due to homozygosis of recessive lethal), and increases overall number of marriages (Figure 2). The increase in relative growth of population is due to a relatively higher overall number of married women (giving birth to children who survive to reproduce) than the offset from relative increase of deaths of inbred children in first cousin families.

To further analyze relative positive growth in small inbreeding populations, we examined their marriage structure. In large populations practicing first cousin marriages, we increased the mortality rate, causing it to gradually shrink in size. As population size decreased, the overall fraction of married individuals decreased while the fraction of those married to first cousin stayed unchanged (Figure 3). The decrease of overall number of marriages was solely due to a decrease in the number of non−first cousin unions, most noticeably in populations of very small sizes.
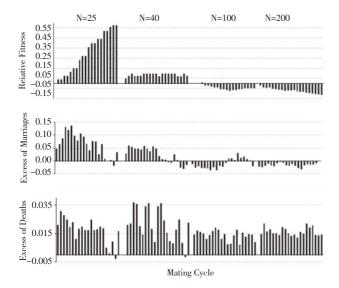
Figure 2. Excess of population size, all marriages and deaths in consanguineous vs. non–consanguineous populations of different sizes (N).
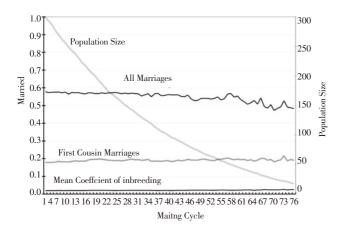

Figure 3. Fraction of all and first cousin married individuals at different sizes of the population.

Evidently, decreasing the number of non–first cousin marriages (all marriages minus first cousin marriages) in smaller populations is due to a decreasing number of available biologically unrelated mates of marriageable age.

3.3 Effect of family size on the rates of first cousin marriages and inbreeding

How family size affects the rates of consanguineous marriages and inbreeding in human populations was not previously analyzed. In this study, we controlled the size of family by changing child mortality and used for the reference point the family size at which population does not grow (family size=1). To eliminate the affect of population size on number of marriages, all analyses were performed in large populations of the same size (N~375). The frequency of first cousin and FBD marriages and the mean coefficient of inbreeding are directly related to the average size of family (Figure 4).
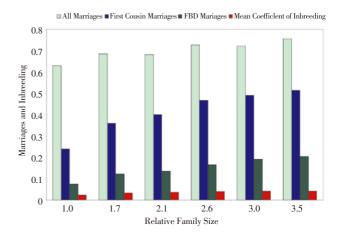

Figure 4. Effect of family size on the frequencies of first cousin and FBD marriages, and the mean coefficient of inbreeding in a large population.

4. Discussion

The purpose of the study was to gain insight into population dynamics of consanguineously marrying groups (tribes, castes, brotherhoods). This was done through computer simulation and comparisons with non–consanguineously marrying groups of equal sizes.

4.1. Groups size and its growth

Our main finding is that the growth of small consanguineous populations was faster compared to similar sized non–consanguineous populations. In small populations, allowing first cousin marriages resulted in a higher total number of marriages. This means that in small groups there is a relative scarcity of biologically unrelated marriageable mates. The additional (kin) marriages produced more viable offspring despite excessive deaths due to inbreeding (Figure 2); therefore, increased reproductive success of individuals who married kin resulted in a faster growing population. In large populations, first cousin marriages depressed the relative population size. This occurred because arrangement of first cousin marriages hardly affected the overall number of marriages due to the large pool of unrelated potential spouses available. The total number of infants born was not affected, but their mortality increased due to the excess of homozygotes of recessive lethal alleles; hence, decreased reproductive success of individuals married to kin resulted in a relative decline in the population. Our results support the view that inbreeding and outbreeding are adaptive responses to a changing ecology [13]. In human populations, consanguineous pairing increases after populations decrease in size due to natural (e.g., cholera, famine) or man–made (e.g., the Second World War) calamities that make potential mates scarce [7,14,15] . A similar scarcity of mates resulting in kin unions are found in geographical isolated regions (e.g., islands, remote mountainous villages) [6]; here, mate scarcity is due to physical unavailability of mate and high cost of search for mate outside the isolate. Mate selection within a displaced group with a 'tribal mentality' explains kin marriages among Pakistanis in the densely populated city of Birmingham, United Kingdom [16].

While our main finding may be obvious post hoc –more marriages result in overall more offspring despite increased

loss due to inbreeding −it provides a basis for a novel explanation of human consanguinity.

4.2. Novel explanation for consanguineous marriages

It is well recognized that consanguinity and tribalism (the partitioning of population into smaller groups) coexist and are related to poor socioeconomic conditions [1,17]. This association can be elucidated within the framework of our results and sociobiological principles of cooperation (social contract), ethnocentrism and mate selection [18−20].

In any society, to complete any social contract a full cooperation between the participants is essential. The honoring of such 'business deals' is expected to bring economic prosperity of a society, while a defaulting will cause economic stagnation. Broadly, marriage is a social contract between spouses (and their respective families) and its dissolution can result in grave biological, social and economic consequences. In societies with untrustworthy individuals, people become distrustful and suspicious; therefore, they turn to kin in arranging most social contracts, which are more reliable. A higher success rate of social contracts with kin (than non−kin) result in formation of kinship units and partitioning of population into many small groups (tribalism) that compete for limited resources (territoriality). This further increases mistrust between the members of different groups (e.g., tribes, subtribes, brotherhoods, castes). Tribalism and territoriality have direct affect on arrangement of marital contracts.

A potential mate cannot be selected from another kinship group because, in most societies, families are patrilocal (upon marriage women moves into husband's house), and women and her children becomes the member of another (competitively opposing) group. This would strengthen one (husband's parents') group and weakens another (wife's parents') group. Occasionally, inter−group marriages are arranged when the members of two groups are expected to benefit through kinship link of groups' leading families ('political marriages'). In tribal societies with matrilocal families, the husband moving to his wife's household creates similar asymmetry of relative strengths of the two groups. Consequently, in all tribal societies inter−group marriages are socially banned, and a potential spouse must be selected from within the group. Thus a lack of trust among the non−kin explains tripartite association of the economic underdevelopment, tribalism and endogamy in human societies.

However, within each group, spouses are selected based on principles of mate selection theory: women more often marry men of a higher socioeconomic status, while men more often marry women of a lower status; therefore , poor men have more difficulty finding spouse and are more often unmarried [18,21, 22]. In addition, the frequent practice of polygyny in human societies, which is more common among higher status men, further lowers availability of a potential spouse for a poor man. The logical conclusion is that, out of a compulsion to procreate, poor men marry a close kin more often than men of higher social status. Indeed, higher rates of consanguinity among socioeconomically more deprived families are well documented [1,17].

In small kinship groups, all potential spouses are either close kin (e.g., first cousins, resulting in consanguineous unions) or distant kin (conventionally, beyond second cousin, resulting in endogamous unions); back tracking of kinship becomes progressively difficult for people and distant kin merges into non−kin within the group. In small groups, the number of available marriageable individuals is also smaller; the number of close kin is unaffected by the size of a group unless this size becomes smaller than the size of extended family. Thus after stochastic arrangement of marriages with distant/non−kin, many marriageable individuals were left without a potential spouse −unless they chose to marry a close kin. Our study has shown that marriage to a close kin increases the reproductive success of such individuals −despite increased loss of the offspring due to inbreeding −and is a biologically viable alternative to staying single and childless.

Our proposed explanation of human consanguinity elucidates its association with poor socioeconomic status and tribalism; it clarifies marriage substructure in consanguineous populations. It explains why arrangement of kin marriages is rational behavior ecologically, and how inbreeding elevates rather than depresses specific human populations. The model does not contradict many previously proposed explanations of consanguinity (e.g., preservation of economic wealth, better protection of family, better treatment of wife, easier marriage arrangements) but fit them within a single explanatory framework based on sociobiological principles of cooperation, territoriality, mate selection and the all important human drive to procreate. The model also suggests that public measures that increase trust between non−kin could simultaneously increase economic development and decrease human inbreeding.

4.3. Family size and inbreeding

A second finding of our study is that the relative rate of consanguineous marriages in a population depends on the average size of the family; populations with large families could have higher rates of first cousin marriages and a higher mean coefficient of inbreeding, and vice versa (Figure 4). Only one study has shown the correlation between family size and inbreeding [23]. In many other studies on human consanguinity, the effect of family size on the rate of consanguineous marriages has not been considered. For example, in a prosperous Gulf country, the rate of consanguineous marriages has increased over time, which is contrary to prediction of socioeconomic theory of consanguinity [12]. This increase of intra−family marriages is likely due to an increased size of families produced by decreased child mortality. In contrast, in an equally prosperous Japan, consanguinity rates plummeted which was expected as per the socioeconomic model of consanguinity [24]; however, family size decreased years before the drop in consanguinity rates, and this most likely contributed to the decline of consanguinity [25]. Future studies on consanguinity should provide information about family size in order to allow longitudinal as well as cross−sectional comparisons.

4.4. Potential limitations of the study

As in all experiments, ours is a simplified representation of reality. For example, in the model, the size of effective population at which relative fitness changes from depression to elevation was somewhere between 40 and 100 individuals. The comparison of our finding with real life data is not possible as such data is unavailable. Nonetheless, the purpose of the study was to create an insight into the principles of dynamics of population and not to predict the size at which this fitness transition occurs as many other factors affect population growth as well. For instance, polygyny decreases the pool size of potential mates for unmarried males in both non−

consanguineous and consanguineous populations. Thus, polygyny may have favored emergence of kin marriages as a mating strategy. In the model, migration was not considered because in consanguineous societies, inter–group (e.g., tribe, caste) marriages are rare. Nonetheless, when migration in and out of a population is equal, its size remains unchanged. However, migration into a population increases the number of biologically unrelated mates available which may not favor kin marriages. Fertility is a contentious issue in studies on consanguinity. A lower level of inbreeding is associated with a higher fertility [26]. However, apparent higher fertility seen among some inbred consanguineous families is difficult to explain; the confounding effect of associated poorer socioeconomic conditions and earlier age of marriage cannot be excluded. The increased loss of children due to inbreeding could have resulted in more compensatory pregnancies [10,27]. Further, inbreeding lowers the frequency of recessive lethal alleles in population faster than outbreeding, which increases the number of surviving offspring in a consanguineous population [10]. Therefore, in the two populations of our model, fertility was kept the same, compensatory pregnancies were not allowed, and the frequency of recessive lethal alleles was kept constant. Other factors could affect dynamics of consanguineous populations [28]. In this study, the aim was limited to the effect of family and group size on population growth.

4.4. Summary

In small isolated populations, there is a relative shortage of biologically unrelated potential spouses. This results in many individuals remaining single and childless – unless they marry a kin. Kin unions increase the overall number of marriages and the average number of offspring lost due to inbreeding is considerably smaller than the number of surviving inbred offspring. Consequently, in small populations, kin unions increase the reproductive success of individuals, who otherwise would be left single without any children.

Conflict of interest statement

Authors declare no conflict of interest.

Acknowledgment

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