Supporting Information

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SI Text 1

Population of Ile aux Coudres. ***Historical landmarks and demography.*** The history of the island can be divided into the three main periods (1) presented below.

1728–1790: foundation and population. The first settlement on île aux Coudres was prompted by increasing demographic pressure from nearby riparian parishes along the St. Lawrence River. At the time of the foundation, the Québec territory was structured according to the "*Seigneurial*" system of land distribution. Under this system, the land remained the property of the king of France. A given piece of land (here the island) was attributed to a *seigneur* (lord), who then subdivided it among tenants (the peasants). The tenants concluded a contract with the lord whereby they were allowed to settle on typically long and narrow strips of land, the *concession*, and to exploit them for their own subsistence. In return they paid taxes (i.e., products of agricultural, fishing, or other activities) to the lord.

The lord of île aux Coudres was not a single person but a society of priests who managed the Québec seminary. They did not inhabit the island. The island's population was founded by a total of 30 couples/families who immigrated between 1720 and 1773 (1, 2). The land was divided evenly among these families. The population grew steadily until 1790 (Fig. S1). Whereas immigration constituted the main source of new households, especially before 1765, local reproduction contributed the major part of the population's rapid subsequent growth (the first recorded births on the island occurred as soon as the 1720s) (3).

1790–1870: demographic "stability." The island became saturated around 1790 because all of the land had already been divided among tenants. Any further attribution could only proceed at the expense of the division of a formerly established estate. When this occurred, it generally implied a father transferring part of his land to a child. Because of this saturation, the growth of population slowed down for about 80 y, but it did not stop, even though the period is designated as one of "demographic stability" by Martin (1) (Fig. S1). This lower growth was essentially the result of emigration of young people (15–30 y old). Fertility rates remained high (1) (Fig. S3) and were comparable to those typical of the province of Québec (4).

1870–1950s: demographic "expansion." After 1870, emigration decreased as a consequence of the progressive diversification of occupations that resulted in an increase in the carrying capacity of the island (see below). This resulted in an acceleration of population growth relative to the former period.

Occupations. From 1720 to 1870, the economy was based essentially on subsistence farming. Interdependency networks constituted a central element of the rural economy. Nearly all heads of household were farmers, and the production relied on the extended family. Thus, brothers, uncles, cousins, and sometimes neighbors participated in activities necessitating important labor (5).

A few other professions were also reported on the island, such as the priest and some handicraftsmen. Farmers often did other complementary activities such as fishing, milling, or navigation in the area (1, 2). The St. Lawrence River being agitated by very strong currents on the northern part of the island, farmers were often hired by foreign captains to pilot their ships up to Québec City harbor as early as the 18th century (6). These activities provided extra resources for subsistence or as income that could serve in building a heritage for all children (see below).

After 1870, nonagricultural activities undertook some expansion (3). Navigation progressively gained in importance. Islanders used sailing boats (schooners) to provide good transportation services along the St. Lawrence River. Sons of farmers who could not follow their fathers' living style because of the lack of land found increasing opportunities in seasonal labor (dockers, timbermen, or sailors) off the island. Therefore, instead of emigrating permanently as before, many could raise a family on the island, in a house built on a piece of land with no adjoining agricultural fields (3). This diversification of occupations took place slowly and accelerated around the Second World War (3). For couples retained in the subfecundity and migration datasets (*SI Text 2*), the profession of the male spouse, when declared, was farmer in 85% and 81% of the cases, respectively, with or without a second profession [sailor or laborer (7)].

Resources. Le Querrec (5) underlines that the distribution of the island territory provided each family with an optimal access to land and river resources. Agriculture was first dominated by wheat. Between 1830 and 1870, there was a shift in favor of the potato culture as the soil impoverished (3) (secondary cultures included oak, barley, and beans). Production was sufficient to feed the population and people were not living in poverty, but neither were they experiencing resource overabundance (2, 3).

Around the 1750s, the intertidal zone, which provided good-quality pasture, was split among the tenants (by the Québec seminary) in a way to equilibrate as much as possible the resources available to each family (2). A second split occurred in 1801. How the distribution of these patches changed later is unclear, but they remained the property of the Québec seminary until 1977 (5).

Fish were abundant around the island (eels, pilchards, cod, smelt, etc.). In particular, setups to catch eels during the fall surrounded the island. Each setup was managed by a team (often people from the same family), who paid part of their catch to the Québec seminary (2). Owing to the diversity of species caught and techniques used, fishing provided a steady input that helped to buffer the variations in agricultural production (5).

Sea mammals also constituted an important resource. Some seals were caught, but the main species hunted was the beluga (*Delphinapterus leucas*). This species furnished oil highly valued by the lords of the island. A bylaw promulgated by the lords stipulated the setting of four fishing units in which the inhabitants of île aux Coudres were roughly equally divided (2, 3). The revenues from this activity reached a peak between 1800 and 1830 and then declined, due to fluctuations in the abundance of belugas and in the market (3).

Wealth transmission. Desjardins-MacGregor (6) studied wealth transmission patterns at île aux Coudres before 1800. In brief, inheritance rules followed the legal tradition of the "Coutume de Paris," which stipulated an egalitarian split of wealth among the children. However, to secure a future to all their children, parents could not divide the land indefinitely. Therefore, they adopted various strategies. Typically, they selected one heir, often the eldest son (but not always), who inherited the land (this may have included a house, animal, or farm tools). Sometimes more than one child inherited the land, depending on the resources available to the family. Other children could inherit fishing shares or land patches located outside the island (bought by the parents for this purpose) and various possessions (e.g., boats). To achieve a fair split of the familial wealth, the child who inherited the land often had to compensate his/her sibs with some donation. Children who emigrated could use their part of the heritage to buy land outside the island. When the occupations began to diversify on the island (see above), small patches of land with no adjoining agricultural field represented another type of legacy, providing an opportunity for sons engaging in jobs other than farmer to raise their family on the island.

Patterns of marriage and kinship. Perron (8) studied marriage patterns at île aux Coudres from 1741 to 1971 and found that women born on the island were, in the majority, involved in endogamous unions because they had limited opportunities to meet men who were not from the island. Because of this endogamy and of the limited size of the population, kinship between spouses increased linearly with time (9). Here we shall distinguish between close and remote kinship. The threshold for defining close kinship corresponds to the minimal degree of relationship between spouses for which spouses needed a dispensation from the church to marry. Close kinship was defined differently over time: A dispensation was needed for fourth-level cousins (or more-related individuals) before 1917 and for third-level cousins (or more-related) after. These types of unions were avoided whenever possible. However, as a result of endogamy, the probability that two individuals shared at least one ancestor more than three generations in the past increased with time. Consequently, remote inbreeding became unavoidable: After 1800, more than 80% of marriages occurred between individuals related to some degree. By the 1950s, the average inbreeding coefficient of islanders reached 0.012, composed in the majority of the remote inbreeding component (9).

Selective context. The island experienced a natural fertility regime in the sense of an absence of sociocultural control on family size (i.e., non-Malthusianism). The onset of reproduction was determined by marriage and its termination by the menopause of the woman or the death of either spouse. Birth control methods were not in use (10). Until the end of the 19th century, the island did not differ from other French-Canadian communities in these respects (11).

The high fertility of French Canadians is sometimes attributed to the ascendancy of Catholic priests who, supposedly, discouraged couples from postponing the next conception beyond the amenorrhea period. However, the reality was likely more complex. Indeed, completed family sizes at île aux Coudres were comparable to those found in other non-Catholic Western societies at that time (12, 13). Nevertheless, the Catholic type of socialization based on the extended family probably contributed to postponing the decline in fertility of French Canadians relative to other Canadian populations during the first half of the 20th century (13). At île aux Coudres, fertility did not decrease as elsewhere but rather increased.

Within the context of natural fertility and population growth at île aux Coudres, earlier age at first reproduction (AFR) may have been advantageous in two ways: (*i*) because of its positive correlation with lifetime reproductive success (LRS) through fertility (as shown in this study); and (*ii*) through shorter generation times that may confer a selective advantage in expanding populations (14). However, regarding the first point, producing more children on the island implied that more of them would likely have to emigrate, in particular between 1790 and 1870 (see above). Therefore, if the number of children a woman had did not make a difference as far as the total number of them who were later able to settle on the island, then a higher LRS would not confer any selective advantage (at the scale of the island). Therefore, a long-term response to selection was only possible if the LRS of a woman correlated positively with the number of her female children who settled (i.e., married) on the island. This was indeed the case: Both traits were significantly correlated (subfecundity dataset: $r = 0.61$, $P << 0.0001$; migration dataset: $r = 0.53$, $P << 0.0001$). For the subfecundity dataset, the correlation was even greater for women married before 1870 ($r = 0.68$, $P << 0.0001$), that is, during the period when emigration was the most important, than afterward ($r = 0.58$, $P << 0.0001$). For the migration dataset, it was similar for both groups (before 1870: $r = 0.54$, $P << 0.0001$; after 1870: $r = 0.55$, $P << 0.0001$). This suggests that emigration did not impede the potential for a response to selection.

Theory predicts that the optimal age at maturity will depend not only on fecundity but on survival rates as well (15). Because LRS integrates both fecundity and viability components of natural selection, the very strong association between LRS and fertility suggests that viability selection was weak on AFR over the long term (assuming a positive correlation between fecundity and fertility). The particular context associated with population foundation, the pattern of resource distribution that prevailed on the island, and the fact that the population surplus was regulated by emigration perhaps contributed to level off variation in mortality risks among women (or their offspring) starting reproduction at different ages. Mortality rates were indeed lower on the island for the period 1790–1870 than in the rest of Québec (1).

SI Text 2

Data-Filtering Criteria Used in This Study. In this study, we filtered the data using the same set of restrictions as Boisvert and Mayer (16) in their study of inbreeding effects on infant mortality conducted on the same database. Among the 2,001 marriages reported in the île aux Coudres database for the period extending from 1728 to 1973, we kept only those celebrated after 1799, as the genealogical depth is highest after this date, and before 1940, to make sure that the couples retained had completed their family before the records ended. We also excluded those:

- *i*) without any recorded offspring, as the age at first (AFR) and last (ALR) reproduction of the wife is missing (by definition);
- *ii*) without an exact recorded date of marriage, as these marriages were possibly celebrated outside the island before the couple immigrated;
- *iii*) without a known month of birth for one or more of their children, as some of these children were possibly born outside the island;
- *iv*) with an unknown year of birth for the wife, as we wished to study age-related female life-history traits; and
- *v*) where the wife had been married more than once, to control for the confounding effects of multiple marriages.

This left us with a restricted dataset of 572 marriages with 4,002 offspring births. These numbers differ slightly from those of Boisvert and Mayer (16) owing to the continued effort to improve the linkage and precision of the records.

The dataset above is referred to as the *subfecundity hypothesis* (average female life-history traits in Table 1) because it assumes that the long birth intervals observed for some couples truly reflect a reduced fecundity. However, these intervals will be overestimated if some births went unrecorded, which can happen if a couple did not spend its entire reproductive life on île aux Coudres (7). Indeed, emigration was common after 1790 because of land saturation (1). Actually, 3.8% of the women showed an unusually long marriage–first birth interval (MFBI; >4 y; see below). Some of these longer intervals might reflect temporary emigration rather than delayed reproduction, in which case AFR would be overestimated. More importantly, the subfecundity hypothesis will underestimate the fertility and the LRS of couples who emigrated (temporarily or permanently; but see below) after the birth on the island of one or more of their children but before the end of their reproductive life (7).

Therefore, in addition to the previous restrictions, we generated a second dataset assuming that unusually long gaps between (*i*) marriage and first birth, (*ii*) two successive births, or (*iii*) the last birth and the end of reproductive life could be due to emigration. Here reproductive life was considered to end with the death of one of the spouses or when the wife reached 45 y old (i.e., the presumed age at menopause). Henry (17) proposed specific threshold values that define these "unusually long" intervals for a French preindustrial population. Boisvert (7) and Boisvert and Mayer (16) refined them for île aux Coudres by comparing the information from church registers with that of nominal censuses. This allowed them to verify, for a subset of marriages, whether the couple was indeed present on the island during a given long birth interval. Following these authors, we thus excluded couples in which:

i) the marriage–first birth interval was greater than 48 mo;
ii) at least one interbirth interval was greater than 48 mo, if the wife was under 35 y of age;
iii) at least one interbirth interval was greater than 84 mo, if the wife was over 35 y of age (because birth intervals increase with approaching menopause); and
iv) the interval between the last recorded birth and the time when the woman reached 45 y old was greater than 84 mo, if both spouses were known to have survived at least until the wife was 45.

This left 363 marriages with 3,110 offspring births for the *migration hypothesis* dataset (average female life-history traits in Table 1). This dataset considers the status of couples with long intervals as uncertain and excludes them. Although this largely corrects for the problem of unrecorded births (7), it also introduces a bias into our analyses. Because they will show at least one interval that is unusually long with respect to the above criteria, truly less fecund couples who never left the island will be excluded, causing the truncation of the lower end of the natural distribution of LRS. Evidence for the existence of such couples comes from the nearly twice longer average marriage–first birth interval in couples included in the subfecundity set but excluded from the migration set (Table 1). Given the respective advantages and drawbacks of the subfecundity and migration hypotheses, we conducted our analyses using both datasets.

Measure of lifetime reproductive success. We calculated the LRS of a woman (or, equivalently, of the couple) as the number of her children who survived to age 15 y old, that is, approximately the minimal age at marriage at île aux Coudres. Death events that occurred on the island were recorded in the church registers. Therefore, we assumed that individuals for whom no death record existed were either still alive in 1973 (i.e., the last year covered by the registers) or survived at least to age 15 and emigrated afterward [men generally emigrated between 15 and 30 y old and women between 20 and 30 y old (3)]. Under the migration hypothesis this assumption is reasonable because most, if not all, couples who emigrated during their reproductive life, probably taking young children with them, would be excluded from the analysis. However, considering the couples retained under the subfecundity hypothesis, it is possible that some children born on île aux Coudres emigrated with their parents. If some of them died off the island before age 15, their births but not their deaths would appear in the register of île aux Coudres. This would inflate the LRS of their mother. However, children in this situation are apparently too few to affect our conclusions, as attested by the similar path coefficients obtained in the phenotypic selection analysis under the subfecundity and migration hypotheses in the path analysis (*Materials and Methods*).

Depth of pedigree information. We used the entropy S and its variance (18) to measure the genealogical information available in the two datasets. Entropy is the expected number of generations separating an individual (i.e., one of the spouses) and a founder in its pedigree:

$$S = -\Sigma P_i \log P_i,$$

where P_i is the probability that a gene carried by this individual originates from the founder i, and where the log is in base 2. The deeper the pedigree, the higher S is. The variance in S provides an indication of the symmetry of the pedigree; a zero indicates that exactly the same number of ancestors is known for each generation back along maternal and paternal lineages. Average S was 4.6 generations with a Var(S) of 1.26 under both subfecundity and migration filtering. These values are taken from the complete pedigree of île aux Coudres and provide a measure of the information available to estimate inbreeding coefficients, although not all relationships will be informative to estimate genetic variance parameters.

1. Martin Y (1957) Île-aux-Coudres: Population and economy. *Cahiers de Géographie*, 2: 167−195 (in French).
2. Mailloux A (1998) *History of Ile-aux-Coudres* (Comeau & Nadeau, Montréal); reprinted (1879) (in French).
3. Richard C, Ayotte R (1964) *Ile-aux-Coudres: 1728–1961: A Demographic and Occupational Study* (Centre de Recherches en Sociologie Religieuse, Université Laval, Québec City) (in French).
4. Henripin J (1954) *The French-Canadian Population at the Beginning of the 18th Century* (Presses Universitaires de France, Paris) (in French).
5. Le Querrec J (1981) Ile aux Coudres: Towards an ethno-ecological divorce? *Anthropol Soc*, 5:165−189 (in French).
6. Desjardins-MacGregor L (1992) *Heritage transmission at Ile-aux-Coudres during the 18th century.* Master's thesis (McMaster University Hamilton, ON) (in French).
7. Boisvert M (1993) *Infant mortality and consanguinity in an isolated population in Québec.* Master's thesis (Université du Québec à Montréal, Montréal) (in French).
8. Perron M (2000) *Mating in the insular environment: Isle-aux-Coudres (1741–1971).* Master's thesis (Université Laval, Québec City) (in French).
9. Philippe P, Gomila J (1972) Inbreeding effects in a French Canadian isolate. I. Evolution of inbreeding. *Z Morphol Anthropol* 64:54−59.
10. Philippe P (1973) Statistical analysis of marriage–first birth and interbirth intervals at Isle-aux-Coudres. *Population (Paris)*, 28:81−93 (in French).
11. Henripin J (1957) From acceptance of nature to control: The demography of the French Canadians since the seventeenth century. *Can J Econ Polit Sci* 23:10−19.
12. Frisch RE (1978) Population, food intake, and fertility. There is historical evidence for a direct effect of nutrition on reproductive ability. *Science* 199:22−30.
13. Fournier D (1990) For the 'revanche des berceaux'? The sociability hypothesis. *Recherches sociobiographiques* 30:171−198 (in French).
14. Brommer JE, Merilä J, Kokko H (2002) Reproductive timing and individual fitness. *Ecol Lett* 5:802−810.
15. Stearn SC, Koella JC (1986) The evolution of phenotypic plasticity in life-history traits: Predictions of reaction norms for age and size at maturity. *Evolution* 40: 893−913.
16. Boisvert M, Mayer FM (1994) Infant mortality and consanguinity in an endogamous population in Québec. *Population (Paris)*, 49:685−724 (in French).
17. Henry L (1958) Intervals between confinements in absence of birth control. *Eugen Q* 5:200−211.
18. Kouladjian K (1986) *A Measure of Genealogical Entropy* (Société Interuniversitaire de Recherches sur les Populations, Université du Québec à Chicoutimi), Document III-C-43 (in French).
19. Philippe P (1969) *Inbreeding structure at Ile-aux-Coudres.* Master's thesis (Université de Montréal, Montréal) (in French).

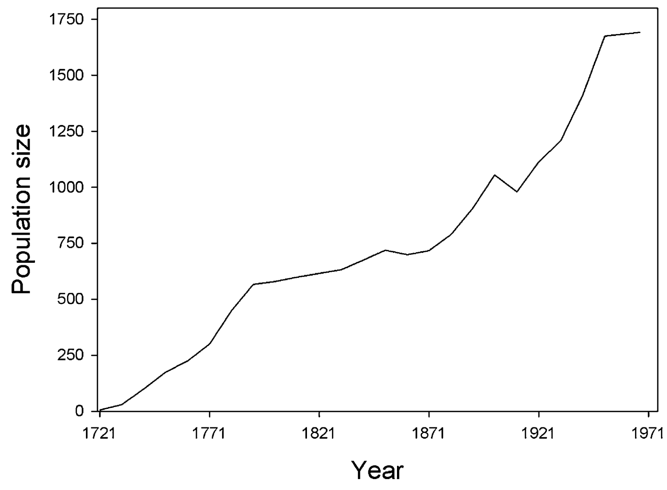

Fig. S1. Population size at île aux Coudres from foundation up to 1967. Canadian censuses were carried out every 10 y from 1851, and hence the time interval between each value used to build this graph was 10 y. For the period anterior to this date, the value for a given decade was extrapolated from censuses conducted by different authorities at varying intervals (1). The last census reported on this graph was conducted in 1967 by Philippe as part of his study on inbreeding (19).

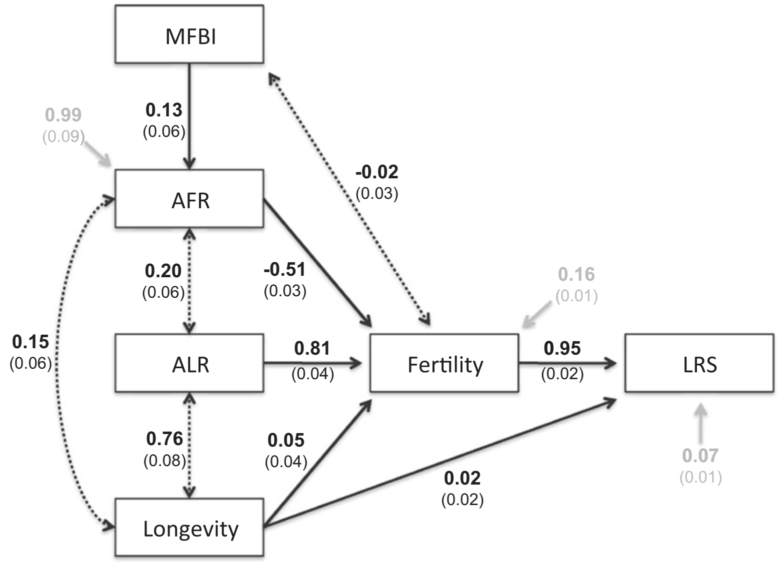

Fig. S2. Path diagram describing the selection exerted on female life-history traits at île aux Coudres. Results are for the migration dataset (n = 251; *Materials and Methods*). Values (±SEM) next to solid arrows are standardized regression coefficients (direct effects for selection gradients) and values next to dashed arrows are correlation coefficients. Values (±SEM) and arrows in gray are for unmeasured causes (residual variance) of endogenous variables. See Fig. 1 for further description of the diagram and the life-history traits. The path coefficients are similar to those obtained with the subfecundity dataset (Fig. 1) except for the direct effect of MFBI on AFR (0.13 instead of 0.30). This difference was expected because the migration dataset excludes many of the less fertile couples and therefore exhibits a lower variation in the MFBI (*SI Text 1*). Because MFBI has a direct effect on AFR (the latter being equal to age at marriage + MFBI), the limited variation in the former under the migration hypothesis will likely not be able to reveal the full effect of this trait on the latter.

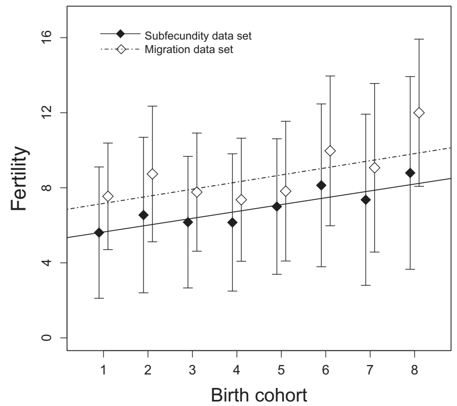

Fig. S3. Temporal trend in fertility (completed family size) in the population of île aux Coudres for couples married between 1800 and 1939. The average value (±SD) is shown for each of eight 20-y female birth cohorts for both the subfecundity (regression slope = 0.37, $P < 0.0001$) and migration datasets (slope = 0.38, $P = 0.0004$). See *SI Text 2* for a description of the two datasets.

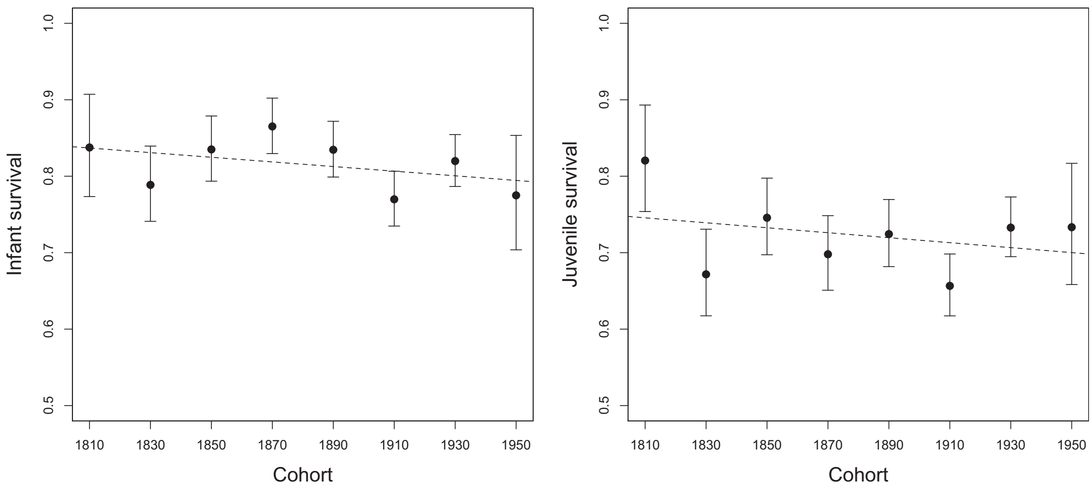

Fig. S4. Infant (0–1 y) and juvenile (0–15 y) survival (±95% confidence interval) at île aux Coudres for the offspring born to couples married between 1800 and 1939 (subfecundity dataset; *SI Text 2*). The year corresponding to the midinterval of a birth cohort is indicated on the *x* axis. Survival curves were fitted using data on the status (alive or dead) of 2,557 individuals when they last appear in the registers. Thus, for an individual whose death date is unknown, the last record attesting that he/she was very likely alive was used. This was either the date of his/her marriage or the date of birth of his/her last known child. Individuals with only one observation (i.e., their birth date) were considered to have lived at least 15 y (for a justification, see *SI Text 2*). Kaplan–Meier survival functions were fitted separately for eight 20-y cohorts using the Survival package in R (1). Survival curves differed significantly across cohorts ($\chi^2 = 40.3$, df = 7, $P < 0.0001$), but there was no evidence for a temporal (linear) trend in infant (regression slope = −0.006, $P = 0.28$) or juvenile (regression slope = −0.006, $P = 0.45$) survival.

1. Therneau T, Lumley T (2009) Package Survival (R Project; http://www.r-project.org), 2.35-7.

Table S1. Standardized linear selection differentials and gradients for female life-history traits in the preindustrial human population of île aux Coudres

Trait	Observed selection differential	Model-inferred selection differential	Direct selection gradient	Indirect selection
Marriage–first birth interval	−0.204	−0.057	−0.144	0.087
Age at first birth	−0.323	−0.314	−0.486	0.172
Age at last birth	0.747	0.667	0.707	−0.040
Longevity	0.595	0.422	0.084	0.338
Fertility	0.966	0.958	0.956	0.002

The observed selection differential is the empirical phenotypic correlation between the trait and fitness (LRS). Direct selection gradients were calculated by multiplying coefficients along each direct path between a life-history trait and lifetime reproductive success in Fig. 1 and by summing the value for all paths. Indirect selection was obtained similarly along indirect paths. Model-inferred selection differential is the sum of direct and indirect selection coefficients. As shown by this table, for all traits except marriage–first birth interval the observed selection differential was in large part explained by the model-inferred selection differential. The selection gradients on both age at first reproduction and age at last reproduction are larger than the selection differentials, because the direct selection on one trait was counterbalanced by selection on the other trait. Goodness-of-fit tests indicate a good fit of the model [$\chi^2 = 9.14$, df = 5, $P = 0.10$; adjusted goodness-of-fit index = 0.954; root mean square error of approximation (RMSEA) index = 0.054].

Table S2. Path analyses of selection on female life-history traits at île aux Coudres

	Selection gradient or correlation coefficient			
	Subfecundity dataset		Migration dataset	
Traits	1800–1870 *n* = 125	1871–1939 *n* = 158	1800–1870 *n* = 118	1871–1939 *n* = 133
MFBI > AFR	0.22 (0.09)	0.37 (0.07)	0.07 (0.09)	0.18 (0.09)
AFR > fertility	−0.57 (0.05)	−0.50 (0.04)	−0.56 (0.04)	−0.49 (0.03)
ALR > fertility	0.78 (0.06)	0.68 (0.06)	0.86 (0.06)	0.76 (0.05)
Longevity > fertility	−0.04 (0.06)	0.15 (0.06)	−0.04 (0.06)	0.13 (0.05)
Fertility > LRS	0.94 (0.03)	0.97 (0.02)	0.94 (0.03)	0.96 (0.03)
Longevity > LRS	0.03 (0.03)	0.02 (0.02)	0.02 (0.03)	0.03 (0.03)
MFBI <> fertility	−0.01 (0.05)	0.01 (0.04)	−0.03 (0.04)	−0.01 (0.03)
AFR <> ALR	0.21 (0.09)	0.18 (0.08)	0.20 (0.09)	0.18 (0.09)
AFR <> longevity	0.13 (0.09)	0.16 (0.08)	0.11 (0.10)	0.18 (0.09)
ALR <> longevity	0.62 (0.11)	0.71 (0.10)	0.74 (0.11)	0.78 (0.11)

Path analyses conducted separately for couples married before 1870 (demographic "stability" period; *SI Text 1*) and after 1870 (demographic "expansion" period). Results are shown for both the subfecundity and migration datasets (*SI Text 2*). The sample size is indicated at the top of each column. The values reported (±SEM) are standardized regression coefficients (i.e., selection gradients) for pairs of traits related by one-way arrows and correlation coefficients for pairs of traits related by two-way arrows. Life-history traits are: AFR, age of the woman at first reproduction; ALR, age of the woman at last reproduction; longevity, woman's lifespan; fertility, completed family size; LRS, lifetime reproductive success; MFBI, marriage–first birth interval.