A Reward-driven Model of Darwinian Fitness

Jan Teichmann[1], Eduardo Alonso[2] and Mark Broom[1]
[1]*Department of Mathematics, City University London, London EC1V 0HB, U.K.*
[2]*Department of Computer Science, City University London, London EC1V 0HB, U.K.*

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Abstract: In this paper we present a model that, based on the principle of total energy balance (similar to energy conservation in Physics), bridges the gap between Darwinian fitness theories and reward-driven theories of behaviour. Results show that it is possible to accommodate the reward maximization principle underlying modern approaches in behavioural reinforcement learning and traditional fitness approaches. Our framework, presented within a prey-predator model, may have important consequences in the study of behaviour.

1 INTRODUCTION

In an evolutionary context, models such as optimal foraging theory (OFT) look at behaviour from the point of view of maximizing Darwinian fitness (e.g., Orr, 2009). On the other hand, the fact that animals show clear reward driven motivations has been extensively reported (Barto et al., 1990; Sutton and Barto, 1998). From the evolutionary perspective models assume a monotonically increasing functional relationship between rewards and fitness. In such a scenario optimization of rewards seems like a straightforward choice. Nevertheless, the success of reward mediated learning as an omnipresent adaptation to the environment can easily deceive the observer into believing that this assumption, that animals just optimize rewards, is generally true (Staddon, 2007), and, very little is still known about the relationship between behavioural and genetic traits. To fully understand the evolution of animal behaviour we require both mechanistic and functional approaches. The mechanistic approach tries to quantify the influence of genetic and environmental factors on the phenotype, whereas the functional approach tries to describe how the interaction of phenotypes and their environment affects fitness. Functional approaches towards understanding behaviour have received very little attention (see, for example, Dingemanse and Réale, 2005). Similarly, it is evident that, notwithstanding the accomplishments of computational theories of reinforcement learning in modelling neural and psychological factors (e.g., Dayan and Daw, 2008; Rangel et al., 2008; Schultz, 2008), the use of rewards in this area is a great simplification of the true nature of rewards (Teichmann et al., 2014). Although new ways to enrich the reinforcement learning ontology with ethological and evolutionary information have been reported (Alonso et al., 2015), the problem of integrating reward-driven approaches and fitness theories has not been tackled so far. It is apparent that whereas rewards reflect some fitness component, a general relationship between strength of rewards and fitness needs to be established.

The question is: is it possible to determine the fitness component of rewards from the environmental set-up and the behaviour of predators? In order to solve this conundrum we have assumed that predators generally show evolved behaviour adapted to their environment and that without the occurrence of new mutants selection is of a stabilizing nature: the end-result is a stable system of balanced interactions of co-evolved predators and all their prey. We use the stability argument to infer the fitness components of subjective rewards. The observed environment is interpreted as an evolutionarily stable snapshot without the presence of any mutants with fitness advantages/disadvantages. The resulting model has been used previously to model the outcome of reward driven learning (Teichmann, 2014) and the aim of this paper is to compare the results of reward driven learned behaviour with the prediction of the

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fitness component of this model assuming energy balance and evolutionary stability.

2 THE PREDATOR LIFETIME MODEL

This section introduces the lifetime model of an individual predator and the definition of the individual's fitness based on its interaction with the environment in the form of payoffs and additional aspects of its behaviour, metabolism, and lifetime traits, age specifically.

We model a situation where the predator faces different types of prey. These are either aposematic, which are prey with invisible defences (such as toxins) advertised by a clear signal (such as bright colouration), or Batesian mimics, which are undefended. We shall simply refer to the former type as "models" and the latter as "mimics". The predator feeds on prey it encounters, as it cannot distinguish between models and mimics based on their appearance. However, the predator has the option to move around freely in its environment to avoid encounters with possibly aversive defended prey based on its experience. Under the assumption of interim stability without the presence of mutants it follows that

$$t_0 \frac{dT}{dk} - E(u) + R = 0, \tag{1}$$

with $t_0 \frac{dT}{dk}$ representing the metabolic cost of the predator as time T passes during interaction k with the prey, $E(u)$ the behavioural expenditure (an energy related quantity defined as the energetic cost of behaviour including, amongst others, locomotion and reproduction), and R being the influx of some fitness quantity from predation. These terms can be interpreted as a form of energy and, generally, $t_0 \frac{dT}{dk} < 0$ and $R > 0$. If this condition is not met, and the l.h.s. in Eq (1) is positive, the population of predators would grow; and if the l.h.s. is negative, the population of predators would shrink. In a coupled system of co-evolution this would lead to changing selective pressure on the prey population, which is assumed to be stabilizing. For simplicity we assume that the system has reached a stable point of balanced interactions between predator and prey.

It must we noted that co-evolutionary dynamical systems, in particular with multiple prey species, can have many possible solutions, including cycling and species extinction as well as a unique equilibrium. We have focused only on the fitness of the predator, through Eq. (1), and have not given the equivalent functions for the different prey species at all. These could take a wide number of forms. We don't mean to imply that under any given prey fitness function there would be a stable equilibrium; only that there would be a range of plausible scenarios which would yield a stable equilibrium, and that we concentrate on these cases only. In particular, an extreme case would be if the fitness of the prey does not greatly depend upon the fitness of our predator (they may have many predators, others of which are more numerous, or their mortality will be driven by internal competition), when the system approximates to a single species system given by Eq. (1). The results in the next section will hold for all cases which yield an equilibrium, but also for cycles of sufficiently small amplitude. Of course, there can be systems with species persistence and significant oscillations where our results do not hold.

The total available prey from the prey population i is given by,

$$G_i = \int_x \int_y g_i(X,Y)\,dx\,dy = 2\,p_i \pi \sigma_{i,x} \sigma_{i,y}, \tag{2}$$

where π is a normalization factor and the dispersion of each prey population i within the environment is described by a Gaussian function

$$g_i(X,Y) = p_i \exp\left(-\left(\frac{(X - x_{i,0})^2}{2\sigma_{i,x}^2} + \frac{(Y - y_{i,0})^2}{2\sigma_{i,y}^2} \right) \right), \tag{3}$$

with $(x_{i,0}, y_{i,0})$ being the centre of the prey population with density p_i, and $(\sigma_{i,x}, \sigma_{i,y})$ the spread of the prey. The payoff, aka the reward, is defined as

$$R = \sum_i G_i d(t_i)\left(r^* - t_i^2\right), \tag{4}$$

with r^* being the assumed fitness component of the payoff, t^2 the cost incurred by ingesting toxins, and $d(t)$ the probability of ingesting a prey individual of toxicity t after taste sampling as given by

$$d(t) = \frac{1}{1 + d_0 t}. \tag{5}$$

We assume that r^* is related to the fitness of the prey. For example, if fitness is measured in terms of energy the predator has a high fitness influx from a prey which also had a great amount of energy

reserves for reproduction. Moreover, if $r*$ relates to the fitness of the prey this value has to be equal for different types of prey under the assumption of stability. If the fitness contribution of a type of prey would be greater than the fitness of other prey types it would be advantageous for the predator to feed exclusively on this prey. It is apparent that fitness in such an interpretation is not equivalent to the standard idea of fitness of the number of offspring surviving to reproductive age. Here $r*$ is better interpreted as an energetic quantity from which individuals can allocate towards the cost of predator defences, reproduction, metabolic costs of toxin ingestion, or behavioural expenditures.

In summary, the fitness component $r*$ for a predator prey interaction with just a single type of prey is given by

$$r^* = \frac{1}{Gd\lambda(A)} \left(\begin{array}{l} E(u) + t_0 + \\ G\left(t_0 t_s + d\left(t^2\lambda(A) + t_0\left(t_t + t_h\right)\right)\right) \end{array} \right). \quad (6)$$

Eq. (6) consists of a scaling factor and the sum of the predator's behavioural expenditure, its basal metabolic cost, and the additional costs of foraging such as the sampling of prey t_s, the handling of prey t_h, and the recovery from ingested toxins t_t. $\lambda(A)$ represents the age dependent agility of the predator, given by

$$\lambda(A) = \frac{1}{1+A}. \quad (7)$$

In short, we solve Eq. (1) for $r*$ by substituting for R with the definition in Eq. (6). Consequently, $r*$ needs to be higher when (i) a predator feeds on toxic prey; (ii) when the prey requires lengthy handling; (iii) prey is rare; (iv) the predator has a high metabolic rate t_0; (v) the predator utilizes costly behaviour; or (vi) when predators live longer. On the predator's side $r*$ can be termed the nutritional value of prey within this context.

If we consider a predator feeding on an aposematic prey in the presence of a Batesian mimic the lifetime model needs to be refined to accommodate the fact that the predator cannot distinguish between the two prey populations and has to use experience obtained from previous exploration. As such both prey populations experience some levels of predation. Moving to multiple food sources i under the assumption of stability gives the following condition

$$0 = \sum_i R_i - t_0 \frac{dT}{dk} - E(u). \quad (8)$$

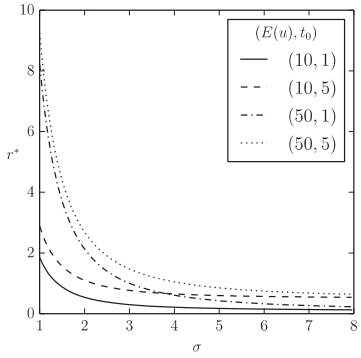
As discussed, we assume that both types of prey contribute the same value of $r*$ whereas the models allocate parts of their energy inventory towards the cost of their anti-predator defences and mimics have to allocate greater amounts towards reproduction to compensate for higher levels of predation, especially in the case of predators which are able to taste-sample their prey. Consequently, $r*$ in the model-mimic system is given as follows:

$$r^* = \frac{1}{\sum_i Gd\lambda(A)} \left(\begin{array}{l} E(u) + t_0 + \sum_i G_i \left(\begin{array}{l} t_0 t_s + d_i \\ \left(\begin{array}{l} t_i^2\lambda(A) + \\ t_0\left(t_{t,i} + t_{h,i}\right) \end{array} \right) \end{array} \right) \end{array} \right). \quad (9)$$

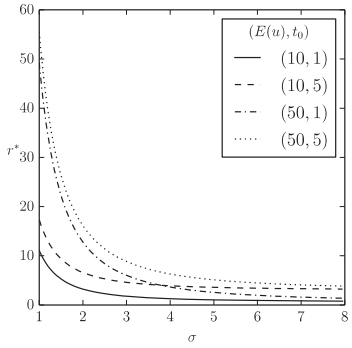
That is, the case of multiple prey types is a direct extension of the case of a single prey type in Eq. (6) where the scaling factor and the outcome of interaction with the prey is the sum over all the contributing prey types.

3 RESULTS

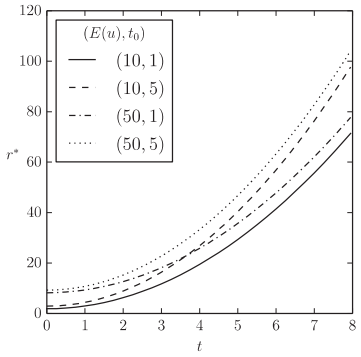
The results in Figure 1 show the effects of different aspects of the lifetime model on the nutritional value $r*$ in the context of a single prey type. We see that increasing prey abundance σ reduces the required nutritional value of prey. Nevertheless, there is a minimal nutritional value prey must have which depends on the metabolic rate of the predator t_0 and which is independent of the predator's behavioural expenditure $E(u)$ and the prey's abundance σ (Figures 1a and 1b). If prey is rare, the predator's behavioural expenditure $E(u)$ has a much greater impact on $r*$ than its metabolic rate t_0. The age distribution or longevity of predators acts as a simple multiplicative factor in this context. Figures 1(c) and 1(d) show the effects of prey toxicity *t* on the nutritional requirement $r*$. Generally, increasing prey toxicity *t* requires higher nutritional values $r*$ for stability. In the case of less toxic prey the predator's behavioural expenditure $E(u)$ again has a greater impact on $r*$ than its metabolic rate. With increasing prey toxicity the predator's metabolic rate has greater impact on $r*$. The age distribution or longevity of predators acts not just as



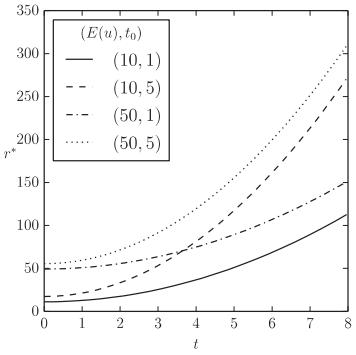
(a) The fitness component r^* of a single prey type with respect to the prey population's abundance σ, the predator's behavioural costs $E(u)$, and the predator's metabolic rate t_0. Hence there is no ageing, i.e., $\lambda(A=0)=1$.



(b) The same as 1(a) with age distribution given by $A=5$.



(c) The fitness component r^* of a single prey type with respect to the prey population's toxicity *t*, the predator's behavioural costs $E(u)$, and the predator's metabolic rate t_0. Here we have $\sigma=1$, and no ageing, $\lambda(A=0)=1$.

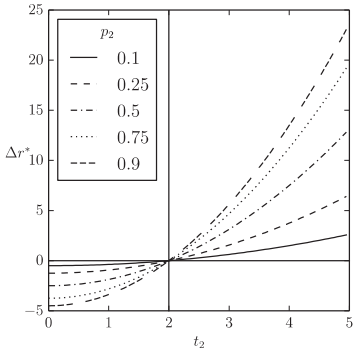


(d) The same as 1(c) with age distribution given by $A=5$.

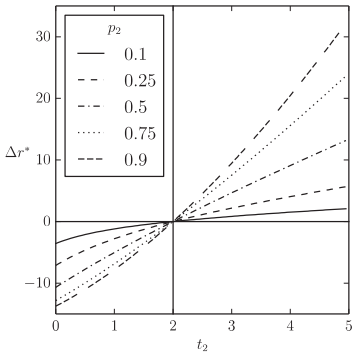
Figure 1: Effects of a single aposematic prey population on the fitness component r^* in a stable predator-prey environment without taste sampling: $d(t)=1$, $t_s=0$, $t_h=0.1$, and $t_t=0.1$.

a simple factor relating to prey toxicity, as it was the case in prey abundance.

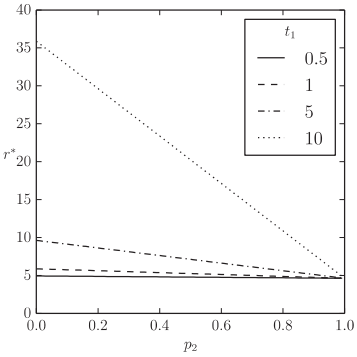
Figure 2 shows the results of Eq. (9) on the dependency of different parameters of the model. The overall prey abundance is held constant in all charts. Figures 2(a) and 2(b) show the effects of a second aposematic type of prey in comparison to an environment with only one aposematic prey type. In the case that the second aposematic prey is less (more) toxic than the first prey type it reduces (increases) r^* overall. An increasing fraction of the second prey type amplifies the effects on r^*. Additionally, taste sampling also amplifies the effect of the second prey type on r^*. However, the impact of taste sampling is greater if the second prey type is less toxic than the first prey type. Figures 2(c) and 2(d) show the effects of mimics. Generally, the presence of mimics lowers r^* and mimics have an increasing impact on r^* with increasing toxicity of the aposematic model t_1. In the case of non-taste-sampling predators the effect of mimics on r^* is linear with respect to the fraction of mimics in the overall prey population p_2. Taste-sampling generally increases r^* and the effect of mimics on r^* becomes non-linear with increasing impact in the case of mimics being rare.



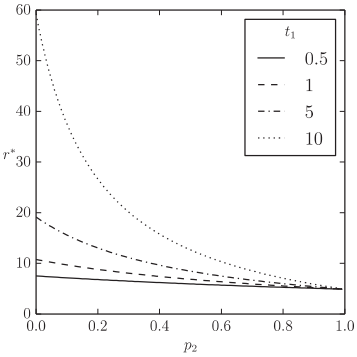
(a) Effects of a second aposematic prey population with respect to its level of defence t_2 and density p_2. The horizontal line $\Delta r^* = 0$ and the vertical line $t_2 = 2$ indicate no differences. Here there is no taste sampling $d(t) = 1$, with $t_s = 0$, $t_1 = 2$, and $p_1 = 1 - p_2$.



(b) The same as 2(a) but with taste sampling with $d_0 = 1$, and $t_s = 0.1$, $t_1 = 2$, and $p_1 = 1 - p_2$.



(c) The effects of mimics within an aposematic prey population with respect to the mimics density p_2 and the models toxicity t_1. Here there is no taste sampling $d(t) = 1$, and $t_s = 0$, $p_1 = 1 - p_2$.



(d) The same as 2(c) but with taste sampling with $d_0 = 1$, and $t_s = 0.1$, $p_1 = 1 - p_2$.

Figure 2: Effects of aposematic prey expressed as the relative change in the fitness component Δr^* in a stable predator-prey environment with multiple prey populations when compared to an environment with a single prey-population. Here $t_h = 0.1$, $t_t = 0.1$, $t_0 = 0.25$, $E(u) = 25$, $\lambda(A = 0) = 1$, and $\sigma = 1$. The total prey abundance $\sum_i G_i$ is held constant.

4 CONCLUSIONS

In this paper we have presented a predator lifetime model including traits such as metabolic costs, locomotion, prey handling, and toxin recovery, which had been abstracted away in the previous studies of behaviour. The fitness quantity is obtained by assuming a stabilizing co-evolution between predator and prey and can be interpreted as a form of energy. On the predator's side this might be the nutritional value of prey and on the prey's side it might be interpreted as an energy inventory which the prey can allocate towards the costs of defence and reproduction. Aposematic prey allocate a greater amount towards the cost of its defence whereas the mimics have to allocate a greater amount towards their reproduction due to higher predation risks from experienced predators. The presence of mimics generally lowers the value of r^* needed for such a system to be stable. If models and mimics co-exist with an unchanged r^* we predict that the models will be better defended than in the corresponding scenarios without mimics.

If mimics and models co-exist but with unchanged levels of defence then models are predicted to be smaller and have lower nutritional value than in a system without mimics. Taste-sampling as a strategy increases r^* if mimics are

rare or if models are only moderately well defended. However, the impact of taste sampling is non-linear especially in systems with highly defended models. In such situations taste-sampling lowers r^*. Consequently, under the assumption of a fixed value for r^* and stability, a predator evolves a taste-sampling strategy because mimics are less common or models are better defended than in a comparable stable environment where predators do not utilize taste sampling.

Another interesting aspect is the effect of different age distributions: in general longevity in predators increases r^*. The effects are linear with regards to prey abundance but non-linear with regards to prey toxicity where behavioural expenditure gains increasing impact in the case of defended prey and older predators, whereas metabolic costs have an increased impact in the case of non-defended prey. The main conclusions of this paper are as follows:

- On the predator's side r^* is related to the nutritional value of prey and on the prey's side it relates to an energy inventory which can be allocated, amongst other things, towards the cost of defences or reproduction;
- Behavioural expenditure has a greater impact than metabolic costs when prey is rare and undefended;
- Metabolic costs have a greater impact when prey is abundant or highly defended;
- Longevity of the predator increases the importance of behavioural expenditure in the case of highly defended prey and the impact of metabolic costs if prey is undefended;
- Mimics generally lower r^* which leads to less nutritional prey or better defended models if r^* is meant to be unchanged;
- Predators utilize taste sampling if mimics are rare or models are highly toxic.

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