

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

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

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Nettle *et al.* [1] explored the conditions under which it could be adaptive for humans to calibrate the development of life history traits (for example, reproductive timing) on the level of adversity experienced in early life. They concluded that external predictive adaptive responses (PARs)—in which early cues are employed to forecast the adult environment—can only evolve if environmental states show ‘almost perfect’ levels of year-to-year autocorrelation, in the order of 0.95 or greater. They suggested that annual autocorrelations could be empirically estimated from environmental time-series datasets; consistent findings of autocorrelations smaller than 0.95 would argue against accounts of human life-history plasticity that involve external PARs.

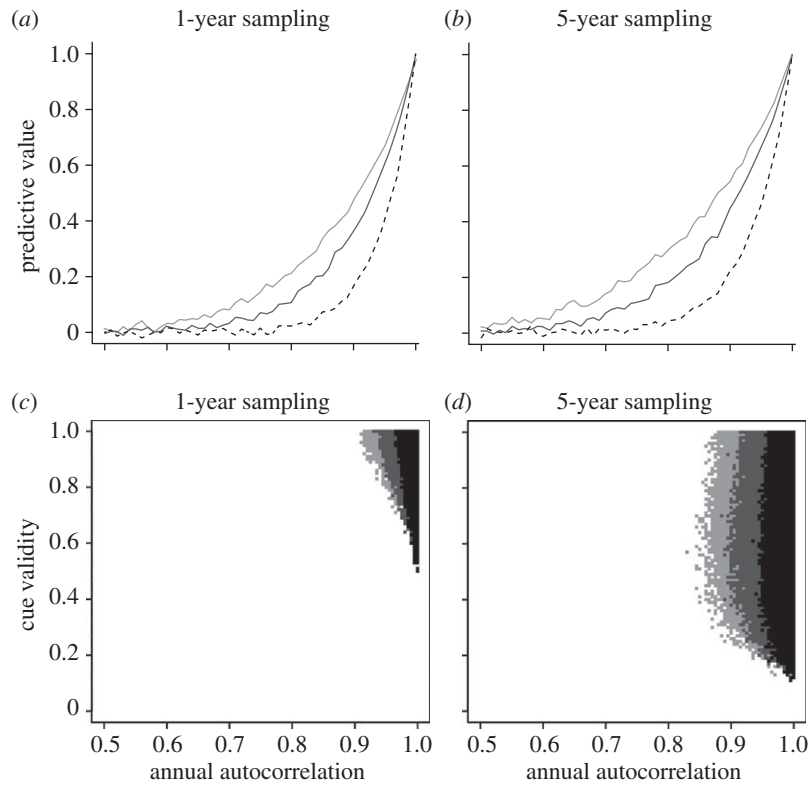
The model by Nettle *et al.* is a welcome contribution to the human literature on life history plasticity and the authors should be commended for their emphasis on testability and quantification. Indeed, their model offers conceptual clarity and quantitative predictions in an area where vague verbal claims are the unfortunate norm. However, it is important to understand to what extent the present results may depend on specific assumptions in the model, and critically evaluate the plausibility of the latter. This is especially true for quantitative predictions (for example, the 0.95 threshold) that lend themselves to be employed as heuristics for the interpretation of empirical findings.

Here, I argue that the model by Nettle *et al.* makes some unrealistic assumptions about the structure of environmental change and present a simple revised model in which past events can have both immediate and delayed effects on subsequent environmental states. I show that when delayed effects are incorporated in the model, the predictive value of early cues shows a notable increase and external PARs can evolve with annual autocorrelations in the order of 0.85 (or even 0.80) instead of 0.95. While the qualitative results obtained by Nettle *et al.* remain valid, the scope for the evolution of external PARs is larger than that implied in their paper. Future theoretical work should strive to clarify the temporal structure of human environments and systematically explore its implications for the evolution of life-history plasticity.

Nettle *et al.* modelled environmental fluctuations with a first-order autoregressive process of the form

$$m_t = \phi_1 m_{t-1} + \sqrt{1 - \phi_1^2} X_t, \quad (1)$$

with  $\phi_1 > 0$ . Coefficient  $\phi_1$  in equation 1 is equivalent to parameter  $r$  in Nettle *et al.* [1]. In this model, the state of the environment in year  $t$  is partly determined by the state of the environment in the previous year,  $t - 1$  (immediate effects). However, earlier environmental states (years  $t - 2$ ,  $t - 3$ , ...) cannot affect the present state if not indirectly—that is, through their long shadow on the state of the environment at  $t - 1$ . In other words, the ‘memory’ of the environment only extends to the previous year, and there is no way for more distant events to exert delayed effects on the present. This assumption is unrealistic if one considers the structure of human social and physical environments. For example, infectious diseases can have incubation periods longer than one year, can be transmitted from mother to fetus and can have delayed effects



**Figure 1.** (a,b) These graphs show the predictive value of early experience for adult environment as a function of the annual autocorrelation. Dotted black line, original model by Nettle *et al.* [1] (no delayed effects;  $\phi_2 = 0$ ); dark grey line, revised model with weak delayed effects ( $\phi_1 = 2\phi_2$ ); light grey line, revised model with strong delayed effects ( $\phi_1 = \phi_2$ ). For simplicity, simulations in (a,b) assume perfect cue validity [1]. Data represent 10 000 simulated lifetimes for each 0.01 increment of the annual autocorrelation. (c,d) These figures show the regions of the parameter space in which an external PAR outperforms a genetically fixed strategy matched to the long-term environmental mean [1]. Black area, original model by Nettle *et al.*; dark grey area, revised model with weak delayed effects; light grey area, revised model with strong delayed effects. Data represent 2000 simulated lifetimes for each parameter combination.

on mortality (e.g. systemic infections in childhood may increase the risk of heart failure in adulthood). As humans are able to store and preserve food for long periods of time, a single year of abundance can have delayed positive effects on food availability over multiple years. Also, both intergroup and intragroup conflicts have long-term dynamics that include revenge, truces, alliances and so forth; because of these social dynamics, past conditions can have a wide range of delayed effects on present levels of violence and aggression. Even exogenous factors, for example temperature, usually exhibit small to moderate amounts of positive autocorrelation from one year to the next [2,3], violating the assumption that stochastic fluctuations ( $X_t$  in equation 1) are independently distributed across years.

The restrictive assumption that only immediate effects contribute to environmental stability can be relaxed by introducing higher-order terms in equation 1 [4,5]. The minimal extension of Nettle *et al.*'s model is a second-order autoregressive equation, in which the state of the environment at  $t$  is jointly influenced by previous states at  $t - 1$  and  $t - 2$

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

with  $\phi_1, \phi_2 \geq 0$ . As in equation 1, the distribution of environmental states generated by equation 2 has mean 0 and variance 1 (see the electronic supplementary material). The relative strength of immediate ( $t - 1$ ) versus delayed ( $t - 2$ ) effects in the revised model is determined by coefficients  $\phi_1$  and  $\phi_2$ . When  $\phi_2 = 0$ , equation 2 reduces to equation 1 and the model describes a first-order autoregressive process (no

delayed effects). When  $\phi_1 = \phi_2$ , delayed effects have the same weight as immediate effects ('strong' delayed effects). A reasonable intermediate case is that of  $\phi_1 = 2\phi_2$ , where immediate effects are twice as large as delayed effects ('weak' delayed effects). As discussed in the electronic supplementary material, the environmental fluctuations generated by equation 2 have a spectral distribution consistent with those observed in natural animal populations [6,7]. Furthermore, adding a second-order term captures the dynamics of correlated exogenous factors (i.e. non-independent  $X_t$ ) when those factors can *themselves* be described by a first-order model [8,9]. Intriguingly, the temporal structure of exogenous climatic factors, such as temperature and precipitation, is often more consistent with a first-order autoregressive process than with a power-law function, in contrast with standard assumptions ([2]; see also the electronic supplementary material); this suggests that equation 2 provides a plausible model of stability and change in natural environments.

In second-order autoregressive models [4,5], the annual autocorrelation ( $\rho_1$ ) is given by

$$\rho_1 = \frac{\phi_1}{1 - \phi_2}. \quad (3)$$

Thus, by choosing appropriate values of  $\phi_1$  and  $\phi_2$ , it is possible to obtain the same annual autocorrelation from equations 1 and 2 (see the electronic supplementary material). For example, an annual autocorrelation of 0.80 may result from  $\phi_1 = 0.80$  and  $\phi_2 = 0$  (original model without delayed effects),  $\phi_1 \cong 0.57$  and  $\phi_2 \cong 0.29$  (revised model with weak delayed effects), or  $\phi_1 = \phi_2 \cong 0.44$  (revised model with

strong delayed effects). However, even when the annual autocorrelation is the same, the autocorrelation function of equation 2 decays less steeply across successive years than that of equation 1 [5]. In other words, when the correlation between  $m_t$  and  $m_{t-1}$  is the same in the two models, the revised model exhibits larger correlations between  $m_t$  and  $m_{t-2}$ , between  $m_t$  and  $m_{t-3}$ , and so forth (see the electronic supplementary material). As a consequence, early cues provide more information about future environmental states and their predictive value increases accordingly.

Figure 1 compares the results of Nettle *et al.*'s [1] original model with those of the revised model, for both weak ( $\phi_1 = 2\phi_2$ ) and strong ( $\phi_1 = \phi_2$ ) delayed effects. As shown in figure 1*a,b*, the predictive value of early cues shows a distinct increase in the revised model. For annual autocorrelations between 0.50 and 0.95, the average predictive value increases about 2.5-fold when delayed effects are weak (1-year sampling: 2.50; 5-year sampling: 2.40), and about 3.5-fold when delayed effects are strong (1-year sampling: 3.71; 5-year sampling: 3.52). Improved predictive values are reflected in the results of evolvability simulations: as shown in figure 1*c,d*, the region of parameter space in which PARs outperform genetically fixed strategies expands when delayed effects are included in the model, especially when individuals average cues over the first five years of life (figure 1*d*). With strong delayed effects and 5-year sampling, annual autocorrelations in the order of 0.85 can favour the evolution of external PARs. Whereas the parameter space of third- and higher-order

autoregressive models is more difficult to examine systematically [4,5], exploratory simulations with third-order effects showed additional increases in predictive value compared with the equivalent second-order models, from about 1.5-fold with weak delayed effects to about twofold with strong delayed effects. **As a result, external PARs could meet evolvability criteria with annual autocorrelations in the order of 0.80.**

In conclusion, the qualitative results of Nettle *et al.*'s [1] model are robust, but the conditions for PAR evolution derived by these authors should be partially revised. Whereas high year-to-year autocorrelations are still required for the evolution of external PARs, they do not have to be prohibitively high in order for prediction to be adaptive. Simple revisions of the model suggest a threshold of about 0.85 (or even 0.80) instead of 0.95. However, the revised models discussed here are still limited and somewhat unrealistic; more accurate models of temporal variation (for example, incorporating longer delays and long-term environmental cycles) might produce even lower estimates. The general point is that annual autocorrelations only provide a partial picture of the temporal structure of the environment; a more sophisticated description of environmental fluctuations will require a broader range of tools, including autocorrelation functions [4], spectral coefficients [2,3,6,7] and so forth (see the electronic supplementary material). Clarifying the temporal structure of human environments and exploring its implications for the evolution of life history plasticity should become top priorities for future work in this area.

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