Evidence for evolution in response to natural selection in a contemporary human population

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It is often claimed that modern humans have stopped evolving because cultural and technological advancements have annihilated natural selection. In contrast, recent studies show that selection can be strong in contemporary populations. However, detecting a response to selection is particularly challenging; previous evidence from wild animals has been criticized for both applying anticonservative statistical tests and failing to consider random genetic drift. Here we study life-history variation in an insular preindustrial French-Canadian population and apply a recently proposed conservative approach to testing microevolutionary responses to selection. As reported for other such societies, natural selection favored an earlier age at first reproduction (AFR) among women. AFR was also highly heritable and genetically correlated to fitness, predicting a microevolutionary change toward earlier reproduction. In agreement with this prediction, AFR declined from about 26–22 y over a 140-y period. Crucially, we uncovered a substantial change in the breeding values for this trait, indicating that the change in AFR largely occurred at the genetic level. Moreover, the genetic trend was higher than expected under the effect of random genetic drift alone. Our results show that microevolution can be detectable over relatively few generations in humans and underscore the need for studies of human demography and reproductive ecology to consider the role of evolutionary processes.

reproductive timing | heritability | *Homo sapiens* | life-history traits | lifetime reproductive success

Darwinian evolution is often perceived as a slow process. However, there is growing awareness that microevolution, defined as a genetic change from one generation to the next in response to natural selection, can lead to changes in the phenotypes (observable characters) of organisms over just a few years or decades (1, 2). This likely applies to humans as well because (*i*) natural selection operates on several morphological, physiological, and life-history traits in modern societies through differential reproduction or survival (3, 4), and (*ii*) a number of these traits show heritable genetic variation (4–7), attesting the potential for a microevolutionary response to selection. This evolutionary potential of modern humans has major implications. First, it signifies that we should consider the role of evolutionary processes that might underlie any observed trends in phenotypes. Second, it may produce eco-evolutionary feedbacks modifying the dynamics of modern populations (2, 8). This also means that the accuracy of forecasts, for instance those pertaining to demography or epidemiology, and on which public policies may rely, could well depend on our knowledge of contemporary evolution.

However, identifying which traits are evolving in which population is technically difficult. First, it requires information on phenotype, pedigree links, and fitness over a sufficient number of generations (9), which is rarely available. Second, robustly demonstrating a response to selection is challenging. Typically, phenotypic trends observed in populations are compared with evolutionary predictions based on selection and heritability estimates, for example, using the breeder's equation (10, 11). However, selection measured at the phenotypic level does not necessarily imply a causal relationship between the trait and fitness (12, 13) and, as a consequence, such predictions will often be inappropriate in the case of natural populations (14). This also implies that phenotypic changes, even those occurring in the predicted direction, may not provide robust evidence of evolution, as they may not be indicative of underlying genetic trends (15–17). These problems are likely exacerbated in long-lived species such as humans, where within-individual plastic responses to environmental variation, or viability selection, can drive phenotypic changes over the timescale of a study in the same direction as that predicted for genetic responses to selection (15).

To overcome these problems, recent studies of wild birds and mammals have tested for microevolution by directly measuring changes in breeding values (16–22; see ref. 23 for a review). The breeding value (BV) of an individual is the additive effect of his/her genes on a trait value relative to the mean phenotype in the population, in other words the heritable variation that parents transmit to their offspring (11). In quantitative genetic (QG) notation, the phenotypic measurement can thus be written as $z_i = \mu + a_i + \varepsilon_i$, where μ is the population average, a_i is the breeding value of individual i, and ε_i is a residual term that may include environmental and nonadditive genetic effects and measurement error. By definition, observing a change in BVs in the direction predicted by selection would constitute direct evidence for microevolution. However, true BVs are not observable and must be predicted using QG models. Although a handful of studies have documented trends in predicted breeding values (PBVs) consistent with a microevolutionary response to selection (e.g., 19–21), it has become apparent that the statistical tests used in these studies were highly anticonservative (23, 24). Moreover, thus far studies have not excluded the possibility that observed genetic changes are similar to those expected under genetic drift, that is, the random sampling of genes between generations.

It follows that empirical support for microevolution from longitudinal studies of long-lived species remains sparse and controversial (15, 23). Here we investigate the genetic basis of age at first reproduction (AFR), a good candidate for an evolving trait in humans (4). We used a recently advocated Bayesian quantitative genetic approach (23) to test whether advancement in women's AFR that occurred over a 140-y period in a French-Canadian preindustrial population was attributable to microevolution. We uncovered a genetic response to selection in this key life-history trait, with potentially important demographic consequences for this population.

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Population of Ile aux Coudres

Ile aux Coudres is a 34-km^2 island located ~80 km to the northeast of Québec City along the St. Lawrence River (Canada). Thirty families settled on the island between 1720 and 1773 and the population reached 1,585 people by the 1950s (25) (Fig. S1). This population is ideal to study the genetic basis of life-history traits (LHTs) (Table 1). First, church registers provide exceptionally detailed records of dates of births, marriages, and deaths. Second, the long-term data and endogamy (marriages within the population) provide a deep and intricate pedigree to facilitate the separation of genetic and environmental influences on LHTs (26). Third, the population was very homogeneous among families, particularly in traits known to correlate with the timing of reproduction (social class, education, and religion) (3, 27). In addition, the split of resources among families was quite even due to the type of land distribution, and the number of professions was limited (*SI Text 1*). This relative homogeneity should minimize confounding socioeconomic or shared environmental influences within quantitative genetic analyses.

We examined the life history of women married 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 (in 1973). Following ref. 28, we used two different datasets that make different assumptions regarding unusually long interbirth intervals in the demographic records. The "subfecundity" dataset (n = 572 women) assumes that unusually long interbirth intervals reflect subfecundity. The "migration" dataset (n = 363 women) assumes that long intervals may also reflect emigration from the island and excludes families with such length intervals (see *SI Text 2* for data-filtering criteria and Table 1 for average life-history trait values).

Selection on Age at First Reproduction

The adaptive significance of the timing of reproduction is well-established within evolutionary biology (29), including in humans (30). In particular, selection in favor of earlier AFR has been previously documented in several pre- and postindustrial human societies (3, 4, 7, 27, 31). French-Canadian preindustrial societies exhibited a natural fertility, that is, non-Malthusian, regime (32). In the absence of birth control methods, the full reproductive potential of couples can be expressed. Consequently, earlier reproduction may lead to bigger family size and confer higher fitness, in particular at time of population expansion (33), provided that fertility correlates with fitness (*SI Text 1*).

On île aux Coudres, selection indeed strongly favored women with earlier AFR. A path analysis (34) accounting for selection on other life-history traits correlated to AFR showed a negative association between AFR and fertility (completed family size), whereas fertility is itself strongly associated with lifetime reproductive success [LRS; used as a proxy for fitness (4)] [results for the subfecundity dataset in Fig. 1 and Table S1; the migration dataset led to similar results (Fig. S2)]. Therefore, AFR is negatively associated with fitness through fertility (direct standardized selection gradient: –0.486; Table S1). There was also a positive association between age at last reproduction (ALR) and LRS (again through fertility), indicating a fitness advantage to women with longer reproductive lifespan (Fig. 1). However, the existence of an evolutionary tradeoff between reproduction and maintenance functions (35) is suggested by the positive phenotypic correlation between AFR and ALR (Fig. 1), meaning that women who began reproducing at a younger age also tended to stop at a younger age. As a result, selection on one trait was counterbalanced by selection on the other trait (Table S1). Marriage–first birth interval (MFBI), used as a proxy for fecundity (capacity to conceive; *Materials and Methods*), had a significant direct effect on AFR (Fig. 1), suggesting that the variation in AFR is partly due to variation in fecundity among women (or couples). However, MFBI was very weakly and not significantly correlated to fertility, suggesting that the reproductive lifespan has a greater influence on fertility than fecundity per se, or that factors other than fecundity (e.g., lactation amenorrhea) (36) had an important influence on the reproductive rates beyond the first child. Finally, longevity had a small direct effect on fitness but was under strong indirect and positive selection owing to its strong correlation with ALR (Fig. 1; Table S1).

AFR was significantly heritable, predicting a microevolutionary change toward earlier first reproduction given that the trait is under directional selection. We used a Bayesian implementation (37) of linear mixed-effects animal models (26) to estimate the heritability in AFR and LRS while controlling for the effects of shared familial environment, inbreeding, temporal trends, and whether a woman gave birth to twins (*Materials and Methods*). Heritability was high for AFR (0.30 and 0.55, depending on the dataset used) and low for LRS (<0.01 and 0.04; Table 2). The presence of a strong negative genetic correlation between AFR and LRS (Table 2) further supports the potential for a genetic response to selection (14), although some uncertainty is associated with this correlation resulting from uncertainty in estimates of the heritability in LRS in our models (*Materials and Methods*). The shared familial environment had a negligible effect on both traits (Table 2).

Genetic Response to Selection

Average AFR advanced from about 26 to 22 y over the study period (Fig. 2), therefore in the direction predicted by selection. We tested for a genetic response to selection by comparing temporal trends in the breeding values predicted by our Bayesian models (PBVs) with trends in breeding values randomly generated along the pedigree under a scenario of pure random genetic drift (RBVs) (23). We found a negative trend in PBVs that was steeper than expected under drift alone (Fig. 2). Remarkably, the estimated genetic change in AFR corresponded to a decline of up to 3 y between the first and last cohorts (Table 2), thus explaining a substantial part of the observed phenotypic change between 1800 and 1939.

Table 1. Average phenotypic values (±SD) for female life-history traits in the preindustrial human population of île aux Coudres

Trait	Migration dataset*	Subfecundity dataset	Women included under the subfecundity hypothesis only
Marriage–first birth interval (mo)	13.9 ± 6.2 (360)	17.8 ± 22.0 (564)	25.7 ± 34.6 (204)
Age at first birth (y)	23.4 ± 3.9 (363)	23.8 ± 4.3 (572)	24.5 ± 4.9 (209)
Age at last birth (y)	38.7 ± 6.7 (363)	36.1 ± 7.3 (572)	31.6 ± 6.1 (209)
Longevity (y)	56.9 ± 22.2 (252)	58.2 ± 21.6 (301)	65.1 ± 17.0 (49)
Fertility (completed family size)	8.6 ± 3.9 (363)	7.0 ± 4.1 (572)	4.3 ± 2.9 (209)
Lifetime reproductive success (offspring living to age 15)	7.0 ± 3.4 (363)	5.1 ± 3.5 (363)	3.5 ± 2.6 (209)

Sample size is in parentheses.
*See *SI Text 2* for dataset description.

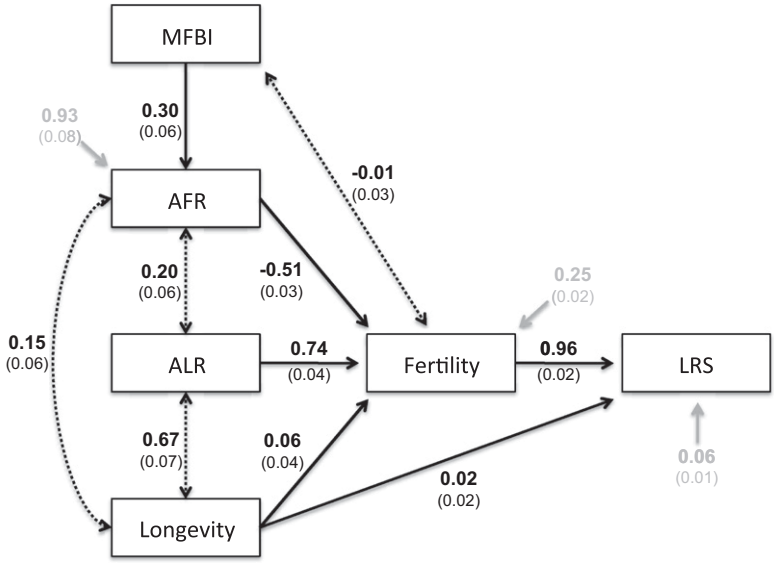

Fig. 1. Path diagram describing the selection exerted on female life-history traits at île aux Coudres. Solid one-way arrows show presumed causal relationships between variables, and dashed two-way arrows are noncausal correlations. Values (±SEM) next to solid arrows are standardized regression coefficients (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. Direct paths are those passing through causal relationships only (e.g., AFR > fertility > LRS), whereas indirect paths pass through at least one correlational relationship (e.g., AFR <> ALR > fertility > LRS). Life-history traits are: AFR, age of the woman at first reproduction; ALR, age of the woman at last reproduction; fertility, completed family size; longevity, woman's lifespan; LRS, lifetime reproductive success; MFBI, marriage–first birth interval. Results are for the subfecundity dataset ($n = 283$; *Materials and Methods*); the migration dataset led to similar path coefficients (Fig. S2).

Lifetime reproductive success showed a phenotypic increase by three to four children over the study period (i.e., from 4.7 to 7.9 children for the subfecundity dataset, and from 6.3 to 10.6 for the migration dataset; Fig. 2). Moreover, the trend in the PBVs of LRS was positive and steeper than expected by drift, suggesting a temporal increase in fitness under the effect of selection on AFR (Fig. 2).

The difference between the slopes in PBVs and RBVs was significant in the subfecundity dataset for both AFR and LRS ($P < 0.01$; Table 2). Using the migration dataset, the difference was nearly significant for AFR ($P = 0.058$) and the strong genetic trend in PBVs was quite robust to modifications of the model settings or Bayesian priors (*Materials and Methods*). However, the difference was not significant for LRS. Differences between the two datasets are likely to be due to the fact that, by definition, the migration dataset excludes a part of the natural life-history variation of the population (particularly in LRS), which likely reduces the power to measure heritability and detect a trend (*SI Text 2*).

Discussion

Throughout the history of île aux Coudres, there was a progressive advancement of age at first reproduction: Women giving birth to their first child around the 1930s were about 4 y younger than those who began to reproduce around 1800. There was a concomitant increase in lifetime reproductive success as women who began their reproduction earlier generally had more children surviving to adulthood. Whereas little information on AFR is reported for other Québec populations, the age at marriage of women apparently remained stable in the countryside and increased in urbanized areas (38). AFR likely followed the same historical pattern because it should correlate positively with age at marriage when marriage marks the onset of reproduction. On île aux Coudres, both traits were strongly correlated (sub-

Table 2. Genetic parameters and response to natural selection in woman's age at first reproduction and lifetime reproductive success at île aux Coudres between 1800 and 1939

		Heritability		Shared familial environment effects		Genetic correlation between AFR and LRS		Genetic response	
Dataset	Response variable	Mode	Interval	Mode	Interval	Mode	Interval	Trend PBVs	Prob. drift ≥ obs.
Subfecundity	AFR	0.55	0.30–0.90	0.01	0.00–0.15	−0.81	−0.97 to −0.48	−2.95	0.009
	LRS	0.04	0.00–0.43	0.00	0.00–0.07	—	—	+0.28	0.009
Migration	AFR	0.30	0.08–0.73	0.01	0.00–0.12	−0.81	−0.99 to 0.16	−1.74	0.058
	LRS	<0.01	0.00–0.12	0.00	0.00–0.02	—	—	+0.08	0.144

For heritability, shared familial environment effects, and genetic correlation, the mode of the posterior distribution (i.e., the point estimate of the parameter) and the 95% Bayesian posterior interval of highest density are reported separately for each dataset. The genetic correlation involves both traits and is only shown once for each dataset. The genetic response is the difference in mean PBVs between the first and last women's birth cohorts computed from the slope of the regression of PBVs on eight 20-y cohorts (means are over all women of a cohort and 1,000 MCMC samples). The trend in PBVs is in years for AFR and on the latent scale (Poisson model) for LRS. "Prob. drift ≥ obs" indicates the probability of observing a trend as strong or stronger due to random genetic drift alone (two-tailed test).

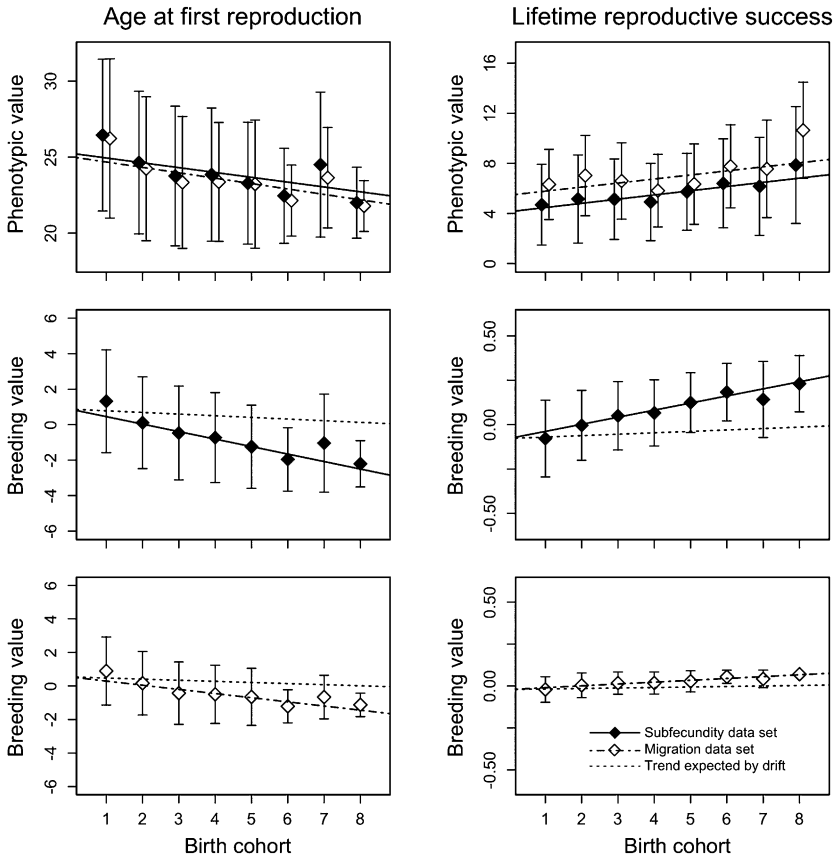

Fig. 2. Temporal trends in the phenotypic and breeding values of woman's age at first reproduction and lifetime reproductive success in the population of île aux Coudres between 1800 and 1939. All values are in years for AFR. For LRS, phenotypic values are in numbers of offspring reaching age 15, whereas PBVs are on the latent scale (Poisson model). PBVs are genotypic deviations from the population average over the study period [zero values correspond to no deviation; diamonds are averages from 1,000 MCMC samples (±SD)]. The genetic trend expected under random genetic drift alone (i.e., in randomly generated breeding values) is also shown by a dashed line. For the sake of visual comparison of slopes, the intercept of the drift trend was set to the same value as the intercept for the observed trend.

fecundity dataset: $r = 0.90$ [95% confidence interval (CI): 0.88–0.91]; migration dataset: $r = 0.98$ [CI: 0.98–0.99]). Moreover, the trend in LRS is associated with an increase in fertility, that is, completed family size (Fig. S3), which is also at odds with what is generally reported for Québec, especially in the first half of the 20th century (39, 40). Consequently, the trends in LHTs at île aux Coudres suggest that factors operated on the island in opposition to socioeconomic or cultural trends operational at a larger scale (39). Indeed, our results provide evidence that those changes resulted, at least partly, from a microevolutionary response to natural selection on AFR.

Crucially, the above conclusion relies on the reliability of PBVs. Here we used a Bayesian analysis intended to avoid the anticonservatism characterizing previous tests of microevolution (23, 24). One potential issue with this approach is its sensitivity in the choice of prior distributions for variance parameters (41). However, the test of microevolution in AFR was robust for various weakly to moderately informative priors. Another potential problem is that when limited information from relatives is available or when relatives share similar environments, PBVs can grasp part of the variation due to nongenetic sources (24, 42). However, the animal model is robust to this kind of bias when supplied with deep and intricate pedigrees because it uses all degrees of relatedness among individuals to estimate genetic parameters. In addition, nongenetic sources of variation can be accounted for explicitly. Here we controlled for temporal trends in traits that might arise from other causes than a change in BVs (24) and for shared familial environment effects that could bias heritability estimates. Actually, there is accumulating evidence that PBVs measured from such multigenerational pedigrees are measuring genetic effects (e.g., 43).

Nongenetic Hypotheses for Life-History Trends. Although the trend in breeding values we observed is consistent with a microevolutionary response to natural selection, other factors could nevertheless have contributed to the temporal trends in AFR and LRS. Most importantly, the advancement of age at maturity, as well as increases in fertility, may reflect plastic responses to improvements in nutritional conditions, such as those observed during the 19th and 20th centuries in Western societies. Better-fed women grow faster, mature earlier and in a better physiological state, and are more fecund (44). Importantly, alongside such plastic responses in reproductive traits, we would expect an increase in infant and juvenile survival rates with time (45). Despite some fluctuations, infant and juvenile survival rates on île aux Coudres were not higher at the end of the study period than at the beginning (Fig. S4). Furthermore, there is no evidence that the population underwent a demographic transition of the sort observed elsewhere during the 19th and 20th centuries. This would involve a decline in fertility and mortality alongside increasing urbanization, none of which occurred on île aux Coudres (Figs. S3 and S4; *SI Text 1*). Therefore, there is limited support for the idea that reproductive plasticity in response to changing conditions can explain the trends in LHTs we observed.

Whereas a vast majority of men were farmers before 1870, a diversification of occupations after that date progressively increased the carrying capacity of the island (*SI Text 1*). If it also meant more resource available per family, it perhaps contributed to the rise in fertility. However, we have no clear indication from the literature that this was the case. In addition, when considering couples married before and after 1870 separately, selection gradients on AFR, ALR, and fertility were in the same direction and of similar magnitude for the two periods (Table S2), indicating no substantial change in the selective regime after 1870. Reproductive compensation by inbred couples, which were hypothetically exposed to higher infant mortality, could have increased fertility rates (39) (note that we control for infant mortality in our selection analyses), but evidence for this hypothesis is inconclusive (28). Wealth transmission patterns possibly contributed to create within-family variation in life history (*SI Text 1*). However, this alone would not explain how a nongenetic effect could be strong enough to mimic a high heritability without being detectable as phenotypic resemblance among full sibs. Finally, cultural transmission of fitness (CTF) can cause nongenetic inheritance in human traits, and was documented in the nearby Saguenay-Lac-St-Jean French-Canadian population (46). However, we would have expected CTF to be partly reflected in family effects, which again were negligible in all of our analyses.

Life-History Evolution in Modern Humans. Very few empirical investigations of secular changes in life-history traits in humans have considered microevolutionary hypotheses. Certainly, these should not be discarded a priori simply because an immediate nongenetic explanation may exist. In particular, natural selection on reproductive timing appears to be widespread in humans, whereas AFR was found to be heritable in several contemporary populations, with an across-study average of 0.11 (4). Moreover, at least one other study uncovered a negative genetic covariance between AFR and LRS [in an American population (7)], which is a better predictor of the response to selection than the breeder's equation (14). Clearly, the potential for genetic responses of the kind observed here is not just limited to the île aux Coudres population. However, only through the wider application of the approaches used here to other human populations can we establish their generality.

Our study, as well as previous investigations, raises the question of why a trait like AFR would be heritable. Actually, heritable traits such as growth rate and birth weight likely correlate positively with age at maturity in humans (44, 45). Age at menarche could play a pivotal role here, as it also correlates with these traits on the one hand (e.g., 47) and with both age at marriage and AFR in human societies with drastically different cultures (48). Incidentally, age at menarche was repeatedly found to be heritable (typical heritability around 0.5) (49).

Our study supports the idea that humans are still evolving. It also demonstrates that microevolution is detectable over just a few generations in long-lived species. For instance, a large proportion of the phenotypic trend in age at first reproduction at île aux Coudres appears to be attributable to a response to natural selection. Modifications in the timing of reproduction can have important effects on the demography of a population (e.g., 50). Therefore, human studies need to carefully consider the role of microevolutionary processes underlying any observed trends in traits and their potential feedback on population dynamics.

Materials and Methods

Lifetime Reproductive Success. We calculated the LRS of a woman 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 (see *SI Text 2* for further details).

Phenotypic Selection Analysis. We fitted univariate general linear models (GLMs) for women's fertility (completed family size) and LRS to control for temporal fluctuations and other sources of variation based on preliminary analyses of the data. We thus controlled for year of marriage, whether or not a couple gave birth to twins, and infant mortality (0–1 y). Inbreeding is a structural characteristic of the population of île aux Coudres (51) and shows complex relationships with LHTs (28, 52). Therefore, we also included linear and quadratic terms of kinship between spouses (i.e., the inbreeding coefficient of their children). We also controlled for the common familial environment shared by sisters (random effect) but dropped this term because of its small and nonsignificant effect. The analysis was conducted on women for which longevity was known and data were available for all other traits (subfecundity dataset: $n = 283$; migration dataset: $n = 251$; *SI Text 2*). We used the residuals of fertility and LRS from the GLMs in a path analysis (34) of phenotypic selection on correlated traits (53) using LRS as a fitness proxy (an analysis on raw data instead gave very similar results but yielded models with slightly poorer fit; hence, we only report the results for the analysis on residuals). We conducted the analysis using the SEM package for R (54) and the path model described next.

We built a modified version of a path diagram of causal relationships between female life-history traits and fitness that was applied by Pettay et al. (3) to a Finnish population. In this model (Fig. 1), AFR, ALR, and longevity have direct effects on fertility and an indirect effect on LRS through fertility. Longevity also has a direct effect on fitness because it may affect the duration of parental care, and thus offspring survival. AFR, ALR, and/or longevity are expected to be correlated (35), and thus these correlations were included in the path diagram. One distinction with Pettay et al.'s original model is the exclusion of the proportion of surviving offspring, because its effect should be mainly mediated through interbirth intervals. Mean interbirth interval (MIBI) is itself the product of other traits already included in the model: MIBI = (ALR – AFR)/fertility. Another distinction with Pettay et al.'s model is the inclusion of the MFBI as a trait correlated to fertility (i.e., noncausal). The rationale is that MFBI reflects fecundability to some degree (i.e., the probability of conceiving in a given month) (39), as opposed to interbirth intervals, which also depend on lactation amenorrhea (36) and perhaps on care demands by older children. In turn, fecundability should be tightly related to fecundity, the physiological capacity to conceive. Consequently, MFBI is perhaps the best proxy that we have for fecundity for the île aux Coudres population (i.e., MFBI should decrease with increasing fecundity).

Estimation of Genetic Parameters. We fitted bivariate "animal" models (26), a type of generalized linear mixed-effects model (GLMM), to estimate the additive genetic variance (V_a) of AFR and LRS and their genetic correlation, as well as the breeding values for each woman. The animal model uses the information from all pedigree relationships to specify the expected phenotypic resemblance between relatives. It has several advantages for the study of wild populations, including its power to separate environmental from genetic sources of resemblance between relatives (especially with an intricate pedigree structure), its applicability to unbalanced sampling designs, and its robustness to departures from distributional assumptions (11, 26). The Bayesian implementation of GLMMs in the MCMCglmm R package (37) was used to fit models independently for the subfecundity and migration datasets. Again, we controlled for temporal trends of environmental origin by entering the year of marriage (24) and for inbreeding (quadratic effect). Whether a woman gave birth to at least one pair of twins was found to affect LRS in the above GLMs, and hence this factor was entered in the LRS models. We controlled for the familial environment shared by sisters (V_{CE}) by entering the marriage identification of the woman's parents (here confounded with maternal effects because only full sibs are known in this population). The distribution of AFR was modeled as Gaussian and that of LRS as Poisson. Samples were taken from the posterior distributions of V_a, V_{CE}, and the residual variance (V_r) every 7,500 iterations of the Markov chain after an initial burn-in of 1,500,000 iterations, for a total of 1,000 samples. For each Markov chain Monte Carlo (MCMC) sample from bivariate models, the narrow-sense heritability (h^2) of AFR was calculated as V_a/V_p, where $V_p = V_a + V_{CE} + V_r$ is the phenotypic variance, whereas h^2 of LRS was calculated on the latent scale as $V_a/(V_p + \ln(1/\exp(\beta_0)+1))$, where β_0 is the intercept of the Poisson model (55). The shared familial environment effects were calculated likewise, except that V_a was replaced by V_{CE} in the numerator. The genetic selection gradient is reported here in the standardized form of the genetic correlation (r_G). The posterior mode of h^2 and r_G was used as point estimates, whereas Bayesian 95% intervals of highest density were used to test whether these estimates differed significantly from zero.

Testing for an Evolutionary Response to Selection. We used a method recently advocated by Hadfield et al. (23) to test for a response to selection while accounting for drift: the posterior estimate of V_a from a given MCMC

sample from the bivariate model of AFR and LRS fitted above was used to randomly generate breeding values along the pedigree of île aux Coudres under a scenario of pure random genetic drift (RBVs), using the rbv function of the MCMCglmm package. Then, mean RBVs were regressed against cohort (eight 20-y cohorts), and the slope coefficient (β_{RBV}) was compared with that (β_{PBV}) of the regression of PBVs against the cohort for the same MCMC sample. This procedure was repeated for all MCMC samples. The proportion of times where the absolute value of β_{RBV} was as high or higher than the absolute value of β_{PBV} was taken as the probability of obtaining the observed genetic trend (i.e., in PBVs) as the result of drift only (i.e., two-tailed test).

Bayesian Prior Choice and Testing. Several priors were tested to finally retain the least informative ones leading to proper posterior distributions for variance parameters in the Bayesian models. Thus, in bivariate models, we used moderately informative priors: Variance parameters (*V*) were set to 1 (and covariances to zero) and the degree of belief (*nu*) to 2. We also ran univariate models with various weakly informative priors (e.g., $V = 1$, $nu = 0.002$). The trend in PBVs of AFR was robust and significantly higher than drift whatever the priors used in uni- or bivariate models (except for the migration model in Table 2, where the trend is close to significance: $P = 0.058$). The trend in PBVs of LRS was always higher than expected by drift but not always significantly so. This greater fluctuation of LRS with prior choice is likely explained by the fact that the heritability of LRS is low and because Bayesian parameter estimation is more difficult in those cases.

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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.

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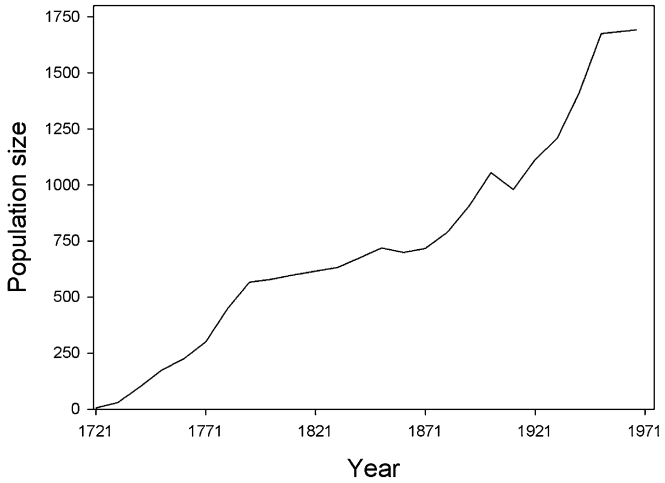

Fig. S1. Population size at île aux Coudres from foundation up to 1967. Canadian censuses were carried out every 10 y from 1851, and hence the time interval between each value used to build this graph was 10 y. For the period anterior to this date, the value for a given decade was extrapolated from censuses 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).

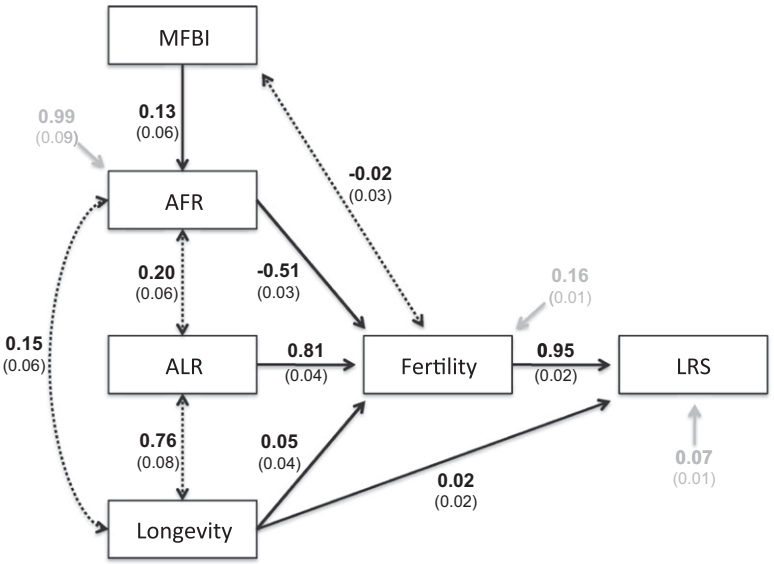

Fig. S2. Path diagram describing the selection exerted on female life-history traits at île aux Coudres. Results are for the migration dataset (n = 251; *Materials and Methods*). Values (±SEM) next to solid arrows are standardized regression coefficients (direct effects for selection gradients) and values 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.

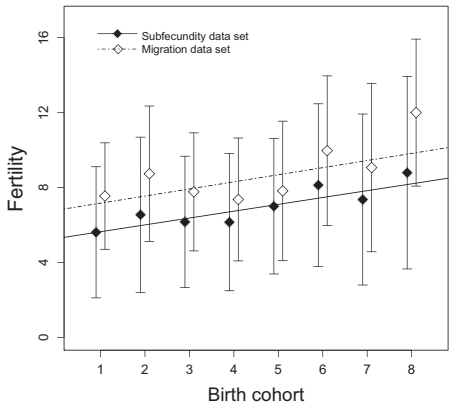

Fig. S3. Temporal trend in fertility (completed family size) in the population of île aux Coudres for couples married between 1800 and 1939. The average value (±SD) is shown for each of eight 20-y female birth cohorts for both the subfecundity (regression slope = 0.37, $P < 0.0001$) and migration datasets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

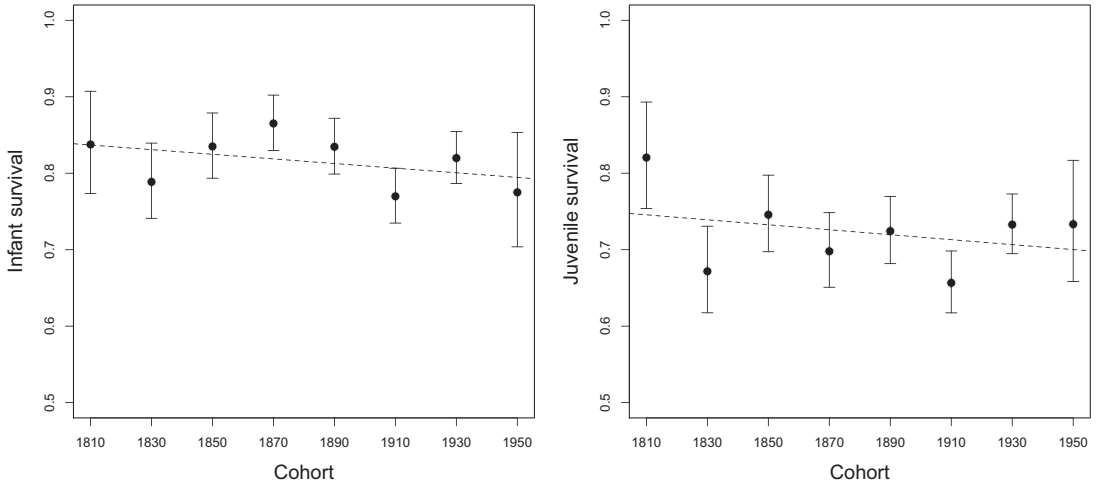

Fig. S4. Infant (0–1 y) and juvenile (0–15 y) survival (±95% confidence interval) at île aux Coudres for the offspring born to couples married between 1800 and 1939 (subfecundity dataset; *SI Text 2*). The year corresponding to the midinterval of a birth cohort is indicated on the *x* axis. Survival 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.