
Relatedness and Kin-Structured Migration in a Founding Population: Plymouth Colony, 1620–1633

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Abstract To test the common assumption of no genetic relationship in a founding population, we calculated average relatedness (r) for the emigrants to Plymouth Colony from Europe on seven voyages from 1620 to 1633. Of 355 individuals, 255 could be individually identified and 4 generations of genealogic depth accounted for. Mean r was 0.00399 (S.D. = 0.00395) and ranged from 0 for 76 individuals to 0.01574 for a single female. There was a strong sex difference in relatedness; 91 females had a mean r of 0.00557 (S.D. = 0.00428), and 161 males had a lower mean r of 0.00308 (S.D. = 0.00349) ($t = 4.71, p < 0.001$). The major difference was in the lower proportion of females with no relations ($n = 12, 13.2\%$) compared with males ($n = 64, 39.8\%$) ($t = 5.05, p < 0.001$). If relatedness is calculated only for those with relations, females still have a significantly higher mean r value (0.00641, S.D. = 0.00393) than males (0.00511, S.D. = 0.00312) ($t = 2.38, p < 0.05$). Thus a higher proportion of females had relatives migrating to the colony, and relatedness is significantly higher among them. The majority of kin links (79.8%) were those within the nuclear family—parents, children or siblings. For the continuity of kin-structured migration, relatedness was highest among voyagers in the same boat load and lower between voyages, with no apparent time trend. The low relatedness value of the Plymouth migrants is a result of community history and recruitment practices for the new colony. For this European population average relatedness was approximately an order of magnitude below that of traditional groups, and the assumption of no genetic relationship is not unwarranted.

A common simplification of genetic models for founding populations is that they are composed of randomly chosen and effectively unrelated individuals [e.g., Rogers and Jorde (1987)]. Subsequent population inbreeding values then accumulate from the time of colony formation. However, it is obvious that founding populations are not genetically random at formation but are composed, at least in part, of related individ-

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uals. Meggitt (1962) proposed that Highland New Guinea group fission and splitting would be characterized by division among patrilineages. Chagnon (1975) found that Yanomamö groups fissioned along kin lines. Among the Amish, schisms leading to new colony formation tend to follow familial and theologic group lines (Hurd 1983). A similar process was observed among macaque monkeys (Chepko-Sade and Oliver 1979). In general, fissioning produces smaller, more highly related groups and increases genetic variance for the total population.

Migration between existing populations may also involve comigration of kin, as seen in local (Fix 1975; Neel and Salzano 1967), national (Whiteford 1976), or international migration (Bell 1979, pp. 204–205). For smaller anthropologic groups Fix (1978) coined the term “kin-structured migration” for migration with a significant familial component between existing populations. Neel (1967, p. 5) called the comigration of unilineal kin among the Xavante the “lineal effect.” Indeed, even during a stepped migration across the eastern United States, some Scottish-Irish families maintained marital ties over several generations (Reid 1988). The question, then, is not whether migrants to existing populations or founders of new ones are related but rather the extent of the relatedness and the circumstances under which the relatedness varies.

Most of the previous examples are tribal or traditional populations whose fissions or intergroup migrations are expected to produce localized microevolutionary changes. English migration to distant American colonies was of a somewhat different character (Langdon 1966; Cressy 1987). The original intent was to use the Americas for economic exploitation rather than as a terminus for permanent settlement, as envisioned for Virginia. However, the migration of religious dissidents to Plymouth in 1620 began a different trajectory, with a concerted attempt to establish not only a viable colonial exploitive base but also a “plantation” of those who desired to relocate permanently as individuals or families in an English-speaking colony (Langdon 1966, pp. 12–25). Migrants to a specific colony were recruited from the cosmopolitan populations of Europe (Flinn 1981), and their reasons for emigrating differed (Cressy 1987, pp. 74–106). Because of the different motives for migration and the origins and types of personnel required to establish an economic colony, we would expect fewer family associations and a lower level of relatedness than in more socially and historically homogeneous small “anthropologic” populations.

In this article we present relatedness values for an early successful founding population, the Separatists and Puritans of Plymouth Colony. Although they formed a single historic and religious community, the known 255 migrants to Plymouth show very low average relatedness ($r = 0.00399$, S.D. = 0.00395) at emigration. Females had a higher mean value (0.00557, S.D. = 0.00428) than males (0.00308, S.D. = 0.00349)

and a greater absolute number and relative frequency of kin links. Relatedness was higher among migrants on the same voyage than among those between voyages, although there were demonstrable intervoyage links.

Cultural and Historical Background

Between 1620 and 1633, 355 individuals left Europe to settle in Plymouth Colony in eastern Massachusetts (Willison 1964). Of these, the names and minimal genealogic information is available for 255 individuals; nothing is known for the remaining 100, although some identifications may be inferred indirectly (Stratton 1986).

The first 101 individuals voyaged to the New World on the *Mayflower I* with a "northern Virginia" destination, but, to avoid all contact with officials of the Church of England, they landed in inhospitable country to the north after a bad voyage. One died at sea before landfall, three children were born before landing or soon after arrival, and over half of the entire group died during the first winter (McCullough and Barton 1990). Once the colony was established, seven subsequent ships brought other settlers over during the next thirteen years; however there were only two large loads with named passengers after the *Mayflower I*.

Although they were soon supplemented by later migrants to Plymouth and by concurrent migration to the rival Massachusetts Bay Colony based in Boston (Langdon 1966; Cressy 1987), the colonists were for a time a separate legal, social, religious, and economic community. As a founding population, they had an important influence on the genetic composition of the American colonies and, later, the modern United States (Huntington 1959, pp. 107–136). Thus they constitute the founders of Plymouth Colony in a historic sense and a founding population in a genetic sense.

Materials and Methods

We define an emigrant as anyone who left Europe and subsequently resided or died in the colony or en route. This definition includes purposeful migrants of all vessels and crew members of the *Mayflower I* only; some crewmen died during the first winter and are traditionally included as part of the "Company."

The passenger lists for the six boats having named passengers were gathered from several sources, including the *Mayflower Compact* and William Bradford's journal (Bradford 1912, v. 1, pp. 189–192), and have been systematized in several recent volumes (Willison 1964; Stratton 1986). All those emigrants included in the "Pilgrim Company" (Willison

1964, Appendix A) were kept in the sample, with several exceptions. Mr. Ford, who died while sailing to Plymouth with his family on the *Fortune*, was not included in Willison's list but is added here because he was an emigrant by our definition.

Five children were born en route or soon after arriving; because these children are technically not independent emigrants from Europe, they are excluded. Willison (1964, p. 485) includes Dorothy and Mary Browne as dependents of John Browne; Stratton (1986, pp. 253–255) shows that the association is erroneous, and these two were removed from the sample. A servant girl and two men whose names are not known were also excluded as identities because their familial relations could not be determined. As a result of insufficient information or reappraisal of older data, we follow relational exclusions for Susanna (née Fuller) White, Catherine (née White) Carver, and John Allerton, as outlined elsewhere (McCullough and Barton 1990).

A coefficient of genealogical relatedness (F_g) was calculated for each pair of individuals, as described by Chagnon (1975) in his adaptation of Wright's (1922) coefficient of inbreeding (F). Individual F_g values were ascertained principally from genealogical records for the Plymouth Company, as recorded on family group sheets on file at the Family History Library in Salt Lake City, and from Willison's (1964, pp. 470–487) description of family relationships. Stratton (1986) has taken particular pains to verify individual identities, origins, and genealogic information, and his suggestions have largely been accepted.

Average relatedness (r) was calculated for each individual following the method of Berté (1988, p. 92): the sum of all F_g values for that individual divided by sample size (n) minus the individual (that is, $n - 1$). This is equivalent to Chagnon's $F_{g(\text{ALL})}$ (Chagnon 1988, pp. 987, 991). No r values are calculated over more than four generations, so the results represent minimal values. Because the Company was composed of individuals who generally originated from different community clusters, there are undoubtedly some deeper consanguineous links, but inadequate historical records preclude further pursuit.

Differences were tested using a simple χ^2 (Siegel 1956, pp. 42–47), a two-tailed t -test (Blalock 1960, pp. 144–149), and a ratio test for proportions (Bailar and Ederer 1964). For statistical tests a significance level of 0.05 was considered acceptable.

Results

Relatedness. Two-hundred forty-seven individuals could be identified and genealogic relationships with other passengers determined (Table 1). Of these, 76 (29.8%) are not demonstrably related to another colony

Table 1. Average Relatedness Values (r) for the Entire Plymouth Company and for Passengers Arriving on the Three Largest Voyages

Passenger Group	Relatedness (r)		
	n	Mean	Standard Deviation
Total	247	0.00399	0.00395
<i>Mayflower I</i>	101	0.00309	0.00321
<i>Fortune</i>	36	0.00240	0.00293
<i>Anne and Little James</i>	88	0.00513	0.00466

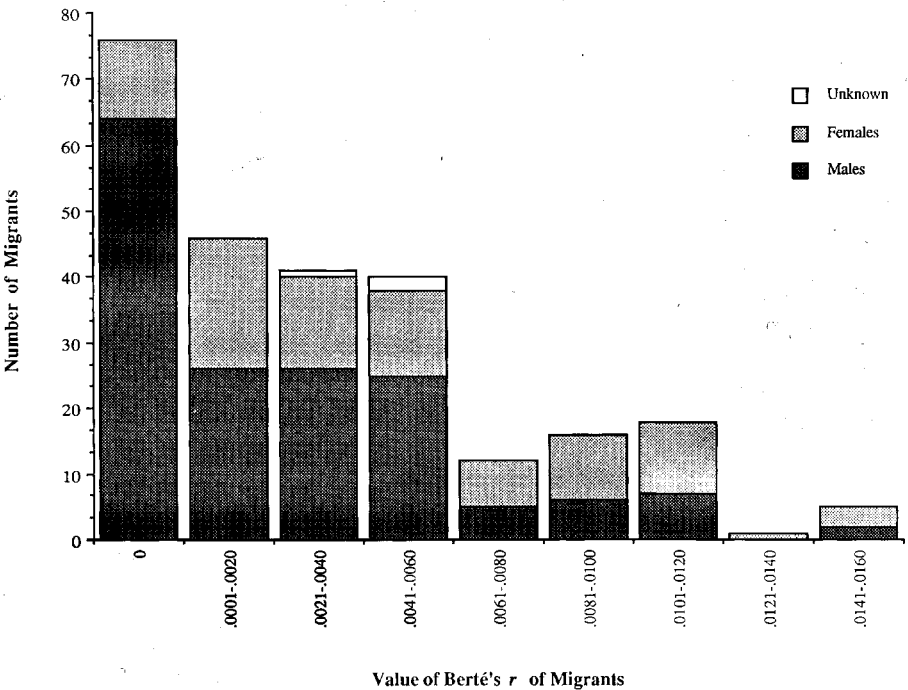


Figure 1. Distribution of relatedness values of Plymouth Company migrants, 1620-1633.

member, and the highest individual F_g value is 4.0, corresponding to an r of 0.01575. The mean value of r for the entire Company was 0.00399 (S.D. = 0.00395). The modal category is 0, which then decays erratically to a frequency of less than 1% (Figure 1). The exact shape of the decline cannot be determined because of small sample size and shallow genealogic depth.

Table 2. Classes of Relationships Found for Males and Females of Plymouth Colony, 1620-1633

	<i>Males</i>	<i>Females</i>	<i>Total</i>	
	<i>n</i>	<i>n</i>	<i>n</i>	%
Son	37	32	69	11.9
Daughter	37	35	72	12.4
Father	37	37	74	12.8
Mother	32	35	67	11.6
Brother	42	32	74	12.8
Sister	32	66	98	16.9
Nephew	6	16	22	3.8
Niece	5	10	15	2.6
Uncle	6	5	11	1.9
Aunt	16	10	26	4.5
Cousin	25	19	44	7.6
Half-brother	2	3	5	0.9
Half-sister	3	0	3	0.5
Total	280	300	580	

The sex of the individuals could be determined for 91 females and 161 males, leaving only 3 undetermined. Males had a significantly lower mean value of r (0.00308, S.D. = 0.00349) than females (0.00557, S.D. = 0.00428) ($t = 4.71$, $p < 0.001$). As seen in Figure 1, the primary difference was the greater number of males who had no relations (64, 39.8%), whereas few females were unrelated (12, 13.2%); the difference in proportions is highly significant ($t = 5.05$, $p < 0.001$). If only those individuals who had relatives are considered, females still had a significantly higher mean relatedness (0.00641, S.D. = 0.00393) than males (0.00511, S.D. = 0.00312) ($t = 2.37$; $p < 0.05$).

The specific classes of relations that males and females had are similar in proportion (Table 2). One category that showed some deviation was like-sex siblings, as opposed to unlike-sex siblings. The sex ratio of siblings for males was 131.25 (42/32), whereas that for females was 48.48 (32/66). Conservatively assuming an expected sex ratio of 100.0, only the low sex ratio among females is significant ($\chi^2 = 11.8$, $p < 0.01$). Forty-four of the 66 sister-sister relationships were generated from the exclusively female sibships of the 5 Warren, 4 Carpenter, and 4 Collier sisters. For both sexes there was a higher proportion of links with nephews than nieces and with aunts than uncles, but, again, no differences were significant.

Females also have an absolutely greater number of kin links (300) than males (280) and a much higher proportion of links per person (3.30)

Table 3. Kinship Linkages within and between Voyages Showing Number of (1) Migrants with Kin Links, (2) Total Number of Kinship Links, and (3) Mean Value of F_g for the Kin Links for the *Mayflower I*, the *Fortune*, and the *Anne and Little James*

Ship Relations On	Ship Migrants Arrived On								
	<i>Mayflower I</i>			<i>Fortune</i>			<i>Anne and Little James</i>		
	(1)	(2)	(3)	(1)	(2)	(3)	(1)	(2)	(3)
<i>Mayflower I</i>	62	132	0.996	2	6	1.500	16	39	0.914
<i>Fortune</i>				13	20	0.769	15	19	0.500
<i>Anne and Little James</i>							60	190	1.442

than males (1.74). The resultant ratio of kin links for females to males is 1.90 [$p < 0.01$, using the ratio test of Bailar and Ederer (1964)].

Kin-Structured Migration. The migration to Plymouth occurred over a period of 13 years. Within that time there were three major shipments of people carried on the *Mayflower I* (1620), the *Fortune* (1621), and the *Anne and Little James* (1623), plus other ships with small numbers of passengers. It is thus possible to test for a short-term time trend in kin-structured migration during settlement. However, as seen in Table 1, no clear time trend for level of relatedness is evident.

The same three-stage migration data were used to test for evidence of Fix's (1975, 1978) kin-structured migration within and between voyages. Three measures of linkage were used to test the hypothesis: (1) the number of individuals on the passenger list who had any kin in that or an earlier boat, (2) the number of relational ties between those with links and others on that or an earlier voyage, and (3) the mean individual F_g value of those links.

The number of relatives within a voyage was generally higher than the number of relatives in subsequent voyages (Table 3). Sixty-two of the 101 *Mayflower I* passengers (61.4%) had relatives on the ship. For the *Fortune* the numbers and percentage are lower (13 and 37.1%, respectively) but increase again on the *Anne and Little James* (60 and 60.6%). Relations and links between voyages were weaker than within voyages. Only 2 of the 34 passengers on the *Fortune* (5.7%) had relatives on the *Mayflower I*. There were only 16 onboard the *Anne and Little James* with kin ties to *Mayflower* passengers (16.1%) and 15 (15.2%) with ties to *Fortune* passengers. Clearly, kin-structured migration is most important for those migrating together, although there is a definite attraction for relations migrating later. The number of kin links and mean individual F_g values of passengers are given in Table 3.

Discussion

The total community relatedness value of 0.00399 is very low compared with values from more traditional small "anthropologic" communities (Leslie and Gage 1989). Values for $F_{g(\text{ALL})}$ among Yanomamö villages varied from 0.058 to 0.118 and averaged 0.086 (Chagnon 1988, p. 987), and the mean coefficient of relationship values (F_g) among the Nebraska Amish of Pennsylvania were 0.0648 for the parent group and 0.0767 for the daughter groups (Hurd 1983). Mange (1964) found that for the 68 minimal "founders" of the S-Leut Hutterites there were 5 sib, 33 half-sib or uncle/nephew, and 24 first-cousin relationships. He calculated the average genetic covariance (R) to be 0.0060; however, this measure is not directly comparable to average relatedness because of a series of exclusions imposed on the sampling procedure, and, like the Amish results, differing methods of calculating relatedness make exact comparison difficult. The Plymouth r values are almost an order of magnitude below those of modern K'ekchi' village males ($r = 0.033$) reported by Berté (1988).

The distribution of relatedness values for migrants was J-shaped, with 0 as the modal category followed by a steep decline. This contrasts with the distribution of inbreeding coefficient values in founders of the S-Leut Hutterites, where the mode is well above 0 and the curve shape is positively skewed. Although many individuals of the Hutterite population who subsequently did not contribute genetically to the community were excluded from consideration, the Hutterites had already spent time together as a genetic isolate and were more genetically unified than emigrants to Plymouth. The history of the colonists and, to a lesser degree, the shallowness of genealogic depth are largely responsible for the low relatedness.

The Plymouth Colony originated from the desire of religious zealots to flee from English law. Separatists, who desired to found a new church, and Puritans, who more conservatively wished to "purify" the existing Church of England by removal of Catholic practices, were part of a small but geographically broad movement (Chadwick 1972, pp. 175–187). As such, colonists originated in different areas of England rather than from a single community. Although it is usually assumed that most migrants to New England came from eastern England, such as Yorkshire, Norfolk, Suffolk, Essex, Nottinghamshire, and Cambridge (McCrum et al. 1986, pp. 115–120)—Cambridge University was the intellectual center of Puritanism—there were many from other areas, for example, Gloucestershire and Devon. In addition, some fled to the more congenial legal atmosphere of Holland and acquired adherents; thus two emigrants are Netherlanders and one is a Walloon. Many *Mayflower* crew members, servants, and hired hands were not members of the religious movement

at all, but the non-Puritan financial backers of the voyages insisted on including a substantial number of workers who had no particular interest in the colony beyond employment or economic opportunity (Cressy 1987, pp. 37–73). Last, it is becoming clear that mobility in Europe after the breakup of feudalism was much higher than expected (Flinn 1981, pp. 65–75; Bailyn 1988, pp. 20–26), so that average relatedness for most English communities may have been lower than for the Yanomamö, Hutterites, K'ekchi', or other isolates to begin with. Because of the varied origins of passengers, relatedness values would probably not increase dramatically, even with greater genealogic depth than the four generations available here.

Previous studies have typically found a higher degree of relatedness among males than females [e.g., Hurd (1983)], as most groups thus far studied are patrilineal or at least patronymic, and Neel (1967) coined the term "lineal effect" to describe this biased migration pattern. The Plymouth sample shows a higher value of r for females. One reason is that almost half the males are unrelated to anyone. Some of these unrelated males arrived on the *Mayflower I* as hired hands, servants, or sailors, and a substantial proportion became part of the sample because they died before returning on the next voyage to England; others were the hired workers or merchant adventurers of later voyages. However, even if unrelated individuals are ignored, the females have a slightly and significantly higher value of r . Although the sample is small, it is apparent that female and male kin links must have been important. Even with only about half as many individuals, females had a greater number of kin links than males, suggesting an intensified pattern of female-based kin-structured migration. Given the essentially cognate nature of lower- and middle-class English-American kinship nomenclature [e.g., Read (1984)], this result is not unexpected. Suarez and Hampe (1990) also found that fissioning among midwestern US Amish Mennonites resulted in higher values of ϕ between females than between males.

Fix's (1978) kin-structured migration is strongly evident among those arriving on the same voyage and more weakly evident among those between voyages. Nuclear families tended to migrate together, which would increase individual r values for the same voyage, but there was also an obvious lag effect in that relatives of earlier migrants were found on later ships.

Cressy (1986, 1987, pp. 263–291) demonstrated the importance of kinship relations in contemporary England. Consanguineous and affine ties were regularly invoked to secure favor and advantage in establishing and maintaining ties between England and New England, including such distant relations as siblings of a spouse's former spouse. Once established, the cousinage relationships were important, especially in wealthier families, beyond the end of the century. Cressy (1987, pp. 46–

50) also described family-based communication networks that served to induce relatives, friends, or servants to emigrate. Thus kin-structured migration persisted at least to 1633.

Last, it should be mentioned that the relatedness values presented here for migrants may not be the effective values (Mange 1964) for the early colony. More than half of the *Mayflower* group died during the first winter, and lack of relatedness was a common factor among those who died (McCullough and Barton 1991), leaving survivors who were more interrelated than the original full company of migrants. Although there was never another crisis year of this magnitude, some founders later died without issue, remigrated, were hanged, or simply never married, and it is unlikely that this selection process was random (McCullough 1990).

After arriving, the colonists, along with their neighbors of the Massachusetts Bay Colony to the north, formed an isolated but enlarging socioeconomic community and genetic population (Demos 1965, 1970). From surname analysis it seems probable that the small number of early migrants and favorable demographic conditions created small communities that shared many intertwining kinship links (Smith 1989). Further study may show relatedness values approaching those of other traditional, small anthropologic communities within a few generations (Leslie and Gage 1989), although there are other indications that high European mobility transported easily to the Americas (Bailyn 1988, pp. 20–26, 91–95). We are now pursuing this possibility for Plymouth Colony using genealogic records and surname analysis.

Conclusions

Most of the emigrants to Plymouth Colony were related to at least one other passenger, although there was a substantial proportion of those with no relatives. The largest number of kin links and the highest value of the relatedness coefficient (r) occur among females. Thus, although men organized the expedition, the personnel were more strongly and consistently related through female lines.

Fix's kin-structured migration is strongly supported, even though the majority of kindred migrated together as families in the same voyage rather than serving as attractions for other relatives in subsequent voyages. Because most of the kin links were restricted to those within the nuclear family, this finding is expected.

Even in this situation of migration planned for economic and religious purposes, nearly 70% of the emigrants were accompanied by relatives. However, the average relatedness is low to moderate, much below relatedness values for more traditional anthropologic communities involved in fissioning, such as the Yanomamö, and probably below those communities eventually formed from this early nucleus (Smith 1989).

The genetic implication of these results is that the founding population of Plymouth was composed of individuals related by many close but not extensive consanguineous ties. The low average relatedness in this population suggests that the assumption of nonrelatedness is not seriously violated.

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