Supporting Information for The evolution of Predictive Adaptive Responses in human life history

Daniel Nettle, Willem E. Frankenhuis, Ian J. Rickard

March 8, 2013

1 General description of model

Here and in the main paper, we report a mixture of analytical results and numerical simulations. All numerical simulations were carried out in R 2.10.1 (R Foundation for Statistical Computing, 2009). Code is available from the corresponding author on request.

We calculate m_t , the value of parameter M for year t, using the recurrence relation:

$$m_t = rm_{t-1} + \sqrt{(1-r^2)}X$$
 (1)

- where X is a value drawn from a normally distributed random variable with mean \overline{M} and standard deviation σ . In what follows, \overline{M} is taken to be 0 and σ as 1 unless otherwise specified, since absolute values of M are unimportant for the results we present. For $0 \leq r < 1$, (1) produces sequences such that the correlation between m_{k+1} and m_k is r for all k, the long-term mean is \overline{M} , and the standard deviation over very long runs of years is equal to σ , although over runs of a few years, the standard deviation is inversely proportional to r. With r = 1, the environment never changes and we consider this only as a limiting case.

As figure 1 of the main paper shows, as r approaches 1, there begin to be long sequences of successive good and bad years. We calculated the mean run length \bar{l} (defined as the mean number of successive years which deviated from \bar{M} in the same direction), for 10000 simulated years, and all values of r from 0 to 0.99 in increments of 0.01. The simulated data were well approximated (Pearson correlation 0.98) by the function:

$$\bar{l} = 1 + \frac{1}{(1 - 0.95r)} \tag{2}$$



Figure 1: Mean length of sequences of successive years deviating from \overline{M} in the same direction, as a function of r. Points show results from simulation of 10000 years whilst the line shows the approximating function given by equation (2).

Mean run length as a function of r is shown in figure 1. Every year, a cue q_t of the current state of the environment is available to the individual. q_t varies continuously, and is related to m_t by:

$$q_t = vm_t + \sqrt{(1-v^2)}X\tag{3}$$

- where X is drawn randomly from a normal distribution with mean \overline{M} and standard deviation σ . We consider only the case of $0 \leq v \leq 1$. This means that the correlation between q_t and m_t is v.

What is referred to as the adult environment in the paper is the mean of m_{16} to m_{25} . That is:

$$m_{adult} = \frac{1}{10} \Sigma_{k=16}^{25} m_k \tag{4}$$

The early-life cues are simply q_1 for one-year sampling, and the mean of q_1 to q_5 (notated as $\bar{q}_{1..5}$) for five-year sampling.

2 Predictive value of cues in one year for the state of the environment in a future year

In this section, we consider analytically the predictive value of cues received in one year for the state of the environment k years later. First, let q and m be standardized to their respective long-term means and standard deviations, so that E(q) and E(m) are 0 and σ_q and σ_m are 1. In general, if two random variables have correlation coefficient τ , then:

$$E(Y|X) = E(Y) + \tau \sigma_Y \frac{X - E(X)}{\sigma_X}$$
(5)

Where the expected values are 0 and the σ equal to 1, this reduces to:

$$E(Y|X) = \tau X \tag{6}$$

In the current case, the correlation between m_t and q_t is v and that between m_{t+1} and m_t is r, and so we have:

$$E(m_t|q_t) = vq_t \tag{7}$$

and

$$E(m_{t+1}|m_t) = rm_t \tag{8}$$

Now we can apply the law of iterated expectations with nested conditional sets which states, in the general case, that:

$$E(X|A) = E(E(X|B)|A)$$
(9)

Thus it follows that:

$$E(m_{t+2}|m_t) = E(E(m_{t+2}|E(m_{t+1})|m_t) = r^2 m_t$$
(10)

and more generally:

$$E(m_{t+k}|m_t) = r^k m_t \tag{11}$$

As for the relationship between q_t and m_{t+k} , we again apply the law of iterated expectations with nested conditional sets using (7) and (11), giving the general result that:

$$E(m_{t+k}|q_t) = vr^k q_t \tag{12}$$

By rearranging equation (6), the predictive value β is given in general by:

$$\beta = \frac{E(Y|X)}{X} \tag{13}$$

Applying this to equation (12), we can see that the predictive value of q_t for m_{t+k} in the current case is:

$$\beta = \frac{E(m_{t+k}|q_t)}{q_t} \tag{14}$$

$$=\frac{vr^{k}q_{t}}{q_{t}}\tag{15}$$

$$= vr^k$$
 (16)

The implication of equation (16) is that the predictive value of information received in one year for the state of the environment in the future decays very fast if $r \ll 1$. Figure 2 illustrates this by showing the predictive value of current cues for time points in the future if v = 1 and r takes the four different values shown. Unless ris around 0.95 or above, there is essentially no predictive value in early-life cues for a time point the length of the human developmental period into the future, even if the cues are perfectly reliable in terms of the contemporaneous environment.

3 Why does using early-life cues (usually) lead to a worse prediction of adult environment than ignoring them?

To investigate why using early life cues leads to a larger discrepancy between prediction and subsequent experience than assuming \overline{M} for values of r less than aproximately 0.95, we simulated 2000 lifetimes for r = 0, r = 0.5, and r = 1and examined the frequency distribution of values of m in early-life experience compared to the frequency distribution of m_{adult} . As figure 3 shows, when r < 1, actual adult experience is clustered tightly around \overline{M} , since it reflects ten drawings from a normal distribution with mean \overline{M} , whereas early-life experience, consisting of fewer samples, has a larger variance. Thus, the adult environment is generally less extreme on average than the shorter period of early life would lead one to predict. This effect will become more marked as the ratio of the length of the adult reproductive period to the length of the early-life sampling period increases. Five-year sampling reduces but does not abolish the difference in variances. Only where r = 1 is the variance of actual adult experience equal to the variance in early-life experience.



Figure 2: Predictive value of a cue received in the current year for the state of the environment in a single year at different times in the future, for four different values of the environmental autocorrelation parameter r. The cue validity v is taken to be 1.

4 Optimal use of early-life information

It is possible to imagine developmental strategies which anticipate the regression to the mean of adult experience compared to the briefer period of early-life experience, for example by predicting that the adult environment will be somewhere between $\bar{q}_{1..5}$ and \bar{M} . Do such strategies, which use early-life information and \bar{M} in some weighted combination, lead to a greater region of adaptive utility for external PARs compared to the simple strategy of assuming that adulthood will be the same as early life which is considered in the main paper?

The strategy of assuming that the adult environment will be halfway between early-life experience and \overline{M} does indeed lead to a slightly larger region of the parameter space in which using early-life cues improves the fit between prediction and actual adult experience. Figure 4 shows that the minimum value of r required



Figure 3: Histogram of values of m in early-life experience (white) and subsequent adult experience (black), for r = 0, r = 0.5 and r = 1. The top row represents one-year sampling and the bottom row fiveyear sampling. Data represent 2000 simulations at each parameter combination.

for using early-life cues to be advantageous is reduced from 0.95 to around 0.90 by taking halfway between early-life cues and \bar{M} as the predicted adult environment, rather than taking early-life cues to represent the adult environment.

There are in fact an infinite number of possible strategies which assume the adult environment will be given by some weighted average of \overline{M} and early-life cues and many of these may perform somewhat better than the simple strategy described in the main paper. However, this does not change the conclusion from



Figure 4: Regions of parameter space (shaded dark) in which an individual ends up on average better matched to her adult environment by using early-life cues to set adult phenotype, rather than following a genetically fixed strategy where she develops matched to the mean of conditions experienced by the lineage over evolutionary time. In the top panels, she predicts that the adult environment will be the same as that she experienced in early life (this reproduces figure 3 of the main paper). In the bottom panels, she predicts that the adult environment will be halfway between her early experience and the lineage's long-term mean experience \overline{M} . Data represent 2000 simulations at each parameter combination.

the main paper that an external PAR is unlikely to be adaptive unless r is close to 1 and v substantial. To see why, we here consider what the optimal weight to give to early-life experience in setting expectations about what m_{adult} should be. Let us assume that the long-term mean of Q is \overline{M}_q , the long-term mean of M is \overline{M} , and that M and Q have the same variance. It follows from equation (5) that:

$$E(m_{16}|q_1) = \bar{M} + r(q_1 - \bar{M}_q) \tag{17}$$

- where r is the correlation coefficient between q_1 and m_{16} . The formula for r is given in equation (16). Thus,

$$E(m_{16}|q_1) = \bar{M} + vr^{15}(q_1 - \bar{M}_q)$$
(18)

The adult environment is in fact the mean of ten years of observations, so we can generalise equation (18):

$$E(m_{adult}|q_1) = \bar{M} + \frac{v}{10} \Sigma_{k=16}^{25} r^k (q_1 - \bar{M}_q)$$
(19)

Unless r is close to 1, powers of r of 15 and above will be extremely close to zero (see SI figure 2). Thus, where $r \ll 1$ (or $v \approx 0$), equation (19) becomes, for all values of q_1 :

$$E(m_{adult}|q_1) \approx \bar{M} \tag{20}$$

If the expected value of the adult environment given any cue values received in early life is approximately \overline{M} , then there is no possible advantage of a plastic strategy which takes these cues into account over a fixed strategy which simply assumes \overline{M} from the outset. Thus, we conclude that there is no strategy under which an external PAR is adaptive if $r \ll 1$ (or $v \approx 0$).

5 Model incorporating effects of internal state on adult outcomes

We expanded the model described in section 1 to allow for a causal impact of early-life experience on the value of M in adulthood. To do this, we defined m_{adult} as:

$$m_{adult} = \frac{1}{10} \Sigma_{k=16}^{25} m_k + d \frac{1}{5} \Sigma_{k=1}^5 q_k \tag{21}$$

That is, the average value of Q over the five years of early life directly contributes to the value of M the individual experiences in adulthood, with weight d, so that as d becomes larger, this influence becomes increasingly strong. We are effectively assuming that only the first five years of life have this impact, and that each of them weighs equally in it. Note that for one-year sampling, it is still only q_1 which the individual uses to form its prediction of adult M, whereas for five-year sampling, it is the mean of q_1 to q_5 . Results from this version of the model are given in the main paper.