

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

Emmanuel Milot^{a,1}, Francine M. Mayer^a, Daniel H. Nussey^b, Mireille Boisvert^a, Fanie Pelletier^c, and Denis Réale^a

^aDépartement des Sciences Biologiques, Université du Québec à Montréal, Montréal, QC, Canada H3C 3P8; ^bInstitute of Evolutionary Biology, University of Edinburgh, Edinburgh EH9 3JT, United Kingdom; and ^cDépartement de Biologie, Université de Sherbrooke, Sherbrooke, QC, Canada J1K 2R1

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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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¹To whom correspondence should be addressed. E-mail: milot.emmanuel@courrier.uqam.ca.

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Population of Ile aux Coudres

Ile aux Coudres is a 34-km² 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 Ile 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 (\pm SD) for female life-history traits in the preindustrial human population of Ile aux Coudres

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

Sample size is in parentheses.

*See SI Text 2 for dataset description.

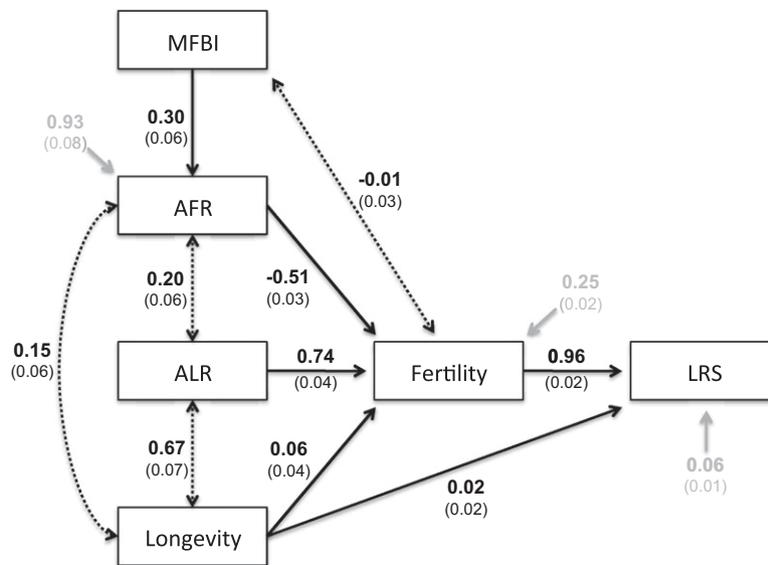


Fig. 1. Path diagram describing the selection exerted on female life-history traits at île aux Coudres. Solid one-way arrows show presumed causal relationships between variables, and dashed two-way arrows are noncausal correlations. Values (\pm SEM) next to solid arrows are standardized regression coefficients (direct effects for selection gradients), and values next to dashed arrows are correlation coefficients. Values (\pm 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 \rightarrow fertility \rightarrow LRS), whereas indirect paths pass through at least one correlational relationship (e.g., AFR \leftrightarrow ALR \rightarrow fertility \rightarrow 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

Dataset	Response variable	Heritability		Shared familial environment effects		Genetic correlation between AFR and LRS		Genetic response	
		Mode	Interval	Mode	Interval	Mode	Interval	Trend PBVs	Prob. drift \geq 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 response 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 \geq obs” indicates the probability of observing a trend as strong or stronger due to random genetic drift alone (two-tailed test).

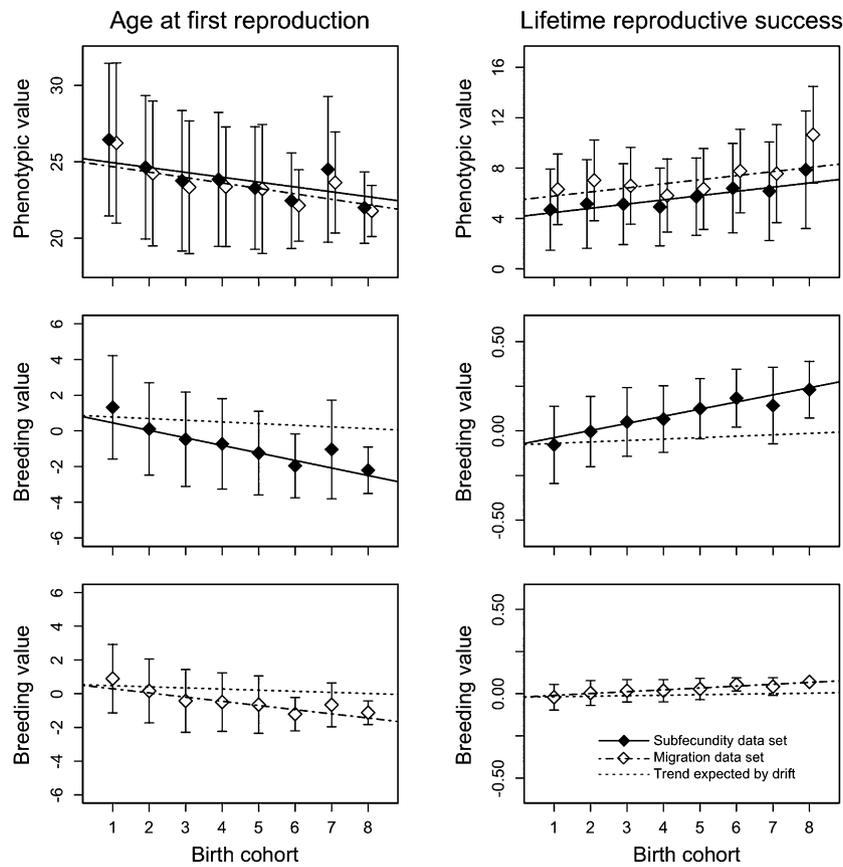


Fig. 2. Temporal trends in the phenotypic and breeding values of woman’s age at first reproduction and lifetime reproductive success in the population of île aux Coudres between 1800 and 1939. All values are in years for AFR. For LRS, phenotypic values are in numbers of offspring reaching age 15, whereas PBVs are on the latent scale (Poisson model). PBVs are genetic deviations from the population average over the study period [zero values correspond to no deviation; diamonds are averages from 1,000 MCMC samples (\pm 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 non-significant 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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- Hairston NGJ, Ellner SP, Geber MA, Yoshida T, Fox JA (2005) Rapid evolution and the convergence of ecological and evolutionary time. *Ecol Lett* 8:1114–1127.
- Carroll SP, Hendry AP, Reznick DN, Fox CW (2007) Evolution on ecological time-scales. *Funct Ecol* 21:387–393.
- Pettay JE, Helle S, Jokela J, Lummaa V (2007) Natural selection on female life-history traits in relation to socio-economic class in pre-industrial human populations. *PLoS One* 2:e606.
- Stearns SC, Byars SG, Govindaraju DR, Ewbank D (2010) Measuring selection in contemporary human populations. *Nat Rev Genet* 11:611–622.
- Pettay JE, Kruuk LEB, Jokela J, Lummaa V (2005) Heritability and genetic constraints of life-history trait evolution in preindustrial humans. *Proc Natl Acad Sci USA* 102:2838–2843.
- Kosova G, Abney M, Ober C (2010) Colloquium papers: Heritability of reproductive fitness traits in a human population. *Proc Natl Acad Sci USA* 107(Suppl 1):1772–1778.
- Byars SG, Ewbank D, Govindaraju DR, Stearns SC (2010) Colloquium papers: Natural selection in a contemporary human population. *Proc Natl Acad Sci USA* 107(Suppl 1):1787–1792.
- Pelletier F, Garant D, Hendry AP (2009) Eco-evolutionary dynamics. *Philos Trans R Soc Lond B Biol Sci* 364:1483–1489.
- Pemberton JM (2008) Wild pedigrees: The way forward. *Proc Biol Sci* 275:613–621.
- Falconer DS, Mackey TFC (1996) *Introduction to Quantitative Genetics* (Longmans Green, Harlow, UK).
- Lynch M, Walsh B (1998) *Genetics and Analysis of Quantitative Traits* (Sinauer, Sunderland, MA).
- Wade MJ, Kalisz S (1990) The causes of natural selection. *Evolution* 44:1947–1955.
- Rauscher MD (1992) The measurement of selection on quantitative traits: Biases due to environmental covariances between traits and fitness. *Evolution* 46:616–626.
- Morrissey MB, Kruuk LEB, Wilson AJ (2010) The danger of applying the breeder's equation in observational studies of natural populations. *J Evol Biol* 23:2277–2288.
- Gienapp P, Teplitsky C, Alho JS, Mills JA, Merilä J (2008) Climate change and evolution: Disentangling environmental and genetic responses. *Mol Ecol* 17:167–178.
- Merilä J, Kruuk LEB, Sheldon BC (2001) Cryptic evolution in a wild bird population. *Nature* 412:76–79.
- Wilson AJ, et al. (2007) Quantitative genetics of growth and cryptic evolution of body size in an island population. *Evol Ecol* 21:337–356.
- Kruuk EB, et al. (2002) Antler size in red deer: Heritability and selection but no evolution. *Evolution* 56:1683–1695.
- Coltman DW, et al. (2003) Undesirable evolutionary consequences of trophy hunting. *Nature* 426:655–658.
- Réale D, McAdam AG, Boutin S, Berteaux D (2003) Genetic and plastic responses of a northern mammal to climate change. *Proc Biol Sci* 270:591–596.
- Garant D, Kruuk LEB, Wilkin TA, McCleery RH, Sheldon BC (2005) Evolution driven by differential dispersal within a wild bird population. *Nature* 433:60–65.
- Teplitsky C, Mills JA, Alho JS, Yarrall JW, Merilä J (2008) Bergmann's rule and climate change revisited: Disentangling environmental and genetic responses in a wild bird population. *Proc Natl Acad Sci USA* 105:13492–13496.
- Hadfield JD, Wilson AJ, Garant D, Sheldon BC, Kruuk LEB (2010) The misuse of BLUP in ecology and evolution. *Am Nat* 175:116–125.
- Postma E (2006) Implications of the difference between true and predicted breeding values for the study of natural selection and micro-evolution. *J Evol Biol* 19:309–320.
- Martin Y (1957) Île-aux-Coudres: Population and economy. *Cahiers de Géographie*, 2: 167–195 (in French).
- Kruuk LEB (2004) Estimating genetic parameters in natural populations using the 'animal model.' *Philos Trans R Soc London Ser B* 359:873–890.
- Kirk KM, et al. (2001) Natural selection and quantitative genetics of life-history traits in Western women: A twin study. *Evolution* 55:423–435.
- Boisvert M, Mayer FM (1994) Infant mortality and consanguinity in an endogamous population in Québec. *Population (Paris)*, 49:685–724 (in French).
- Stearns SC (1992) *The Evolution of Life Histories* (Oxford Univ Press, Oxford).
- Hawkes K, Paine RR (2006) *The Evolution of Human Life History* (School Am Res Press, Santa Fe, NM).
- Käär P, Jokela J, Helle T, Kojola I (1996) Direct and correlative phenotypic selection on life-history traits in three pre-industrial human populations. *Proc Biol Sci* 263:1475–1480.
- 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.
- Brommer JE, Merilä J, Kokko H (2002) Reproductive timing and individual fitness. *Ecol Lett* 5:802–810.
- Scheiner SM, Mitchell RJ, Callahan HS (2000) Using path analysis to measure natural selection. *J Evol Biol* 13:423–433.
- Kirkwood TBL, Austad SN (2000) Why do we age? *Nature* 408:233–238.
- Philippe P (1974) Amenorrhea, intrauterine mortality and parental consanguinity in an isolated French Canadian population. *Hum Biol* 46:405–424.
- Hadfield JD (2010) MCMC methods for multi-response generalised linear mixed models: The MCMCglmm R package. *J Stat Softw* 33, issue 2.
- Charbonneau H (1991) *The Population of Québec from Yesterday to Tomorrow*, eds Henripin J, Martin Y (Presses de l'Université de Montréal, Montréal), pp 11–23 (in French).
- Philippe P (1973) Fertility, fecundability and consanguinity at Isle-aux-Coudres. *Recherches Sociobiographiques* 14:117–123 (in French).
- Henripin J (1991) *The Population of Québec from Yesterday to Tomorrow*, eds Henripin J, Martin Y (Presses de l'Université de Montréal, Montréal), pp 45–50 (in French).
- Gelman A (2006) Prior distributions for variance parameters in hierarchical models. *Bayesian Anal* 1:515–533.
- Mrode RA (1996) *Linear Models for the Prediction of Animal Breeding Values* (CABI, Wallingford, UK).
- Tomkins JL, Penrose MA, Greeff J, LeBas NR (2010) Additive genetic breeding values correlate with the load of partially deleterious mutations. *Science* 328:892–894.
- 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.
- Stearns 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.
- Heyer E, Sibert A, Austerlitz F (2005) Cultural transmission of fitness: Genes take the fast lane. *Trends Genet* 21:234–239.
- Terry MB, Ferris JS, Tehranifar P, Wei Y, Flom JD (2009) Birth weight, postnatal growth, and age at menarche. *Am J Epidemiol* 170:72–79.
- Udry JR, Cluett RL (1982) A cross-cultural examination of the relationship between ages at menarche, marriage, and first birth. *Demography* 19:53–63.
- Towne B, et al. (2005) Heritability of age at menarche in girls from the Fels Longitudinal Study. *Am J Phys Anthropol* 128:210–219.
- Goldstein JR, Schlag W (1999) Longer life and population growth. *Popul Dev Rev* 25:741–747.
- Philippe P, Gomila J (1972) Inbreeding effects in a French Canadian isolate. I. Evolution of inbreeding. *Z Morphol Anthropol* 64:54–59.
- Philippe P (1977) Genetics of fecundity: A demographic approach. *Hum Biol* 49:11–18.
- Lande R, Arnold SJ (1983) The measurement of selection on correlated characters. *Evolution* 37:1210–1226.
- Fox J (2010) Package SEM (R Project; <http://www.r-project.org>), 0.9-21.
- Nakagawa S, Schielzeth H (2010) Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biol Rev Camb Philos Soc* 85:935–956.