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# Transmission of migration propensity increases genetic divergence between populations

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## ABSTRACT

The advent of molecular genetics has brought invaluable information, which is now routinely used by anthropologists in their attempt to reconstruct our demographic past. Since the mitochondrial DNA loci are much more similar between populations than are the Y chromosome loci, it has been suggested that women had a much higher migration rate than men throughout history. Based on an examination of intergenerational migration patterns in three large demographic databases, we bring this inference into question. In some early Canadian settlements (St. Lawrence Valley and Saguenay), and in the past Krummhörn region of Northwest Germany, men whose father was a migrant were more likely to migrate, while the migration probability of women was largely independent of that of their mothers. As a result, men's movements were less effective in preventing genetic differentiation between populations than women's movements. If it is largely prevalent among human societies, this male-specific transmission of migration propensity could partly explain the geographical clustering of Y chromosome distributions. In order to account for its impact, we propose a slight modification of Wright's Island model. We also address the relevance of this model with respect to previously reported measures of population differentiation and we discuss the supporting historical and anthropological literature. We conclude that the widespread patrilocal rules of post-marital residence have generated both a higher female migration rate and a patrilineal dependency in the propensity to migrate.

Through its involvement in sex determination, the Y chromosome is necessarily transmitted by males, whereas mtDNA, which is provided by the mother's egg cell, is transmitted by females. This remarkable contrast, combined with the increasing availability of data on DNA variations, has triggered a number of studies addressing males' and females' specific demographic history (Al-Zahery et al., 2003; Bamshad et al., 1998; Behar et al., 2003; Capelli et al., 2003; Carvajal-Carmona et al., 2000; Fagundes et al., 2002; Helgason et al., 2003; Hurles et al., 1998; Jorde et al., 2000; Mesa et al., 2000; Oota et al., 2001; Seielstad et al., 1998; Stoneking, 1998). From a worldwide comparison, Seielstad et al. (1998) reported a large contrast in the geographic stratification between the two sex-specific markers. The analysis was based on both published (Underhill et al., 1997) and original data of various genetic systems such as RFLP, SNP and micro-satellites. The  $F_{ST}$ , or the identity by descent in sub-populations relative to the total population, were 65% for Y chromosome loci and 19% for mtDNA loci. After having discarded various alternative scenarios like polygyny, natural selection, and mutation rate, they concluded that only a large sex differential in migration rate could account for the discrepancy. Using the "Island model" (Wright, 1951; 1969) they estimated a migration rate for women exceeding that of men by a factor of height in most human societies, throughout most of human history. The migrations referred to here are "matrimonial migrations", by which individuals leave their community of origin to marry, settle, and reproduce in a new community.

In order to explain the counterintuitive view that women have a higher migration rate than men, the widespread practice of patrilocality among human populations was called upon: in about 70% of documented societies, women typically move from their

communities of origin to that of their husbands (Divale, 1984; Murdoch, 1967). This seems plausible because the property of means of production (e.g. land in agricultural societies) is passed down from father to son in most human societies (Bouchard and de Pourbaix, 1987; Wall, 1983). However, a closer look at the implications of patrilocality suggests alternative theoretical perspectives. For instance, the son of an immigrant might find it hard to settle down and gather enough resources for successful provisioning of a family. Because his successful implantation and reproduction depend on his access to means of production, he is more likely to move out of the community than his counterpart who inherited land from a well-established father. On the other hand, the daughter of an immigrant woman may marry and settle into the community without being responsible for the property that will be the basis for family subsistence. As a result, in comparison with matrilineal, immigrant patrilineal are less likely to enter the “core” of a given sub-population (Fig. 1) and the same amount of migration in men and women results in a higher  $F_{ST}$  for the Y chromosome than for the mtDNA.

The propensity to migrate may run in families through ways that are not specifically associated with property as a means of production. If status or occupations are transmitted, and if status or occupations are related to migrating propensity, then migrating propensity may also be transmitted. Chatelain (1976) has shown how seasonal workers inherited both their occupation and migrating status from their fathers in the French 19<sup>th</sup> century Massif Central. More prone to travel from one region to another in order to find work, they were also more likely to find their spouse outside their community of origin than the sons of rich landlords or farmers, who were destined to perpetuate *in situ* the familial holding.

## FIGURE 1 ABOUT HERE

Such evidence for paternal transmission of migration behavior was found in three populations for which extensive demographic data are available: the French Canadian population of the St. Lawrence Valley (1608-1800) and the Saguenay region (1842-1971), and the German population of the Krummhörn region of Ostfriesland (1720-1874). For each of these populations, relative risks of migrating were calculated for men and women whose fathers or mothers, respectively, were immigrants in given areas of the region. Not unlike the “transmission of effective family size” (Austerlitz and Heyer, 1998; Gagnon and Heyer, 2001; Sibert et al., 2002) or the “kin-structured migrations” (Fix, 1978; Fix, 1999), the intergenerational transmission of migration would be a social behavior that can significantly affect the frequency and the distribution of genes. We provide a model that accounts for the impact of this phenomenon on equilibrium values of  $F_{ST}$  and, based on historical and anthropological literature, discuss its prevalence and significance in human societies.

## MATERIAL AND METHODS

### Data

**The St. Lawrence valley** data were taken from the *Registre de population du Québec ancien* (1608-1800), designed by the *Programme de recherche en démographie historique* at the University of Montreal (Charbonneau et al., 1993; Légaré, 1988). This database is made up of 712,000 marriage, birth and death certificates. It covers the vital events and the kinship network of every individual of European ancestry who lived in the



colony before 1765, and the genealogy of every individual who married there before 1800. From this, a number of parent-child pairs were selected, for which the migratory status of both parent and child were known. All the selected parents married and settled between 1720 and 1750 in one or the other of the three following areas: Montreal Island, Quebec City area, or Beaupré/Charlevoix counties. The place of residence of an individual was defined as the place of birth of his/her first child. An individual was said to be a migrant if his/her place of residence was different from that of his/her parent.

The **Saguenay** region (pop. 278,000) is located in the province of Quebec, approximately 200 km north of Quebec City. Settlement in this region began during the second quarter of the 19<sup>th</sup> century (Roy et al., 1988). Until the 1930's, the population was mainly rural, with high fertility levels (average of 7 children per woman). All births, marriages and deaths that occurred in this region since the beginning of settlement until 1971 were registered and linked in the BALSAC Population Register (Bouchard, 1992; Bouchard et al., 1995). This register presently contains 660,000 records from the Saguenay population and more than 1.5 million records from other regional populations of the province of Quebec, covering the 19<sup>th</sup> and 20<sup>th</sup> centuries. The data for this study consist of parent-child pairs (parents born between 1850 and 1880 in the Saguenay region) for which the migratory status was known. A migrant parent (Pm) was defined as a parent whose place of birth was different from that of his/her child. In this case, the place of birth is one of the eight subregions of the Saguenay (for details, see Tremblay et al., 2000). A migrant child (Cm) was considered as a person for whom the place of birth of his/her first child was different from his/her own place of birth.

**The Northwest Germany** data derive from a family reconstitution study based on church registers, as well as on other records of the Krummhörn region (Ostfriesland, 18<sup>th</sup> and 19<sup>th</sup> century). At present, 19 of the 32 parishes of the region are evaluated, for a total of some 23,000 families for which vital and social data are known. In the present analysis, we considered only the men and women whose marriage took place between 1730 and 1830 in one of the studied parishes and for whom the migration status of themselves, their parents and their children was known. Migration status was defined from the place of residence, based such factors as place of birth of all children, place of death of young children, weighted for their particular significance. For details on the database and some main results see Beise (2001) and Volland (1995).

### **The Island model with intergenerational transmission of migration**

In Wright's Island model (Wright, 1951; 1969), an infinite number of sub-populations of equal effective population size  $N$  exchange migrants at a rate  $m$  in each generation. The probability of identity by descent  $F_t$  in sub-populations relative to the total population for haploid DNA at time  $t$  is given by (Crow and Kimura, 1970):

$$F_t = (1 - m)^2 \left[ \frac{1}{N} + \left( 1 - \frac{1}{N} \right) F_{t-1} \right], \quad (1)$$

where  $N$  is the effective population number of males *or* females, whether Y chromosome *or* mtDNA is considered, respectively. The solution of the recurrence equation (1) is:

$$F_{st} = \frac{(1 - m)^2}{N - (N - 1)(1 - m)^2}, \quad (2)$$

which reduces to (Whitlock and McCauley, 1999):

$$F_{st} \cong \frac{1}{1 + 2Nm}, \quad (3)$$

when  $m$  is small relative to 1 and  $Nm$ .

This model has sometimes been declared unrealistic because it ignores the spatial unfolding of migrations and relies on strong assumptions that are rarely met in the real world (ibid; Crow and Kimura, 1970; Fix, 1999). In spite of these limits, the model has extensive ramifications in population genetics that encourage its further specification. Several predictions concerning the magnitude of genetic drift, natural selection and mutation derive from its simple formulation. For example, it shows that a very low migration rate is sufficient to counteract genetic differentiation of populations.

The expression accounting for the dependence of migration across generations is a modification of the above formulation. Let  $\alpha$  be the parameter representing this dependence, with  $0 \leq \alpha \leq 1$ . The higher  $\alpha$  is, the higher are the probability that the child of a migrant will migrate and that the child of a non-migrant will stay in the population. With this intergenerational dependence, the probability of drawing an allele coming from an immigrant at any generation is no more  $m$ : it is reduced to:  $c = (1 - \alpha)m / (1 - \alpha m)$ , with  $\alpha m < 1$ . Conversely, the probability of drawing an allele from a resident is increased from  $(1 - m)$  to  $(1 - c) = (1 - m) / (1 - \alpha m)$ . When  $\alpha = 0$ ,  $c = m$ , there is no dependence in migration over generations (no transmission of migration behavior), while when  $\alpha = 1$ ,  $c = 0$ , there is a complete dependence: all alleles that will form the next generation are drawn from the non-migrant pool and none among the immigrants. If  $\alpha = 0.5$ , the children of immigrants are half as likely to stay in the population as those whose parent was a non-migrant. With these definitions, the classic formula can be modified as:

$$F_t = (1-m)^2 \frac{1}{N^*} + (1-c)^2 \left(1 - \frac{1}{N}\right) F_{t-1}, \quad (4)$$

where  $\frac{1}{N^*} = \frac{1}{N} \left( \frac{c^2}{m} + \frac{(1-c)^2}{(1-m)} \right)$ , i.e., the probability of drawing successively the same allele

under the transmission of migration. The equilibrium value of the recurrence equation is:

$$F_{ST} = \frac{(1-m)^2 \left( \frac{c^2}{m} + \frac{(1-c)^2}{(1-m)} \right)}{N - (N-1)(1-c)^2}, \quad (5)$$

which, when  $m \ll 1$  and  $m \ll Nm$ , reduces to:

$$F_{ST} \cong \frac{1}{1 + 2N(1-\alpha)m}. \quad (6)$$

Thus, the effect of the transmission of migration factor  $\alpha$  is to reduce linearly the impact of migration in preventing divergence between sub-populations. The factor  $(1-\alpha)m$  can be considered as the “effective migration rate”. The equation can also be expressed in terms of the *relative risk RR* of migrating when the parent is a migrant (in relation with the risk of migrating when the parent is non-migrant) by replacing  $(1-\alpha)$  with  $1/RR$ .

Note that when  $c = m$ , that is, when  $\alpha = 0$ , equations (4), (5) and (6) reduce to equations (1), (2) and (3), respectively.

## RESULTS

Sons whose fathers were immigrants to Montreal, Quebec City and Beaupré/Charlevoix had a much higher risk of moving out of these places to marry and

settle elsewhere. For those men for whom place of settlement is known and whose fathers married between 1720 and 1750, the relative risks of emigrating were, respectively, 1.41, 1.23, and 1.50 (Table 1). The figures are relatively substantial and highly significant. However, no such significant tendency was found for Montréal, Québec City or Beaupré/Charlevoix women who married in the same period. In other words, the migrating propensity of a woman was independent of the migrating status of her mother.

Results for the Saguenay areas also point to a higher risk of migrating for individuals whose parents were migrants, although the differences between men and women are not as clear as in the St. Lawrence Valley. Relative risks for Lower Saguenay (1.17,  $p=0.15$ ) and Chicoutimi (1.18,  $p=0.02$ ) men are similar, and a little lower than those of Quebec City men (1.23), but the relative risk for Chicoutimi women, although low (1.13), is significant at the 0.05 level ( $p=0.04$ ).

In the case of the Krummhörn population, analyses were performed at the parish level. Exchanges of migrants between the nineteenth parishes for which data were available for at least three generations were tabulated. The probability of moving out of one of the 19 parishes to settle in another of the other 18 parishes was significantly higher (relative risk,  $RR = 1.56$ ,  $p = 9 \times 10^{-7}$ ) for a man whose father was a migrant than for a man whose father was a non-migrant. No transmission of migration was found for women in this sample ( $RR = 1.06$ ,  $p = 0.32$ ).

#### TABLE 1 ABOUT HERE

Because of the intergenerational dependency in the probability of migration, the pool of migrants is not a random sample. The descendants of immigrants are more likely

to move out, so that Y chromosome variants from the outside are less likely to be found in the next generation. This reduces the effectiveness of migration in preventing differentiation between Y chromosomes in different populations. Interpreting from equation (6) the relative risks (and the corresponding  $\alpha$ ) given in Table 1 in relation with the  $F_{ST}$  and  $Nm$  values given in the literature we gain new insights into the male/female differential in migration rates throughout history. As said above, the Island model rarely matches perfectly the movements of exchange among human groups, and the proposed extension. For this reason, we do not attempt to explore the implications of the model for our sampled populations. Our purpose was not to precisely describe the migration process, but to provide a crude assessment of the effect of its transmission on genetic differentiation of populations. As pointed out by Fix (1999, p.53): “The question remains whether the lack of realism matters when general answers to broad questions are sought”.

#### FIGURE 2 ABOUT HERE

Figure 2 shows the impact of  $\alpha$  on the equilibrium values of  $F_{ST}$ . This impact is minor for extreme (small or high) values of  $Nm$ , the number of migrants per generation. On the other hand, it is quite sizeable within the range of usually reported values of  $Nm$ . For instance, with two migrants per generation a value of  $\alpha = 0.5$  would divide the effective migration rate by two, and nearly double  $F_{ST}$ . A value of  $\alpha \cong 0.36$ , as obtained in Krummhörn, would increase  $F_{ST}$  by about 50% (Fig.2). It is often stated that, as a rule of thumb, a  $Nm > 1$  is sufficient to overcome the effects of genetic drift, although  $Nm > 2$  is probably a more accurate guideline for haploid systems. To take an extreme example, if  $\alpha = 1$  (complete dependence),  $F_{ST} \cong 1$ ; this would mean that a high migration rate would not prevent the gene frequencies in the sub-populations to drift away from one

another. The critical factor is not the number of migrants  $Nm$  but the number of *effective migrants*  $(1 - \alpha).Nm$ .

## DISCUSSION

### **The transmission of migration and the geographical clustering of Y chromosomes**

We showed that in three historic populations, sons inherited their propensity to migrate from their father, while such transmission was largely absent among women. If this male-specific intergenerational dependence has been a common feature of human history, it could explain partly the contrast between Y chromosome and mtDNA geographical clustering. An unlikely large value of the transmission factor ( $\alpha \cong 0.87$ ) would be needed to account for the huge discrepancy reported by Seielstad et al (1998). In other words, in order to increase  $F_{ST}$  from ~20% to ~65%, sons of immigrants would have to be 7.7 times more likely to emigrate than sons of residents ( $7.7 = 1/(1-.87)$ ; see Fig. 2). However, using the same data, Hammer et al. (2001) obtained a  $F_{ST}$  of 0.414 for male-specific DNA. With about two migrants per generation, this corresponds to an  $\alpha$  value of .67, and a more realistic three-fold increase in the probability of migrating for sons of immigrants (Fig. 2). They wrote: “It is not clear why the  $F_{ST}$  value of 0.645 reported by Seielstad et al. is so much higher than the value reported here”. Comparing autosomal, mtDNA and Y chromosome variations, Jorde et al. (2000) obtained a  $F_{ST}$  of 60% for four European populations on Short Tandem Repeats Y chromosome variations. But this was largely due to an extreme reduction of genetic diversity in the two northern populations of the sample (Kittles et al., 1999). All other comparisons within or between

continents yielded  $F_{ST}$  that, for both Y chromosome and mtDNA loci, lay between  $\sim 0.02$  and  $\sim 0.27$ . Within such a range, any scenario involving a reasonable transmission of migration in paternal lines is conceivable, so that the question whether men or women migrate more becomes problematic.

As pointed out by Stoneking (1998), it is not clear if the “patrilocal effect” extends to intercontinental levels. Data from historical demography can also shed light on the “long-distance migrations” (Fix, 1999) that have occurred in recent human history. Spanish records show that, from the late 15<sup>th</sup> to the early 19<sup>th</sup> centuries, the ratio of women to men embarking for the New World was one to ten (Carvajal-Carmona et al., 2000; Sánchez-Albornoz, 1977). Although less extreme, the sex-ratio of the very first French settlers in the St-Lawrence Valley was also male-biased, with about 3 men for one woman (Charbonneau et al., 1993; Gagnon and Toupance, 2002). No study has yet specifically addressed the issue, but these data would suggest a higher level intercontinental mtDNA clustering. Noting that numerous factors could account for the male-female  $F_{ST}$  ratio, Hammer et al. (2001) concluded that patrilocal effects are evident at local and regional scales rather than at the intercontinental level of analysis. The same could be said of the transmission of migration because long-range migrations most likely break the intergenerational dependency.

### **Historical and anthropological evidence**

Little evidence is available concerning the existence of father to son transmission of the propensity to migrate. To our knowledge, this phenomenon has only been reported once (Chatelain, 1976). We argue that the male-biased transfer of means of production reported in most societies (Murdoch, 1967) induce *both* patrilocal post-marital residence



rules and patrilineal transmission of migration. Whether this pattern is realized in most human societies is an empirical question that remains to be answered. Although our sample covers only three populations from the past, there are socio-economic bases for the broader relevance of these conclusions.

The most compelling support comes from the vast historical, demographic, and anthropological literature on the processes of rural family formation and reproduction (see for instance: Goody, 1976; Livi Bacci, 1997; Wall, 1983). In the “European marriage pattern”, Hajnal (1965) presented a model according to which, prior to the demographic transition, sufficient economic means had to be accumulated before starting a family. In the privileged this was obtained through inheritance. Although the rules of heritage and their application varied greatly over time and space in ancient Europe (Goody, 1976), a common feature emerges: typically, whether equality or impartibility prevailed, the sons, not the daughters, were the ones who received a share or the integrity of the family estate. In the Krummhörn region of North East Germany, the youngest son inherited the entire undivided family estate (Volland, 1995). Surrounded by the North Sea and by inhospitable moorlands, population pressure was high, and the response of the inhabitants was to limit the fragmentation of the land by giving preference to one heir (ibid.). As in many other crowded areas of 19<sup>th</sup> century Europe the disinherited sons were often confronted with a harsh fate since they were compelled to look for alternative occupations outside the family estate or to accept a state of permanent celibacy. Some authors even suggested that high-status inhabitants of Krummhörn were prone to commit *male* infanticide, ostensibly to keep their property from being divided (Volland et al., 1991). Still, native fathers had a much better chance to settle their sons in the community than the immigrants: for at least

one of them, there was a strong opportunity. Overall, men had a lower inter-parish migration rate than women, but they also transmitted their propensity to migrate to their sons (see Table 1). This supports our claim for a strong association between sex-biased transfers of means of production, post-marital residence patterns, and the intergenerational transmission of migration.

The gender inequity in the property of means of subsistence was transplanted in colonial North America (da Silva, 1998), where we find the first settlers of the Saint-Lawrence Valley in the 17<sup>th</sup> and 18<sup>th</sup> centuries, and the inhabitants of Saguenay a hundred years later. The rules of inheritance of land among Canadian peasants ranged from a strictly egalitarian division to an integral transmission by a deed to a sole heir, while other received compensation (Dépatie, 2001). However, empirical studies show that in general, sons were more likely to inherit most of the land and were able to establish a new farm in proximity to the father's estate (Bouchard, 1996; Dessureault, 2001). In America, the dominant inheritance system was also the partition into equal shares. But again, this did not necessarily mean that all children, including daughters, received title to land. In this regard, a noticeable gender inequality prevailed in colonial Connecticut (1750 – 1820). By the 1770s, daughters were over four times more likely than sons to receive no land; when they were granted land, they usually received far less than their brothers (Ditz, 1998).

It is somehow surprising to find evidence for paternal transmission of migration in the past Québec population, where, in contrast with Krummhörn, arable lands were largely available (Bouchard, 1996). It could be argued that, without regard to the context of colonization, land tenure customs were directly imported from Europe, which has

created the necessary conditions to induce the intergenerational dependency in migration. In fact, the latter only appeared in the 18<sup>th</sup> century, among the oldest settlements of the St. Lawrence Valley (Montreal, Québec, Beaupré/Charlevoix), i.e., where the demographic pressure on land, although not excessive, was the highest. Elsewhere, on the “pioneer front”, the inheritance of land was by no means a critical necessity; land was owned by those who were willing to clear the forest. This might explain the relatively low intergenerational dependency in migration reported for the Saguenay region (see Table 1). This region has only recently been open to colonization; in the middle of 19<sup>th</sup> century.

Persistent demographic pressure can favor the appearance and the maintenance of paternally-based systems of inheritance. In a seminal comparative study on modes of land tenure in East Africa, Shipton (1984) provided an explanation for the origins of the famous segmentary agnatic lineages, described in Evans-Pritchard’s ethnography, *The Nuer* (1940). He noted that these lineages were most commonly found in areas with relatively high population density. He also wrote:

Land shortage encourages sons to stay, after marriage, on or near the land of their fathers more commonly, and for longer periods, than they would do if land were freely available elsewhere. Staying on and inheriting part of a paternal holding is an easier way of obtaining land than asking the headman of a crowded village or neighborhood. On the other hand, where an abundance of land permits married men and their conjugal families to move easily away from their natal homestead, they will tend to do so (p.620).

Accordingly, we find very little support for male-dominated modes of acquisition and transmission of means of subsistence in low density settings. Studying the sparsely

spread !Kung groups in the Desert of Kalahari, Yellen and Harpending (1972) have argued that the scarcity and heterogeneity of resources make the social organization of hunter-gatherers extremely flexible. The network of kinship is widely extended across space, in such a way that the individuals can access the resources of many different areas. Tight grouping of patrilineal bands would hinder individuals in their response to environmental heterogeneity and variation. In this regard, there is no reason to believe that the level of geographic clustering was higher for Y chromosome than for mtDNA loci among the hunter-gatherers bands of the Paleolithic.

## CONCLUSION

The general conclusion of Seielstad et al. (1998) probably remains true: women ensured most of gene flow throughout history. But it is not necessarily because they had a much higher migration rate than men. Their movements might have been more effective in preventing genetic divergence between populations than those of men. Patrilocality may induce the circulation of women between populations. However, it might also induce the transmission from father to son of the probability of migrating. Together, the two effects may account for the large  $F_{ST}$  difference between the two sex-specific DNA markers.

Based on recently available DNA variations, anthropologists and population geneticists were able to provide important inferences regarding past human colonization and migration processes (Cavalli-Sforza and Feldman, 2003). As pointed out by Renfrew et al. (2000), “it seems remarkable altogether that the history of our species is most

effectively obtained by characterizing the DNA of living populations...”. These analyses, however, depend on assumptions about the genealogical processes that shape the frequencies of alleles over time (Helgason et al., 2003) and can only reveal the net outcome of demographic and evolutionary events, not the detailed history of such events. As shown here, the “past within us”, which is encapsulated in our DNA fingerprints, can be advantageously updated by the actual observation of demographic processes in “real” populations of the past.

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**Table 1.** (On next page). Transmission of migration in the St. Lawrence Valley (parents married 1720-1750), the Krummhörn region of North East Germany (parents married 1730-1830) and the Saguenay region of Quebec (parents born 1850-1879)<sup>1</sup>

<sup>1</sup> PmCm stands as number of “parent migrant/child migrant” pairs, PmCnm as the number of “parent migrant/child non-migrant” pairs, PnmCm as “parent non-migrant/child migrant and PnmCnm as “parent non-migrant/child non-migrant”. A migrant is an individual (son or daughter) whose place of residence is different from that of his/her parent. *RR* is the relative risk of migrating for an individual whose parent was a migrant and  $\alpha$  is a re-scaling of this risk that falls between 0 and 1 ( $\alpha = 1 - 1/RR$ ).

	St. Lawrence valley						Krummhörn	Saguenay					
	Montreal Island		Quebec city Area		Beaupré/Charlevoix			Lower Saguenay		Chicoutimi			
	Men	Women	Men	Women	Men	Women		Men	Women	Men	Women		
PmCm	261	213	1072	430	264	145	137	331	142	123	156	231	
PmCnm	372	497	818	613	131	250	262	406	176	142	236	284	
PnmCm	679	945	751	1033	413	568	264	379	77	94	517	527	
PnmCnm	1647	2439	877	1573	516	944	934	514	124	118	1021	802	
Total	2959	4094	3518	3649	1324	1907	1597	1630	519	477	1930	1844	
<i>RR</i>	1.41	1.07	1.23	1.04	1.50	0.97	1.56	1.06	1.17	1.05	1.18	1.13	
$\chi^2$	33.28	1.25	39.28	0.78	55.55	0.10	24.07	1.00	2.03	0.20	5.25	4.15	
<i>P-value</i>	$8 \times 10^{-9}$	0.26	$4 \times 10^{-10}$	0.38	$9 \times 10^{-14}$	0.98	$9 \times 10^{-7}$	0.32	0.15	0.65	0.02	0.04	
$\alpha$	0.29	-	0.19	-	0.33	-	0.36	-	0.14	-	0.16	0.11	

## FIGURE LEGENDS

**Figure 1.** Core-Fringe model of population (Heyer, 1993). As the sons of immigrants are more likely to move out of the community than sons of residents, incoming patriline are often confined to the fringe of the population. In contrast, since the migratory behavior of a woman is largely independent of that of her mother, matriline may enter the core of the population with more ease.

**Figure 2.** Equilibrium values of population divergence ( $F_{ST}$ ) values on haploid DNA per number of migrants per generation ( $Nm$ ) and for different values of intergenerational dependence in migration propensity ( $\alpha$ )

**Figure 1**

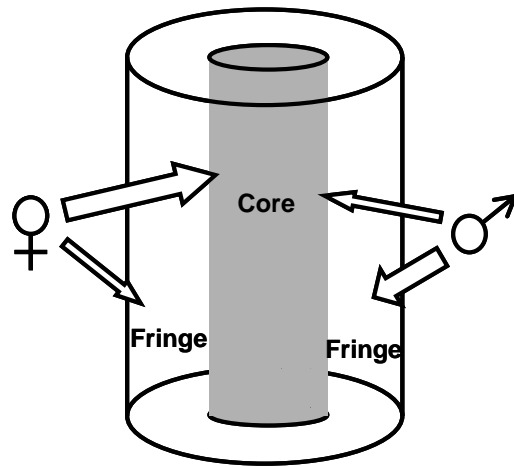




Figure 2

