

## Supporting information for

### *Life history plasticity in humans: the predictive value of early cues depends on the temporal structure of the environment*

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October 15, 2013

#### 1. Second-order extension of Nettle *et al.*'s model

In the first-order autoregressive model by Nettle *et al.* [S1], the distribution of environmental states has mean  $\bar{M} = 0$  and variance  $\sigma^2 = 1$ . When a second-order term is added to the model, the random variable  $X$  has to be multiplied by an appropriate coefficient so that  $\sigma^2 = 1$ . Specifically, the variance of the stochastic term involving  $X$  must equal one minus the variance of the sum of the regression terms:

$$m_t = \phi_1 m_{t-1} + \phi_2 m_{t-2} + \sqrt{1 - \text{VAR}(\phi_1 m_{t-1} + \phi_2 m_{t-2})} X_t \quad (\text{S1})$$

Since  $\phi_1 m_{t-1}$  and  $\phi_2 m_{t-2}$  are correlated, the variance of their sum is given by:

$$\begin{aligned} \text{VAR}(\phi_1 m_{t-1} + \phi_2 m_{t-2}) &= \text{VAR}(\phi_1 m_{t-1}) + \text{VAR}(\phi_2 m_{t-2}) \\ &\quad + 2\rho_1 \text{SD}(\phi_1 m_{t-1}) \text{SD}(\phi_2 m_{t-2}) \end{aligned} \quad (\text{S2})$$

where  $\rho_1$  is the correlation between  $\phi_1 m_{t-1}$  and  $\phi_2 m_{t-2}$ , i.e., the annual autocorrelation. The variance of environmental states is constant over time, so that

$$\text{VAR}(m_t) = \text{VAR}(m_{t-1}) = \text{VAR}(m_{t-2}) = 1 \quad (\text{S3})$$

It follows that

$$\begin{cases} \text{VAR}(\phi_1 m_{t-1}) = \text{VAR}(m_{t-1}) \phi_1^2 = \phi_1^2 \\ \text{VAR}(\phi_2 m_{t-2}) = \text{VAR}(m_{t-2}) \phi_2^2 = \phi_2^2 \end{cases} \quad (\text{S4})$$

The annual autocorrelation in second-order models (see [S2]) is given by:

$$\rho_1 = \frac{\phi_1}{1 - \phi_2} \quad (\text{S5})$$

Eq. S1 can now be rewritten as:

$$m_t = \phi_1 m_{t-1} + \phi_2 m_{t-2} + \sqrt{1 - \left( \phi_1^2 + \phi_2^2 + 2 \frac{\phi_1}{1-\phi_2} \phi_1 \phi_2 \right)} X_t \quad (\text{S6})$$

and rearranged to yield:

$$m_t = \phi_1 m_{t-1} + \phi_2 m_{t-2} + \sqrt{1 - \left( \phi_1^2 + \phi_2^2 + 2 \frac{\phi_1^2 \phi_2}{1-\phi_2} \right)} X_t \quad (\text{S7})$$

## 2. Simulations

All simulations were performed in R 2.15 [S3] with the same equations and parameter values of Nettle *et al.* [S1]. The only difference was that environmental states were generated by Eq. S7 (instead of Eq. 1 in the supplementary material of [S1]). For each value of  $\rho_1$  in the simulation, coefficients  $\phi_1$  and  $\phi_2$  were obtained from Eq. S5. In simulations based on the revised model with *weak* delayed effects,  $\phi_1$  and  $\phi_2$  were set to:

$$\phi_1 = 2\phi_2 = \frac{2\rho_1}{2+2\rho_1} \quad (\text{S8})$$

In simulations based on the revised model with *strong* delayed effects,  $\phi_1$  and  $\phi_2$  were set to:

$$\phi_1 = \phi_2 = \frac{\rho_1}{1+\rho_1} \quad (\text{S9})$$

## 3. Autocorrelation functions of the two models

A key difference between first- and second-order autoregressive models is their autocorrelation function,  $\rho_k$  (see [S2,S4]). In first-order models, the autocorrelation function follows a simple exponential decay:

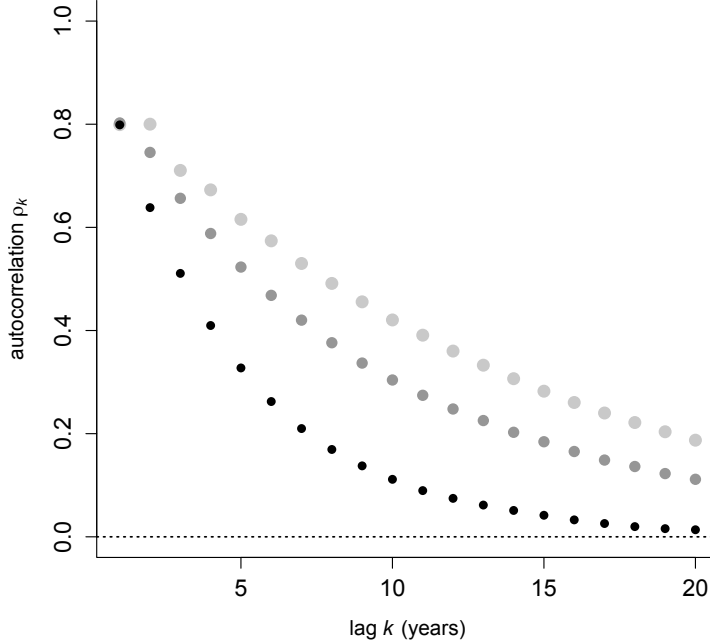
$$\rho_k = \phi_1^k \quad (\text{S10})$$

whereas in second-order models, the autocorrelation function becomes:

$$\rho_k = \phi_1 \rho_{k-1} + \phi_2 \rho_{k-2} \quad (\text{S11})$$

with  $\rho_0 = 1$ . When both  $\phi_1$  and  $\phi_2$  are positive (as in the present model), the autocorrelation function described by Eq. S11 is a mixture of terms that decay exponentially

[S4], resulting in a slower decay over time compared with a first-order model with the same value of  $\rho_1$ . Figure S1 illustrates this by comparing the autocorrelation functions of the original and revised model for  $\rho_1 = 0.80$ .



**Figure S1.** Autocorrelation functions of the original and revised model for  $\rho_1 = 0.80$  and  $k = \{1 \dots 20\}$ . Black dots = original model by Nettle *et al.*, dark grey dots = revised model with weak delayed effects, light grey dots = revised model with strong delayed effects. Data represent simulated time series of 100000 years.

#### 4. The temporal structure of ecological variation

The temporal structure of variation in natural environments has been investigated in the ecological literature (see [S5] for a review). In ecology, the degree of positive or negative autocorrelation displayed by a time series is often described as its “colour”, in analogy with the visible light spectrum [S5-S8]. When successive values are positively autocorrelated, slow fluctuations dominate the frequency spectrum, resulting in “red” or “red-shifted” spectral colour. In contrast, negative autocorrelations produce a disproportionate amount of high-frequency fluctuations and a “blue” or “blue-shifted” spectrum. Time series with zero autocorrelation have a flat frequency spectrum and can be described as “white noise”.

In the literature on temporal variation, it is often assumed that the spectral density of the process under investigation follows a power law function of the form:

$$S(f) \propto \frac{1}{f^\beta} \quad (\text{S12})$$

where  $f$  is frequency and  $S(f)$  is spectral density. The  $\beta$  parameter in Eq. S12 is the *spectral exponent* of the process. White noise has  $\beta = 0$ ; red-shifted spectra are characterized by  $\beta > 0$ , whereas blue-shifted spectra are characterized by  $\beta < 0$  (see [S5]). The  $1/f$  frequency distribution that obtains when  $\beta = 1$  is commonly referred to as “pink noise” [S7, S8] (note that different authors may adopt slightly different definitions of the spectral exponent; for example, some authors employ  $-\beta$  as an index of spectral redness [S7, S8]).

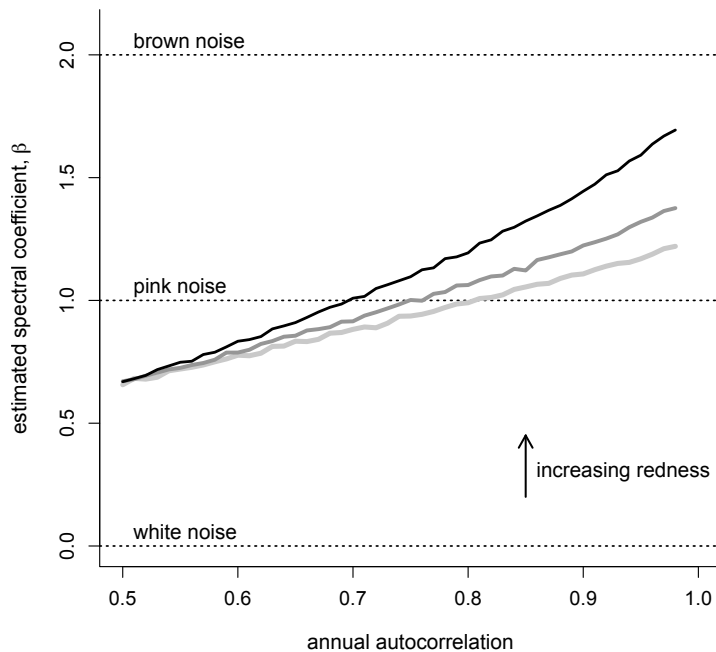
Empirical investigations of temporal variation in natural environments have yielded a number of useful generalizations. Climatic variables such as temperature and precipitation tend to show reddened spectra (i.e., positive autocorrelation patterns), with marine habitats being more red-shifted (typical values:  $1 < \beta < 2$ ) than terrestrial habitats (typical values:  $0.5 < \beta < 1$ ), and coastal habitats falling in between ( $\beta \cong 1$ ) [S6]. Among climatic variables, temperature variation is more red-shifted than variation in precipitation [S6]. Importantly, careful examination of spectral densities reveals that many climatic phenomena show “flattened” spectra at low frequencies, a pattern more consistent with first-order autoregressive processes than with the power law function of Eq. S12 ([S6]; see below). Nevertheless,  $\beta$  is often employed as a measure of spectral colour under the (typically untested) assumption of a  $1/f^\beta$  spectrum.

In animal species, population dynamics (i.e., temporal fluctuations in population size) also tend to show markedly reddened spectra. In a large-scale analysis of population time series [S7], 92% of the investigated species had spectral exponents  $0 < \beta < 2$ , with an overall mean of 1.02 (virtually the same as pink noise) and little difference between terrestrial and marine species [S7]. Also, larger body size (associated with longer generation time) predicts redder dynamics across species [S8]. The fact that population dynamics have redder spectra than exogenous environmental variables suggests that population fluctuations are not entirely driven by environmental fluctuations [S8], and/or that environmental fluctuations are “filtered” by biological processes in ways that emphasize low-frequency variation [S9].

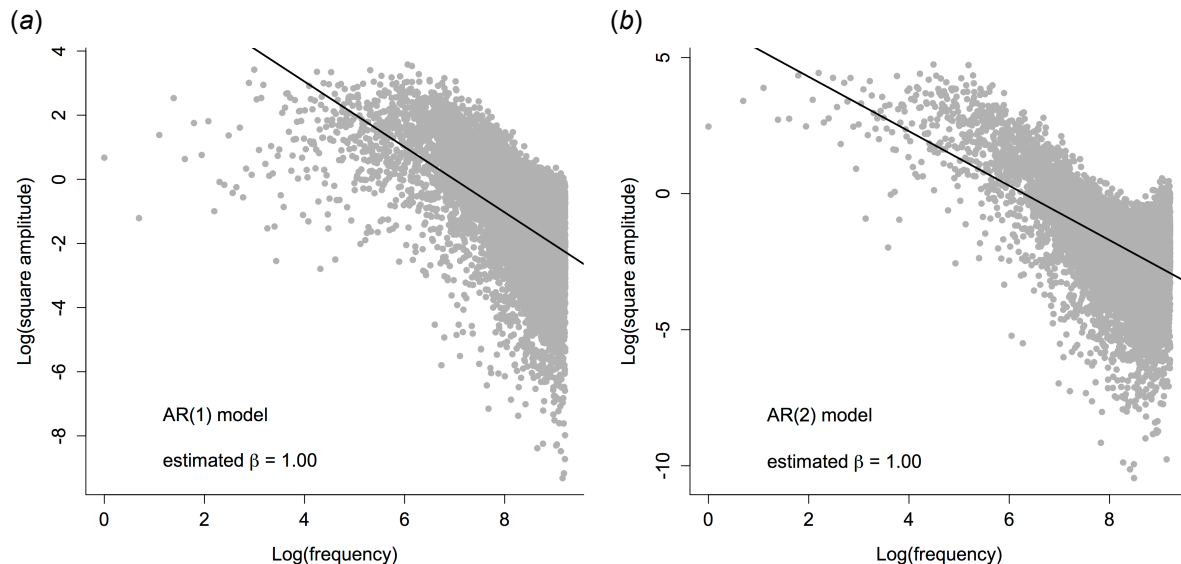
In order to check the plausibility of Eq. S7 as a model of environmental variation, long time series of environmental states were generated for different values of  $\phi_1$  and  $\phi_2$ , and their spectral exponent  $\beta$  was estimated with the least squares method described in [S7] (see the supplementary material of [S7] for details; note that  $\beta$  in [S7] corresponds to  $-\beta$  in Eq. S12). All computations were performed in R 2.15 [S3] with functions from the *GeneCycle* package (version 1.1.2) [S10]. Simulation results are shown in Figure S2. As expected, higher annual autocorrelations correspond to higher values of  $\beta$  (increasing redness). Compared with the original model by Nettle *et al.*, the time series generated by the revised model appear less red-shifted, and remain closer to the spectral exponent of pink noise ( $\beta = 1$ ) as the annual autocorrelation increases. As illustrated in Figure S3, this occurs because second-order autoregressive models deviate more than first-order models from the assumptions of Eq. S12, resulting in a lower *estimated* exponent even in presence of a stronger autocorrelation pattern (compare Figure S1 with Figure S2). It is important to stress that, while the spectral exponents in

Figure S2 underestimate the amount of autocorrelation in the simulated time series, the same applies to exponents estimated from real-world datasets, as the latter often show “flattened” spectra characteristic of autoregressive models [S6]. The critical question is: how do values of  $\beta$  estimated from simulated datasets compare with typical values of  $\beta$  estimated from real-world datasets, given that both are likely to underestimate the true amount of autocorrelation in the data?

Under the assumptions of Nettle *et al.*’s original model, the evolution of external PARs requires levels of annual autocorrelation of 0.95 or greater. Accordingly, the empirical spectral exponent of environmental fluctuations would have to be 1.5 or greater (black line in Figure S2), which is close to the upper limit of ecological fluctuations observed in natural environments. In contrast, the revised model may support external PARs with annual autocorrelations of 0.85 or greater; this corresponds to spectral exponents in the vicinity of 1 (light grey line in Figure S2), closer to the average of empirical estimates in nonhuman species. In other words, the revised model may permits the evolution of external PARs in a more realistic range of environmental conditions. Of course, these estimates are only first approximations based on studies of nonhuman species, and may not accurately reflect the temporal structure of human environments. However, they provide a useful heuristic in absence of more information on the patterns of environmental fluctuations experienced by our ancestors across evolutionary time.



**Figure S2.** Spectral exponent  $\beta$  estimated from simulated time series. Black line = original model by Nettle *et al.*, dark grey line = revised model with weak delayed effects, light grey line = revised model with strong delayed effects. Data represent simulated time series of 100000 years for each 0.01 increment of the annual autocorrelation.



**Figure S3.** Spectral analysis of simulated time series (20000 years) generated by first-order (a) and second-order (b) autoregressive models (see the supplementary information of [S7] for methodological details). The estimated spectral exponent is  $\beta = 1$  in both cases. Black line = expected amplitude for a power law spectrum with  $\beta = 1$  (pink noise; see Eq. S12). Both first and second-order autoregressive processes show flattened spectra at low frequencies; the spectrum of second-order processes (b) also deviates from theoretical expectations at high frequencies.

## References

- S1. Nettle D, Frankenhuys WE, Rickard IJ. 2013 The evolution of predictive adaptive responses in human life history. *Proc. R. Soc. B.* **280**, 20131343 (doi:10.1098/rspb.2013.1343)
- S2. Wei WWS. 2006 *Time series analysis: univariate and multivariate methods* (2<sup>nd</sup> edition). Boston, MA: Pearson Addison-Wesley.
- S3. R Core Team (2012). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL:<http://www.R-project.org/>
- S4. Chatfield C. 2000 *Time-series forecasting*. Boca Raton, FL: CRC press.
- S5. Ruokolainen L, Lindén A, Kaitala V, Fowler MS. 2009 Ecological and evolutionary dynamics under coloured environmental variation. *Trends Ecol. Evol.* **24**, 555-563. (doi:10.1016/j.tree.2009.04.009)
- S6. Vasseur DA, Yodzis P. 2004 The color of environmental noise. *Ecology* **85**, 1146-1152. (doi:10.1890/02-3122)
- S7. Inchausti P, Halley J. 2001 Investigating long-term ecological variability using the Global Population Dynamics database. *Science* **293**, 655-657. (doi:10.1126/science.293.5530.655)

- S8. Inchausti P, Halley J. 2002 The long-term temporal variability and spectral colour of animal populations. *Evol. Ecol. Res.* **4**, 1033-1048.
- S9. Laakso J, Kaitala V, Ranta E. 2001 How does environmental variation translate into biological processes? *OIKOS* **92**, 119-122. (doi:10.1034/j.1600-0706.2001.920114.x)
- S10. Ahdesmaki M, Fokianos K, Strimmer K. 2012 *GeneCycle package 1.1.2*.  
URL:<http://www.cs.tut.fi/~ahdesmak/robustperiodic/index.html>