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Royal Society Publishing

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

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

with $\phi_1 > 0$. Coefficient ϕ_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
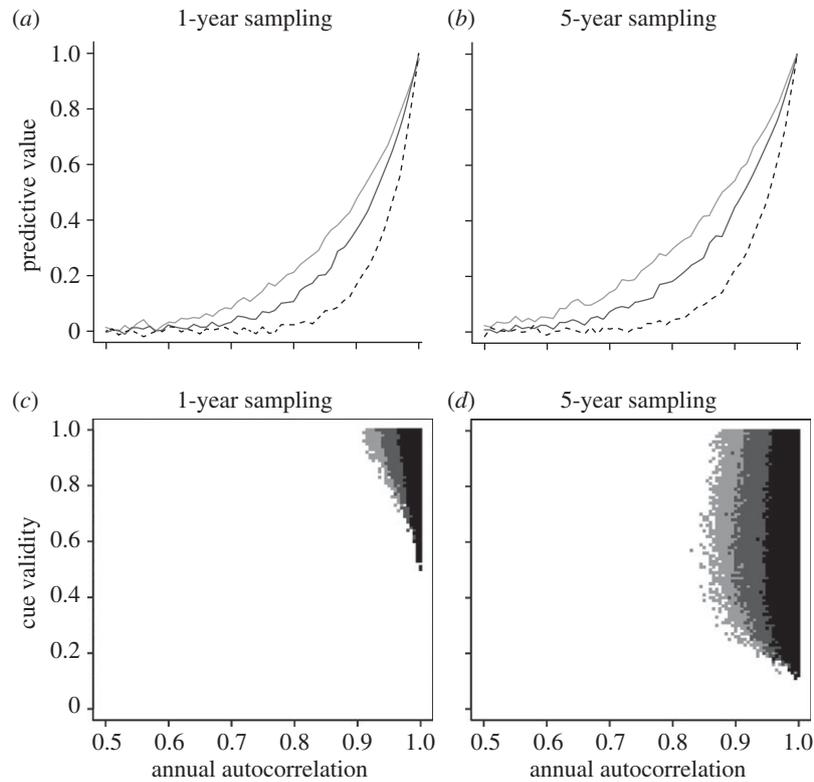
Figure 1. (a,b) These graphs show the predictive value of early experience for adult environment as a function of the annual autocorrelation. Dotted black line, original model by Nettle *et al.* [1] (no delayed effects; $\phi_2 = 0$); dark grey line, revised model with weak delayed effects ($\phi_1 = 2\phi_2$); 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 $t − 2$

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

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 ϕ_1 and ϕ_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 (ρ_1) is given by

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

Thus, by choosing appropriate values of ϕ_1 and ϕ_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

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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 1a,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 1c,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 1d). 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.

References

1. Nettle D, Frankenhuis 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)
2. Vasseur DA, Yodzis P. 2004 The color of environmental noise. *Ecology* **85**, 1146–1152. (doi:10.1890/02-3122)
3. 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)
4. Chatfield C. 2000 *Time-series forecasting*. Boca Raton, FL: CRC press.
5. Wei WWS. 2006 *Time series analysis: univariate and multivariate methods*, 2nd edn. Boston, MA: Pearson Addison-Wesley.
6. 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)
7. Inchausti P, Halley J. 2002 The long-term temporal variability and spectral colour of animal populations. *Evol. Ecol. Res.* **4**, 1033–1048.
8. Royama T. 1981 Fundamental concepts and methodology for the analysis of animal population dynamics, with particular reference to univoltine species. *Ecol. Monogr.* **51**, 473–493. (doi:10.2307/2937325)
9. Williams DW, Liebhold AM. 1995 Detection of delayed density dependence: effects of autocorrelation in an exogenous factor. *Ecology* **76**, 1005–1008. (doi:10.2307/1939363)

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The accompanying comment can be viewed at
http://dx.doi.org/doi:10.1098/rspb.2013.2222.

The evolution of predictive adaptive responses in humans: response

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We welcome the generalization by Del Giudice [1] of our model investigating the evolvability conditions for predictive adaptive responses (PARs) in long-lived species like humans [2]. In our original approach, environmental conditions in 1 year were modelled as the sum of the conditions in the previous year plus a perturbation term to represent exogenous sources of change. The perturbation terms were independent from year to year. If the exogenous perturbation forces are themselves temporally autocorrelated, then environmental change is described by a more complex autoregressive structure than the one used in our original model, one in which conditions in the current year are influenced by conditions in the previous year and the one before that. Del Giudice shows that when dependencies between successive years take this more complex form, the present becomes in effect a better guide to the future than it would otherwise have been. This makes the external PAR (using conditions experienced early in ontogeny as a guide to the likely adult external environment) an adaptive strategy under a somewhat wider range of conditions that those we originally reported.

The objective for our paper was to galvanize theoretical progress in an area where adaptive hypotheses have been discussed for some time without agreement about whether they are likely to be right, and without exposure of the precise assumptions on which they depend. We recognize that our initial model was not exhaustive; it provided a contribution, hopefully, to the eventual construction of a whole library of related models examining how developmental trajectories might evolve under different environmental regimes. It will be this library of cases taken together—rather than any single one—that will lead to general understanding. The modelling endeavour is also not isolated from empirical work. To quote George Box, who died in 2013, 'science is a means whereby learning is achieved, not by mere theoretical speculation on the one hand, nor by the undirected accumulation of practical facts on the other, but rather by a motivated iteration between theory and practice' [3, p. 791]. Our model aimed to make an initial bridge between adaptive hypotheses about PARs, on the one hand, and empirically measurable features of the environments inhabited by humans, on the other. Del Giudice's model is welcome because it creates a second iteration, incorporating more detailed information about how environments vary to refine the model. We hope that his paper and ours will stimulate greater empirical research on environmental variation as experienced by individuals and populations (something that has also been called for elsewhere [4]). It may well be that some environmental forces are well captured by our original model, whereas others are not so well captured and require more complex specifications. Future empirical work will make this clearer.

An even more important thing that George Box taught us was to 'remember that all models are wrong; the practical question is how wrong do they have to be to not be useful' [5, p. 74]. Our model contained a highly simplified representation of how organisms experience the early environment and how that environment might change. Our main conclusions were that, for a long-lived organism, there is only adaptive advantage to using early life as an indicator of the adult environment if (1) the level of annual autocorrelation in the

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environment is very high, and (2) the cues of environmental conditions received in early life are very accurate indicators of the present conditions. Del Giudice shows that allowing for delayed effects in environmental change leaves these two conclusions qualitatively intact, though the precise numbers change. Examining Del Giudice's fig. 1, panels (c) and (d) show that even where strong delayed effects are included, the adaptive advantage of plasticity is found only in the top right quadrant of the parameter space. The quantitative details of our evolvability criteria might need amending if the environmental factor under study were shown to exhibit strong delayed effects; where we specified an annual auto-correlation of at least 0.95, in fact 0.80 might be sufficient. Though this amendment is important, both models concur that there would have to be strong positive annual autocorre-lation (not 0, 0.2 or 0.5, for example) coupled with high cue validities. When models using different assumptions come to qualitatively similar conclusions, it adds to our confidence

about the robustness of those conclusions. We also note that quite different modelling approaches have recovered con-clusions that are in some ways similar to ours [6–8]. Thus, we stick by our contention that conclusions (1) and (2) con-strain the plausibility of the idea that humans use early-life cues to gain information about the likely external envi-ronment in adulthood, and reiterate our call to examine accommodation to the directly detrimental effects of early adversity on health as an alternative explanation of observed phenomena [9].

There has been a flurry of recent papers trying to test empirically what can broadly be characterized as PAR hypoth-eses. These are very diverse in design, character and results. Some find the predicted effects, while many do not [10–14]. Being more precise about the assumptions of the theory may help understand what the exact predictions are for particu-lar systems and particular traits, and, especially, when we should expect to find PARs and when we should not.

References

1. Del Giudice M. 2014 Life history plasticity in humans: the predictive value of early cues depends on the temporal structure of the environment. *Proc. R. Soc. B* **281**, 20132222. (doi:10.1098/rspb.2013.2222)

2. Nettle D, Frankenhuis 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)

3. Box GEP. 1976 Science and statistics. *J. Am. Stat. Assoc.* **71**, 791–799. (doi:10.1080/01621459.1976.10480949)

4. Via S, Gomulkiewicz R, De Jong G, Scheiner SM, Schlichting CD, Van Tienderen PH. 1995 Adaptive phenotypic plasticity: consensus and controversy. *Trends Ecol. Evol.* **10**, 212–217. (doi:10.1016/S0169-5347(00)89061-8)

5. Box GEP, Draper NR. 1987 *Empirical model building and response surfaces*. New York, NY: John Wiley.

6. Baig U, Belsare P, Watve M, Jog M. 2011 Can thrifty gene(s) or predictive fetal programming for thriftiness lead to obesity? *J. Obes.* **2011**, 861049. (doi:10.1155/2011/861049)

7. Moran NA. 1992 The evolutionary maintenance of alternative phenotypes. *Am. Nat.* **139**, 971–989. (doi:10.1086/285369)

8. Leimar O, Hammerstein P, Van Dooren TJM. 2006 A new perspective on developmental plasticity and the principles of adaptive morph determination. *Am. Nat.* **167**, 367–376. (doi:10.1086/499566)

9. Rickard IJ, Frankenhuis WE, Nettle D. 2014 Why are childhood family factors associated with timing of maturation? A role for internal prediction. *Perspect. Psychol. Sci.* **9**, 3–15. (doi:10.1177/1745691613513467)

10. Storm JJ, Lima SL. 2010 Mothers forewarn offspring about predators: a transgenerational maternal effect on behavior. *Am. Nat.* **175**, 382–390. (doi:10.1086/650443)

11. Uller T, Nakagawa S, English S. 2013 Weak evidence for anticipatory parental effects in plants and animals. *J. Evol. Biol.* **26**, 2161–2170. (doi:10.1111/jeb.12212)

12. Hayward AD, Rickard IJ, Lummaa V. 2013 Influence of early-life nutrition on mortality and reproductive success during a subsequent famine in a preindustrial population. *Proc. Natl Acad. Sci. USA* **110**, 13 886–13 891. (doi:10.1073/pnas.1301817110)

13. Hayward AD, Lummaa V. 2013 Testing the evolutionary basis of the predictive adaptive response hypothesis in a preindustrial human population. *Evol. Med. Public Health* **2013**, 106–117. (doi:10.1093/emph/eot007).

14. Sandman CA, Davis EP, Glynn LM. 2012 Prescient human fetuses thrive. *Psychol. Sci.* **23**, 93–100. (doi:10.1177/0956797611422073)