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Inducible plasticity: optimal waiting time for the development of an inducible phenotype

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ABSTRACT

Question: How does an organism that possesses inducible plasticity determine waiting time before the development of a secondary phenotype after changing to the secondary environment, in which the inducible secondary phenotype is suitable?

Model: Maximization of the fitness currency, the survival possibility times the expected amount of remaining energy at terminal time, with respect to waiting time before development of a secondary phenotype.

Key assumptions: If the individual develops the inducible secondary phenotype in the secondary environment, death rate is reduced. The development and maintenance of the inducible phenotype incurs a cost.

Results: The optimal waiting time should be longer under the following conditions: when the inducible phenotype has low effectiveness in improving the survival rate of an organism exposed to the secondary environment; when the cost of development of the secondary phenotype is high; when the time delay required to develop the phenotype is short; or when the total energy that an organism possesses initially is low and fitness will be evaluated far in the future.

Keywords: cost, delay time, inducible defences, inducible plasticity, waiting time.

INTRODUCTION

Phenotypic plasticity is the ability of a single genotype to produce alternative morphologies, physiological states or behaviours in response to different environmental regimes (Gilbert, 2003; West-Eberhard, 2003). Phenotypic plasticity thus refers to the flexible response of a genotype to variety in the environment (Schlichting and Pigliucci, 1998). Inducible plasticity is defined as phenotypic changes in response to an external environmental change (Pfennig, 1992; Gilbert and Schreiber, 1995, 1998; Tollrian, 1995; McCollum and Leimberger, 1997; Slusarczyk, 1999; Michimae and Wakahara, 2002; Kishida and Nishimura, 2005).

Optimization models provide a means of achieving a rational understanding of the conditions necessary for the evolution and maintenance of inducible plasticity (Lively, 1986a; Moran, 1992; Gross and Repka, 1997; Sultan and Spencer, 2002; Hazel *et al.*, 2004). Organisms exhibiting

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inducible plasticity in response to a change in the external environment gain a fitness advantage compared with organisms that possess a non-plastic design, provided that the plasticity itself and the environmental change satisfy certain conditions (Lively, 1986a; Moran, 1992; Pigliucci, 2001). The most persuasive explanation for why an organism changes from an ordinary phenotype to a secondary one when a change of environment occurs is that it receives a cue reflecting the environmental change and then evaluates whether the cost of development and maintenance of the secondary phenotype outweighs the advantage it confers in the new environment.

Despite this rationalized explanation for the evolution and maintenance of inducible plasticity (Lively, 1986a; Moran, 1992; Padilla and Adolph, 1996; Dewitt *et al.*, 1998; Schlichting and Pigliucci, 1998; Schlichting and Smith, 2002), decision making by individual organisms is still an unexplored theoretical topic that has not been adequately addressed in previous studies of inducible phenotypic plasticity (but see Clark and Harvell, 1992; Gabriel, 1999; Jaremo *et al.*, 1999). When an organism encounters an environment more suitable for its secondary phenotype, it has several options.

To determine the appropriate level of adjustable cost for development of the secondary phenotype, the organism must make a strategic decision. An early decision increases the organism's investment, whereas a late decision lengthens the time of exposure to the secondary environment with the less adaptive primary phenotype. Here, I use the word 'decision' figuratively for a conditional response to a changing environment by any type of organism. The time lag between the environmental change and development of the inducible phenotype thus has components in addition to the delay time, which is the time required to complete the secondary phenotype.

My aims in this paper are to clarify that waiting is a strategy for an organism developing the secondary phenotype, and to explore testable predictions of the waiting time before development of a secondary phenotype. I have chosen to investigate this problem in the context of predator-inducible defences (Lively, 1986b; Trussell, 1996; Harvell and Tollrian, 1999; Kishida and Nishimura, 2004, 2005) – that is, the ability of an organism to produce a defensive phenotype in response to a change in predation risk. The prey organism adopts a basic, non-defensive phenotype in the primary environment without a particular predator, but when faced with an environment that includes that predator, it produces an adaptive secondary defensive phenotype to deal with the now harsh environment.

While the terminology I use relates to the context of inducible defences, I argue that the model has general applicability, with or without modification, as appropriate in the circumstances. Since my argument assumes that inducible phenotypic plasticity is favoured over alternative designs for phenotypic expression, I assume that the particular conditions of induction cost and occurrence frequency of the secondary environment favouring inducible plasticity over constitutive designs are implicitly fulfilled, and analyse the timing of the decision to adopt the inducible phenotype after the environment has changed.

THE MODEL

The simplest logically complete model with which we can argue the optimality of an inducible secondary phenotype must incorporate certain minimum conditions. First, I postulate a prey individual with a primary phenotype (non-defensive phenotype) that has just detected the secondary environment (predator environment). If the prey individual does not develop the inducible secondary phenotype (defensive phenotype) in that predator

environment, its death rate is μ_1 . The death rate is reduced to μ_2 by development of the defensive phenotype, where $\mu_1 > \mu_2$. The development and maintenance of the defensive phenotype incurs a cost. I assume that c_1 is the default baseline energy cost to the prey individual per unit time, and c_2 includes the additional costs of building and maintaining the defensive phenotype per unit time ($c_1 < c_2$).

If the prey organism is being induced to develop the defensive phenotype, it may commit one of two types of inappropriate decision making with regard to timing: it may make an early decision, with the result that it pays an excessive cost, c_2 , over the long term; or it may hesitate to make the decision, with the result that the prey organism incurs a high mortality risk, μ_1 , over the long term. We can thus suppose that the prey organism has two main concerns, to reduce the possibility of death by predation and to expend less energy on defence and leave more energy for other physiological processes (e.g. reproduction), at an arbitrary terminal time of fitness evaluation, T .

Suppose that E is the total initial energy budget and c_{0i} is the cost of the plasticity phenotype *per se* (Dewitt *et al.*, 1998). If the habitat of the prey individual has no predator, the prey individual is not being induced to develop the defensive phenotype and it pays only the plasticity cost, c_{0i} , and the default baseline cost, c_1 ; that is, its total cost is $c_{0i} + c_1T$. If the individual decides to develop the defensive phenotype at time t after being exposed to predation threat, its cost is $c_{0i} + c_1(t + \tau) + c_2(T - t - \tau)$, where τ is the delay time (i.e. the time required to complete the effective defensive structure after the decision is made). Here, for simplicity, I assume that the building and maintenance costs are imposed immediately after $t + \tau$ time.

To address the decision making that accompanies the development of the secondary environment, I evaluate the performance of a decision maker adopting decision timing t as the expected survival probability in the predator environment for time interval T , $e^{-(\mu_1(t+\tau) + \mu_2(T-t-\tau))}$. Survival and energy remaining at time T are the elements that determine the value of a fitness currency. The suitable fitness currency, $W(t)$, is equal to the survival possibility at terminal time T times the expected amount of remaining energy:

$$W(t) = e^{-(\mu_1(t+\tau) + \mu_2(T-t-\tau))} (E - c_{0i} - c_1(t + \tau) - c_2(T - t - \tau)) \quad (1)$$

The achievement (survival times the remaining energy) of the decision maker would be converted to another appropriate term of fitness currency for another (non-defensive) type of inducible phenotype.

RESULTS AND DISCUSSION

Optimal waiting time

I now evaluate time t to maximize the fitness. By solving for $\partial W/\partial t = 0$ with respect to t , we can obtain the necessary conditions of the waiting time t^* for the development of the defensive phenotype after the prey organism is exposed to the predation threat to maximize W as

$$t^* = \frac{1}{\mu_1 - \mu_2} - \frac{\tilde{E}}{c_2 - c_1} \quad (2)$$

where $\tilde{E} = E - c_{0i} - c_1\tau - c_2(T - \tau)$ indicates the energy remaining at terminal time T when the prey adopts an immediate decision (i.e. $t = 0$).

The second derivative of W at t^* is $\partial^2 W / \partial t^2 = (c_1 - c_2)(\mu_1 - \mu_2)e^A$, where

$$A = \frac{-(E - c_{0i})(\mu_1 - \mu_2) - (c_1(1 + \mu_2 T) - c_2(1 + \mu_1 T))}{c_1 - c_2}$$

It has a negative value under the conditions of our scenario, $c_2 > c_1$ and $\mu_1 > \mu_2$. Therefore, t^* maximizes the fitness of the prey.

When the relation

$$\tau < \frac{1}{\mu_1 - \mu_2} - \frac{E - c_{0i} - c_2 T}{c_2 - c_1} \quad (3)$$

holds, the optimal waiting time is positive. Otherwise, the prey should make an instantaneous decision at the beginning of the predation threat (i.e. $t^* = 0$).

The above mathematical analysis informs us that the trade-off between energy left and the probability of non-lethality at the terminal time involves the strategic part in the time lag between the environmental change and development of the inducible phenotype. The right-hand side of equation (2) tells us that the optimal waiting time should be longer under the following conditions: when the inducible defensive phenotype has low effectiveness in improving the survival rate of an organism exposed to a predation hazard (i.e. when the value of $\mu_1 - \mu_2$ is small); when the cost of development of the defensive phenotype is high (i.e. the value of $c_2 - c_1$ is large); when the time delay τ required to acquire the defensive phenotype is short; or when the total energy that an organism possesses initially, E , is low and fitness will be evaluated far in the future. These conditions evidently illustrate the characteristics of inducible defences: if the cost of development of the defensive phenotype is high and the induced defence has low effectiveness, the organism should delay initiating development of the defensive phenotype in order to delay incurring the cost as long as possible.

The actual time chosen (strategic waiting time) is not observable. The observable time consists of the sum of the strategic component (waiting time) and the constraint component τ (delay time required to acquire the defensive phenotype). If inequality (3) holds, then the observable total time, \tilde{t} , required to complete the inducible phenotype is

$$\tilde{t} = \frac{1}{\mu_1 - \mu_2} - \frac{E - c_{0i} - c_2 T}{c_2 - c_1} \quad (4)$$

Thus, the observable total time required to develop the defensive phenotype in many cases does not reflect the time delay. Even when the duration of time τ is altered, the total time needed to develop the phenotype reflects the timing decision. In contrast, if time τ is long such that it dominates the total time required to develop the defensive phenotype – that is, if it does not satisfy inequality (3) – then the total observable time $\tilde{t} = t^* + \tau$ is τ , because the prey organism makes an immediate decision at the beginning of the predation threat (i.e. $t^* = 0$).

It is possible to deduce the optimal waiting time for more complex scenarios with some modifications of the model's assumptions. If the energy cost of the induced phenotype is concentrated during the development of the phenotype (i.e. the maintenance cost of expression of the inducible phenotype is small or zero), the optimal waiting time becomes

shorter. In the extreme case in which all costs relating to the induced phenotype are incurred immediately at the time of induction, such as in the case of an escape behaviour, no waiting time is expected if the other assumptions of the present model are kept. However, if there is a possibility that the secondary environment will stochastically go away, then the optimal waiting time should become longer, even if a cost is incurred only during the development of the secondary phenotype. These deductions can also be quantified by the mathematical model with the modifying assumptions incorporated.

Optimal waiting time and the extent of the induced phenotype

Adjustment of the extent of the phenotype developed in response to different levels of predation threat is another decision task. The extent of development of the phenotype is adjusted in accordance with different levels of predation threat by larvae of the frogs *Rana lessonae* (Van Buskirk and Arioli, 2002) and *Rana pirica* (O. Kishida *et al.*, unpublished data), and by the intertidal snail *Littorina obtusata* (Trussell and Nicklin, 2002). These studies considered the adaptive significance of this phenomenon, but they did not consider adjustment of the time to develop the inducible phenotype, which is the strategic aspect of the inducible plasticity. Since inducible defences are a cost-saving strategy (Clark and Harvell, 1992), the extent of the induced phenotype and the waiting time before developing the inducible phenotype for different levels of predation threat are potential decision tasks for organisms with inducible defences.

Both decision tasks are involved in the development of an inducible defence. Suppose that a prey organism is exposed to a high potential predation threat. In these circumstances, the prey must intensify the extent of development of the inducible phenotype. The delay time, τ , for completion of the development of the inducible phenotype can be supposed to be an increasing (or non-decreasing) function of the extent of the induced phenotype, $\tau(x)$, where x is the extent of development of the phenotype on completion. Therefore, intensification of the inducible phenotype under high predation threat lengthens the delay time required. Furthermore, intensification of the extent of the inducible phenotype incurs an additional cost – that is, it increases the value of c_2 , which lengthens the waiting time. These two processes thus tend to lengthen the total time, \tilde{t} , required to complete the inducible phenotype. However, antithetically, the high threat itself tends to shorten the waiting time. These complex interrelations obscure the emerging pattern of decision making about waiting time.

When a prey organism is exposed to a high potential predation threat, the observable time between the environmental change and the completion of the development of the inducible phenotype shows two distinct patterns, reflecting these antithetical mechanisms. If the requirement of additional energy and delay time for intensification of the inducible defence predominates, the observable time for completion of the inducible phenotype becomes long. In this case, we cannot determine whether the prey organism adjusted the waiting time in response to its exposure to a high potential predation threat. In contrast, if little additional energy and delay time for intensification of the inducible defence are required, the observable time for completion of the inducible phenotype becomes short. In this case, we can identify the strategic decision to shorten the waiting time before development of the inducible phenotype.

Because waiting time is affected by the total energy that an organism possesses and the period of time between the decision and the fitness evaluation, the extent of development of

the inducible phenotype is also affected by these factors. An empirical study to detect and quantify the timing decision and the extent of development of the inducible phenotype is needed to further clarify the interrelated decision tasks of inducible plasticity.

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