A MODEL FOR PHENOTYPE CHANGE IN
A STOCHASTIC FRAMEWORK

Graeme Wake

National Research Centre for Growth and Development &
Institute of Information and Mathematical Sciences
Massey University, Private Bag 102904, Albany, Auckland, New Zealand

Anthony Pleasants

National Research Centre for Growth and Development &
AgResearch Limited
Ruakura Research Centre, Private Bag 3123, Hamilton, New Zealand

Alan Beedle

National Research Centre for Growth and Development & Liggins Institute
University of Auckland, Private Bag 92019, Auckland, New Zealand

Peter Gluckman

National Research Centre for Growth and Development & Liggins Institute
University of Auckland, Private Bag 92019, Auckland, New Zealand

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Abstract. In some species, an inducible secondary phenotype will develop some time after the environmental change that evokes it. Nishimura (2006) [4] showed how an individual organism should optimize the time it takes to respond to an environmental change ("waiting time"). If the optimal waiting time is considered to act over the population, there are implications for the expected value of the mean fitness in that population. A stochastic predator-prey model is proposed in which the prey have a fixed initial energy budget. Fitness is the product of survival probability and the energy remaining for non-defensive purposes. The model is placed in the stochastic domain by assuming that the waiting time in the population is a normally distributed random variable because of biological variance inherent in mounting the response. It is found that the value of the mean waiting time that maximises fitness depends linearly on the variance of the waiting time.

1. **Introduction.** Organisms with the same genotype may display different phenotypes in different environments. This phenomenon of phenotypic plasticity benefits an organism's fitness (its ability to survive and reproduce) by matching it more closely to its environment (West-Eberhard, 2003 [7]). However, plasticity may incur costs, both in maintaining the general capacity for plasticity and in generating the alternative phenotype(s). The balance between benefits and costs determines

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whether plasticity is adaptive in particular situations, and previous theoretical studies have explored the conditions under which plasticity is preferable to alternative strategies such as local specialization (Moran, 1992 [3]; Jablonka *et al.* [2], 1995; Sultan & Spencer, 2002 [6]). One particular condition that has been explored is the relationship between the time scale of environmental change and the time lag involved in eliciting an appropriate phenotype for the new environment. For example, Padilla & Adolph (1996) [5] showed that plasticity is more likely to be adaptive when the time to expression of the new phenotype is short relative to the time scale of environmental variability. Nishimura (2006) [4] extended this exploration by using a simple model of a prey in an environment which changes to favor predation, with the assumption that the optimum waiting time to develop an anti-predator phenotype would maximize the product of survival in the new environment and energy remaining to the organism after adapting to the new environment. For example, an individual that adapted immediately to the new environment would utilize more energy to generate and maintain the anti-predator phenotype but would be less likely to be predated, whereas an individual that failed to adapt would retain more energy for non-defensive purposes but would be more likely to be predated. Using this model, Nishimura elucidated conditions that would favor a longer waiting time. The study of Nishimura (2006) [4] considered the effect of waiting time on individual fitness by use of a model involving a deterministic response to the new environment. Here we extend that model by exploring the consequences for mean fitness of variance in the waiting time to develop the defensive phenotype.

We have not in this study attempted the obvious alternative, that is, to analyse the temporal effects of phenotype plasticity of the ecology, and evolution of populations and have not described plasticity in terms of dynamical systems. This will come later. Rather, we have taken the prior view, that is, plasticity is seen as an optimisation problem, albeit over a whole population.

2. **Stochastic model of plasticity.** We follow the notation of Nishimura (2006) [4] and restate the model with slight simplification. The model assumes that in the high-predation environment the death rate of the prey organism will be μ_1 for the unmodified phenotype and μ_2 for the defensive phenotype (with $\mu_1 > \mu_2$) and that the development of the defensive phenotype incurs an energy cost from a base of c_1 to c_2 (with $c_1 < c_2$). Given an initial amount of energy E available to the organism, the fitness function $W(t)$ is to be evaluated at some end-time T in the future. It is assumed to depend on the variable time t ($0 < t < T$) which is the waiting time after the environmental cue (at which time the predation rate and energy consumption rate changes). This gives

$$W(t) = e^{-(\mu_1 t + \mu_2(T-t))}[E - c_1 t - c_2(T - t)] . \tag{1}$$

We have omitted expressions for the cost of maintaining the capacity for plasticity and for the time required to complete the defensive phenotype after time t at which the decision to undertake the response is taken.

Equation (1) is used to find the time t* that maximizes fitness

$$t^* = \frac{1}{\mu_1 - \mu_2} - \frac{E - c_2 T}{c_2 - c_1} .$$

However, this result assumes a deterministic response where there is no variability. In view of the inherent variability, it is more realistic to consider a population of

prey in which the time to develop the defensive phenotype after the environmental stimulus displays biological (genetic, epigenetic or environmental) variance.

Then, restating equation (1)

$$W(t) = e^{-\alpha t - \mu_2 T}[A + ct] \,, \tag{2}$$

where $\alpha = \mu_1 - \mu_2 > 0$, $A = E - c_2 T$, and $c = c_2 - c_1 > 0$.

Let the time t at which the defensive phenotype is developed be a random variable with moment generating function M_t, where $M_t(\alpha) = \mathbf{E}[e^{\alpha t}]$. The choice we make later of normality is of course debatable. However, provided the infeasible region (negative time) is sufficiently small, it provides an easy and realistic framework. Also it has the advantage that when we set the variance of t to zero, it then recovers the deterministic case described by Nishimura (2006) [4]. Notice that we are not assuming that the probability density of fitness is normal.

The expected value of the fitness of the organism is

$$\mathbf{E}[W(t)] = \mathbf{E}[e^{-\alpha t - \mu_2 T}[A + ct]]$$
$$= e^{-\mu_2 T} A \mathbf{E}[e^{-\alpha t}] + c e^{-\mu_2 T} \mathbf{E}[t e^{-\alpha t}],$$

and so,

$$\mathbf{E}[W(t)] = e^{-\mu_2 T}[A M_t(-\alpha) + c M_t'(-\alpha)] \,. \tag{3}$$

Here we have used

$$\mathbf{E}[e^{-\alpha t}] = M_t(-\alpha),$$
$$\mathbf{E}[t e^{-\alpha t}] = \frac{d}{d\alpha}[M_t(-\alpha)] = -M_t'(-\alpha) \,.$$

Equation (3) can be restated as the question: what M_t maximises the expected value of the fitness? This means we need to find the probability density function $p(t)$ which maximises the quantity

$$F(p(t)) = A M_t(-\alpha) + c M_t'(-\alpha) \,.$$

The left hand side of this gives $F(p(t)) = \int_0^\infty e^{-\alpha t}(A + ct)p(t)dt$.

As $e^{-\alpha t}(A + ct)$ achieves its maximum at $t = t^* = \frac{1}{\alpha} - \frac{A}{c}$ the required $p(t) = \delta(t - t^*)$, the Dirac-delta function, a point distribution at the time t^* obtained by Nishimura (2006) [4] in the deterministic case. This means that the deterministic case (with zero variability) is the optimal limit.

In practice $p(t)$ will not be a point distribution. Suppose an optimal distribution is $q(t)$ in the stochastic case, where $q(t)$ is a perturbation bringing with it the essential variability, with small variance (for example, a member of a δ-sequence with support $\ni t^*$).

Accordingly, $\int_{-\infty}^\infty q(t)dt = 1$, and the integral

$$\int_{-\infty}^\infty t(q(t) - p(t))dt = \bar{t}^* - t^*,$$

where $\bar{t}^*$ is the optimal value of the expected time for plastic response in the stochastic case (and t^* is the optimum for the deterministic case).

In the normally distributed case we have $\mathbf{E}\left[e^{-\alpha t}\right] = e^{-\alpha\left(\bar{t} - \frac{1}{2}\alpha\sigma_t^2\right)}$ and $\mathbf{E}[t e^{-\alpha t}] = e^{-\alpha\bar{t} + \frac{1}{2}\alpha^2\sigma_t^2}(\bar{t} - \alpha\sigma_t^2)$, where $\bar{t}$ and σ_t^2 are the mean and variance of t respectively.

We notice that these equations involve t being in the negative domain: however the tail involved will be small in practice and will introduce a small error only, which could be eliminated by use of a truncated normal, a gamma probability density or

722 G. WAKE, A. PLEASANTS, A. BEEDLE AND P. GLUCKMAN

another suitable probability density function. This would be determined by the detailed biology of a particular application. We will not do this here, and use the normal distribution for illustrative purposes, and thereby we can use its nice additive structure. It is conceded that a gamma distribution with no infeasible region might be better.

Then

$$\overline{W}(\bar{t}, \sigma_t^2) = \mathbf{E}[W(t)] = e^{\frac{1}{2}\alpha^2\sigma_t^2 - \alpha\bar{t} - \mu_2 T} \left(A + c(\bar{t} - \alpha\sigma_t^2)\right) \tag{4}$$

Note that equation (4) reverts to the original expression in the deterministic case when $\sigma_t^2 = 0$. Equation (4) has two variables associated with plasticity, the mean waiting time to response after detection of the environmental stimulus ($\bar{t}$) and the variance of this waiting time in the population of interest (σ_t^2). In order to determine the effect of uncertainty on the average plastic response we find the average time for plasticity which maximises the fitness is given by setting the derivative of equation (4) with respect to the average time to plasticity equal to zero, assuming that the variance is given; that is,

$$\frac{\partial \overline{W}}{\partial \bar{t}} = e^{\frac{1}{2}\alpha^2\sigma_t^2 - \alpha\bar{t} - \mu_2 T} \left\{\alpha^2 c\sigma_t^2 + c - \alpha A - \alpha c\bar{t}\right\} = 0 \tag{5}$$

This gives

$$\alpha c \left(\bar{t} - \alpha\sigma_t^2\right) = c - \alpha A$$

and so

$$\begin{aligned} \bar{t}^* &= \frac{1}{\alpha} - \frac{A}{c} + \alpha\sigma_t^2 \\ &= \frac{1}{\mu_1 - \mu_2} - \frac{E - c_2 T}{c_2 - c_1} + (\mu_1 - \mu_2)\sigma_t^2 \ . \end{aligned} \tag{6}$$

This shows that when the time at which the defensive phenotype is developed is stochastic rather than deterministic, the mean time optimizing the expected value of fitness is extended by an amount given by $\alpha\sigma_t^2$ as we would expect: the variability would extend the (mean) waiting time.

Substituting the optimal average time for plasticity into equation (4) gives the maximum fitness for a given level of the variance of the time to plasticity is given by

$$\overline{W}_{max} \sim \text{constant } e^{-\frac{1}{2}\sigma_t^2\alpha^2}.$$

As this variance increases the optimal time for plasticity increases according to equation (6) and also the fitness of the population falls. Thus, other things being equal it appears to be advantageous for a population to have a low variance and a short interval between the stimulus and the expression of plasticity, that is, an instantaneous response to an adverse stimulus.

If in addition, an external variance is introduced into the time between the stimulus and the expression of plasticity, (perhaps because of variation in the strength of the stimulus across members of the population), this results in an optimal population fitness with the time to plasticity being longer than in the deterministic case considered by Nishimura (2006) [4].

Thus maximum fitness is not defined by a unique pair of numbers for mean waiting time and its variance, but rather by a set of numbers lying on a straight line in the plane of mean time and variance. The position of the line in the plane is determined by the available energy E, and its slope is determined by the effectiveness of
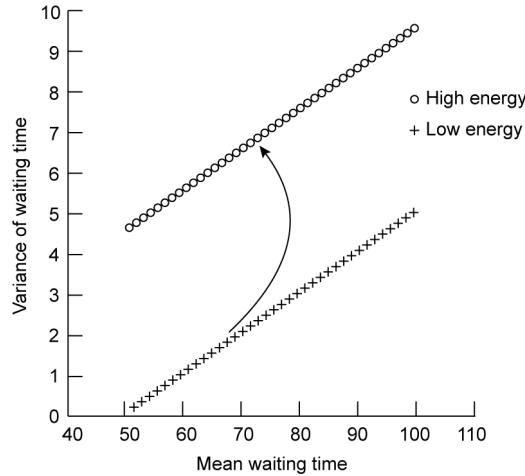
FIGURE 1. The trade-off between the expected value of the time for plasticity and the variance of the time for plasticity in a population subjected to two different energy availabilities, and the optimal path of waiting time mean and variance when the energy available changes from low to high. This diagram is schematic only.

the defensive phenotype, $\mu_1 - \mu_2$. Figure 1 illustrates the mean-variance trade-off in waiting time for optimum fitness of the organism and where the time meets the horizontal axis is the deterministic case.

3. **Path to optimal states in the mean-variance plane.** A population might not be on the optimal mean-variance line for a number of reasons. For example, the average energy available E might change, resulting in a parallel shift of the optimum line, or the predation rate might change, altering the slope. If the population ends up off the optimal line the question arises of the expected path in the mean-variance space that it will take to get to the new optimal line. To calculate this path we assume that the probability distribution of the waiting time for the population remains Gaussian. This means that the new environment induces a similar average change in waiting time across the population, preserving the normal distribution of the probability density. Assuming that the path of the population in mean-variance space proceeds in a direction most favorable to the population, the path from a point $\left(\bar{t}_0, \sigma_{0,t}^2\right)$ to a point on the new optimal line $\left(\bar{t}_1, \sigma_{1,t}^2\right)$ will be perpendicular to the level curves of the expected value of the fitness function (3). As shown in the Appendix the equation of this curve is a transcendental function given by:

$$\frac{3\alpha\left(E_1 + c(\bar{t} - \alpha\sigma_t^2)\right) + 4c}{3\alpha\left(E_1 - E_0\right) + 7c} = e^{\frac{3\alpha}{2}\left(\bar{t} + 2\sigma\sigma_t^2 - \bar{t}_1 - 2\sigma\sigma_t^2\right)} \tag{7}$$

It is also shown in the Appendix that a population starting from a point $\left(\bar{t}_0, \sigma_{0,t}^2\right)$ off the optimal line will meet the new optimal line at the point given by:

$$\sigma_{1,t}^2 = \sigma_{0,t}^2 - \frac{E_1 - E_0}{3(\mu_1 - \mu_2)(c_2 - c_1)} - \frac{2}{9(\mu_1 - \mu_2)^2} \ln \left(1 - \frac{3(\mu_1 - \mu_2)(E_1 - E_0)}{7(c_2 - c_1)} \right)$$

$$\bar{t}_1^* = \bar{t}_0 - \frac{2(E_1 - E_0)}{3(c_2 - c_1)} + \frac{2}{9(\mu_1 - \mu_2)} \ln \left(1 - \frac{3(\mu_1 - \mu_2)(E_1 - E_0)}{7(c_2 - c_1)} \right) \qquad (8)$$

Here the expected value of the energy available in the environment has changed from $\bar{E}_0$ to $\bar{E}_1$. It can be seen from equations (8) that

$$\bar{t}_1 - \bar{t}_0 = 2\left(\mu_1 - \mu_2\right)\left(\sigma_{1,t}^2 - \sigma_{0.t}^2\right)$$

Thus, the greater the difference in predation rates the greater the change in the mean waiting time in the population relative to the variance of waiting time, given the same average energy levels and relative costs of maintaining plasticity. For example, consider a population with $T = 100$ days, an average energy level of 100 units, $\mu_1 = 0.2$ day^{-1}, $\mu_2 = 0.1$ day^{-1}, $c_1 = 0.5$ units/day, $c_2 = 2$ units/day, and standard deviation $\sigma = 8$ days. This will have an optimal mean waiting time to develop the defensive phenotype of 84.1 days (the deterministic calculation is 6.4 days less, that is 77.7 days). If the energy level available from the environment increases to 105 units then from equations (8) the population will move to an optimal mean waiting time of 81.8 days with a standard deviation of 7.2 days. The extra energy available allows a more rapid deployment of the defensive phenotype (reduced lifetime risk of predation) because individuals have more energy to spare on maintaining this phenotype for a longer time.

The form of equation (8) imposes a constraint on the solution if the energy levels decrease. If $E_1 - E_0 < \frac{7}{3}(c_2 - c_1)(\mu_1 - \mu_2)$ then the change in the mean and variance of the waiting time tends to infinity. That is, there is no preferred path when the energy change is too great, but the variance of the waiting time will tend to zero, indicating that there is no advantage for population fitness in maintaining any variation in the waiting time.

4. **Discussion.** The extension of the work of Nishimura (2006) [4] to deal with inducible plasticity and fitness as a stochastic process is a natural step. The Nishimura (2006) [4] model deals with individual optimization of the trade-off between survival and remaining energy (a proxy for fecundity) and we have developed the model by investigating how variance in the set point of this trade-off can affect population fitness. We show that for a given set of initial conditions (energy status and predation rate) leading to a particular value of population fitness, mean waiting time for development of a defensive phenotype is positively correlated with variance in the waiting time, such that maximal fitness can be described by a continuum between early deployment/low variance and later deployment/high variance. Assuming that predation rates are normally distributed random variables within a population makes the frequency distribution of the resulting fitness function asymmetrical when the predation rates are taken to be proportional to the population size. The distribution becomes lognormal through the nonlinear transformation of the exponential function. This introduces the variance of the waiting time, as well as the mean of this variable, into the expected value for the fitness function. Thus, the trade-off between the mean and the variance in the formulation of the optimal fitness describes a subfamily of probability densities. That is, there is a subfamily of asymmetrical probability densities for waiting time which have optimal fitness
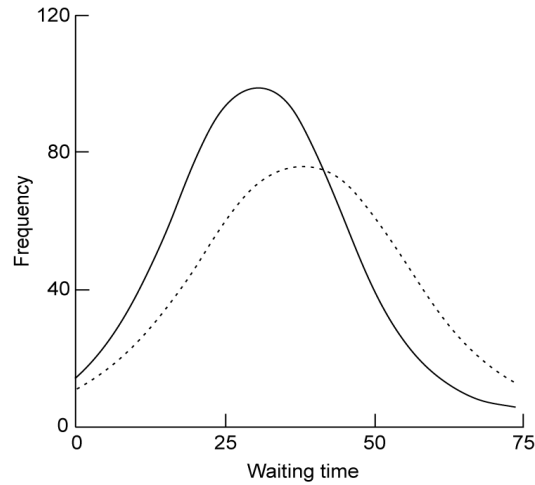
FIGURE 2. Schematic view of the frequency distributions for the waiting time for two populations each having the same optimal expected value for fitness given by equation (4).

for a given energy status and predation rate in the population. This is illustrated in Figure 2, which shows two different probability densities for waiting time in two populations each with a different mean and variance, but which both have the same mean fitness.

The analysis here is dependent on the form of the fitness function. The form adopted by Nishimura (2006) [4] is particularly simple with a high degree of abstraction. In this respect it emphasizes two important features of an inducible defense mechanism. These are the density-dependent predation rate and the proportional increase in energy cost with increasingly early deployment of the defensive phenotype. As shown in this paper, under these conditions the population of organisms will evolve to an optimal fitness dependent on a waiting time described by a subfamily of frequency distributions that conform to the mean-variance relationship derived here.

Biologically this means that one should expect to find a variety of this subfamily of frequency distributions among populations with similar characteristics. In populations selected with respect to the elements of the abstraction formulated by Nishimura (2006) [4] there will not be a unique frequency distribution of waiting times at optimal mean fitness. Furthermore, once a population settles on an optimum frequency distribution of waiting times defined by the mean-variance trade-off derived here it would be expected that, other things being equal, the population will random walk (drift) along the mean-variance line with consequent drift in the frequency distribution of waiting time. Natural perturbations in E, the energy

available to the population, would also induce changes in the frequency distribution.

However, this degree of flexibility in the population also provides scope to initiate other strategies. Because of the effect of the mean-variance trade-off in waiting time on fitness, a population with high mean and high variance of waiting time (implying a population with a high proportion of individuals with long waiting times) will be equally competitive with a population with low mean and low variance of waiting time (implying a population with a low proportion of individuals with long waiting times) in terms of managing fitness due to energy expenditure and predation. Thus, if a longer waiting time was advantageous to other traits not abstracted into the current fitness function, then a population with a mean-variance trade-off favoring a greater frequency of individuals with long waiting times would be favored independently of the effect of predation rate. For example, in a situation where false signals of changes in the environment were common (unreliable cues), long waiting time might be favored. The optimal path-based calculation shows that if the available energy in the environment increases there is a trend for the mean and the variance to increase, albeit by differing amounts. Once the fitness is optimal again the population can maneuver both mean and variance of waiting time along the line defined by the optimal fitness, as shown in Figure 1. Clearly, inevitable fluctuations in energy availability will drive the mean-variance trade-off in waiting time along the optimal paths described here. This provides a mechanism for confining the frequency distribution for the waiting time, since when the environment changes frequently the population will tend to remain on the optimal path.

Most previous studies that have considered stochasticity in the setting of adaptive plasticity have assessed how fitness can be optimized when the environment is stochastic. For example, Yoshimura and Clark (1991) [8] discussed the relationship between geometric mean population fitness (requiring minimization of variance in reproductive rates) and individual average reproductive output and described the role of risk-sensitive behavioral strategies ("bet hedging") in this context. More relevant to the present paper, Hartt and Haefner (1998) [1] considered the effect of genetically determined phenotypic variation in prey traits on prey fitness in a predator-prey system and concluded that increased variance in the traits examined (fecundity and predator evasiveness) enhanced mean population fitness to similar extents as did increases in the mean values of the traits. However, they did not explicitly investigate the trade-offs between trait means and variances.

In summary, we have shown that, in a system of inducible defensive plasticity, prey population fitness is maximized by a trade-off between mean waiting time and variance in waiting time. Populations may achieve equal fitnesses with different frequency distributions of waiting times, which may allow exploration of different environments.

Appendix. To trace the path from any point in plasticity mean time and variance space to the optimal line the point should move in the direction of steepest descent

of the level curves at that point. This is shown in Figure 1. That is, so that the solution $y = f(x)$ is a solution to:

$$\frac{dy}{dx} = \frac{\partial \overline{W}/\partial y}{\partial \overline{W}/\partial x}$$

Here $x = \alpha \sigma^2$ and $y = \bar{t}$. Thus, x and y have the same dimension of time.

Note that this is the gradient of the normal (perpendicular) lines to the contours of the fitness $\bar{W}(x, y) = $ constant. To facilitate the calculations we need to make the time and the variance of time have the same dimensions. Then

$$\overline{W}(x, y) = e^{-\mu_2 T} e^{-\alpha y} e^{\frac{\alpha^2 x}{2}} \left[E_2 + c(y - x) \right]$$

Thus

$$\frac{\partial \overline{W}}{\partial x} = e^{-\mu_2 T} e^{-\alpha y} \left[\frac{\alpha}{2} E_2 + \frac{\alpha}{2} c(y - x) - c \right] e^{\frac{\alpha x}{2}}$$

$$\frac{\partial \overline{W}}{\partial y} = e^{-\mu_2 T} \left[-\alpha E_2 - \alpha c(y - x) + c \right] e^{\frac{\alpha x}{2} - \alpha y}$$

and:

$$\frac{dy}{dx} = \frac{-\alpha E_2 - \alpha c(y - x) + c}{\frac{\alpha}{2} E_2 + \frac{\alpha}{2} c(y - x) - c} = \frac{-2\alpha E_2 - 2\alpha c(y - x) + 2c}{\alpha E_2 + \alpha c(y - x) - 2c}$$

Making a change of variable to $z = y - x$ we obtain:

$$\frac{dz}{dx} = \frac{-3\alpha (E_2 + cz) + 4c}{\alpha(E_2 + cz) - 2c}$$

and so,

$$\frac{\alpha(E_2 + cz) - 2c}{-3\alpha(E_2 + cz) + 4c} \frac{dz}{dx} = 1 \tag{9}$$

Solving the separable differential equation (A1) gives a transcendental equation as the solution in the original variables as

$$\frac{3\alpha (E_1 + c(y - x) + 4c}{3\alpha (E_1 - E_0) + 7c} = e^{\frac{3\alpha}{2}(y + 2x - y_1 - 2x_{1,t})}$$

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E-mail address: `g.c.wake@massey.ac.nz`
E-mail address: `tony.pleasants@agresearch.co.nz`
E-mail address: `a.beedle@auckland.ac.nz`
E-mail address: `pd.gluckman@auckland.ac.nz`

A model for phenotype change in a stochastic framework

Wake, Graeme C.

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