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A theory for investment across defences triggered at different stages of a predator-prey encounter

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Abstract

We introduce a general theoretical description of a combination of defences acting sequentially at different stages in the predatory sequence in order to make predictions about how animal prey should best allocate investment across different defensive stages. We predict that defensive investment will often be concentrated at stages early in the interaction between a predator individual and the prey (especially if investment is concentrated in only one defence, then it will be in the first defence). Key to making this prediction is the assumption that there is a cost to a prey when it has a defence tested by an enemy, for example because this incurs costs of deployment or tested costs as a defence is exposed to the enemies; and the assumption that the investment functions are the same among defences. But if investment functions are different across defences (e.g. the investment efficiency in making resources into defences is higher in later defences than in earlier defences), then the contrary could happen. The framework we propose can be applied to other victim-exploiter systems, such as insect herbivores feeding on plant tissues. This leads us to propose a novel explanation for the observation that herbivory damage is often not well explained by variation in concentrations of toxic plant secondary metabolites. We compare our general theoretical structure with related examples in the literature, and conclude that coevolutionary approaches will be profitable in future work.

Keywords: Sequential defences, predation, herbivory, cost, trade-off.

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Introduction

All organisms face threats from enemies, be they predators attacking animal prey, herbivores eating plant tissue, or pathogens and parasites feeding on host tissues. The coevolution between such enemies is a major driving force in evolution, which has contributed substantially to the diversification of defensive mechanisms deployed by organisms, and indeed of life's forms (Vermeij 1987). A major and important general biological question here is why organisms often invest in several defensive mechanisms, rather than putting all their defensive resources into one highly effective "superdefence". Why, for example, do most animals and plants not merely invest in toxins, but often invest additionally in physical and behavioural defences? One answer is that the components of multiple defence suites each target alternative types of enemy, in which case we could expect a positive association between the number of defences deployed and the number of different classes of enemy. A second answer is that multiple defences act simultaneously and perhaps synergistically, so that a greater total level of protection is achieved per unit invested when an enemy is assaulted by e.g. physical and chemical defences together. Alternatively defences may act one after another, presenting predators with a sequence of barriers that enemies must cross to gain the resources presented to them by the victim. Here we focus on this third explanation, and consider the evolution of multiple, sequentially acting defences.

A good reason for assuming that many defences act sequentially - and hence the focus of this paper - is that interactions between victims and enemies can often be split into a number of stages at which one or more defences can be deployed. Although a variety of different descriptions of this process have been suggested (see Caro 2005 for a review), the most commonly used in the context of animal defence is that given by Endler (1991) who splits the process up into six sequential stages: (i) spatial and temporal proximity of predator and prey, (ii) detection of prey by predator, (iii) identification of prey by predator, (iv) chase or stalking by the predator to close the distance to the prey, (v) subjugation of the prey, and (vi) final consumption. Attack by herbivores on plants can be similarly described in a sequence of stages, though here without the behaviour of chase by the predator.

Defensive traits extend across all phases of attacks. For example, prey can reduce the risks: of spatial and temporal proximity by avoiding habitats where predators are more common; of detection, through lack of movement and cryptic appearance; of identification, through mimicry or masquerade; of predators closing in, through fleeing; of subjugation, through struggle, spines or production of slippery secretions; and finally, prey can prevent the risk of consumption, through chemical toxins. Hence it is possible for prey to employ defences at all stages of the predation sequence in order to curtail attack.

Defences are often thought costly (Ruxton et al. 2004, Caro 2005), and investment in defence acting at one stage in the sequence might reduce the benefit of investment in defences that act at later stages. Hence, it seems logical that investment should be biased towards earlier stages, as was argued by Endler (1991). However, it is clear that in the natural world sometimes there is investment in later-acting defences. Here we ask whether there could be a general framework for understanding investment in defences that act in sequence (as highlighted by Caro 2005). Our aim in this paper is to introduce a simple but general theoretical description of a combination of defences acting at different stages in the predatory sequence in order to make predictions about how prey should best allocate investment across different defensive stages. The model can, in our view, provide a flexible and predictive framework for understanding strategies of investment in multiply defensive systems in many biological contexts, including animal prey. We also explore its application to the evolution of sequentially acting plant defences, proposing a new explanation for the otherwise puzzling lack of effects on herbivory for variation in plant chemical defences (Carmona et al. 2011).

The Sequential Defences Model

We assume that the prey can invest in at most n stages of defence, which the predator experiences sequentially. We denote each defence stage by the order i $(i = 1, \dots, n)$ in which it is encountered (so $i = 1$ is the first defence encountered, and $i = n$ the last). We define s_i $(0 \le s_i < 1)$ as the success probability of the prey's i-th defence, i.e. the probability that, if the predator reaches defence i, then it fails to overcome that defence. The effectiveness of each defence depends upon the level of investment in it. We define I_i as the (non-negative) investment made in defense i, so

$$I_i = I_i(s_i) \tag{1}$$

is a non-decreasing function ($I_i'(.) \ge 0$), so a defence with a higher probability of success requires higher investment by the prey. We also assume that, if the prey invests nothing in a defence, then the success probability of that defence will be 0: $I_i(0) = 0$. It would arguably be more natural to consider the investments I_i as the fundamental variables of the model, and survival s_i as being a function of I_i, but our approach is formally identical (provided $I_i(\cdot)$ is monotonic, so there is a 1-to-1 relationship between I_i and s_i) and turns out to be more convenient to analyse.

Note that while predation pressure does not explicitly appear in the model, it is present implicitly because it affects the survival probabilities (or, more precisely, the relationship between I and s). The optimal strategy might be quite different among different populations, facing different environments and predation pressures. We are interested in the evolutionary defence strategy for a certain population. It is quite often observed that many individuals in a certain colony have the similar kind of defence strategies (e.g. similar level of aposematism or camouflage). We think of this as the optimised defence strategy averaged across generations and across populations. The form of the model is consistent with a single attack, but could also be though to represent a number of attacks. The latter are particularly appropriate for plants mounting defences against herbivores, where there could be many attackers, each of which only does a small amount of damage. In that case we still can still think of defences being "breached" with a certain probability, even though there are many individual attack events. Here, predation pressure affects the probability that a defence is breached as well as the "tested costs" (because it affects the average number of times a defence is tested).

We assume that the prey has a total amount of resource, I_T, available for all defences. We define I_A as the investment in all the defences, so

$$I_A = \sum_{i=1}^{n} I_i(s_i) \leq I_T \tag{2}$$

We define $C(I_A)$ as the fitness cost of making investments across the various defences, in whatever division, so that this total investment amount is I_A. We assume that $C(0) = 0$ (when there is no investment in defence, the investment cost is zero). The residual amount of resources left after investment across all the defences, $I_T - I_A$, can effectively then be used as additional investment in non-defensive fitness-enhancing activities. Thus we assume $C(.)$ is an increasing function of I_A (i.e. $C'(.) > 0$).

We further assume that, if defence i is tested by the predator, then (even if the defence holds) there is a cost c_i (≥ 0), henceforth referred to as "tested cost", that can be considered as the injury risk of being exposed to the predators after defence $i - 1$ is breached. (Note that c_i can be 0, which means that the tested cost is zero; e.g the tested cost of crypsis in a nocturnal moth might be zero.) In this assumption, since there is no defence before the first defence, we think that the first defence is always exposed and tested by the predators (although the tested cost for the first defence can be zero, $c_1 = 0$). Alternatively, c_i can be thought of as the costs incurred when a predator triggers the defences at stage i. These need not be solely risk of injury, but might additionally or alternatively be time, energy or other resource spent in the deployment of the defence. Like the model from Wilkening (1999) discussing layered defences in military use, we calculate the probability that each defence is tested and holds (i.e. is not breached); and we also calculate the corresponding fitness when that defence is tested and holds. Multiplying them together, we get the expected fitness contribution from the eventuality where that defence is tested and holds. The overall fitness which we care about is the sum of all these terms. Here, fitness means the average number of viable offspring that an individual produces, and by assuming that this number decreases as successive defences are tested and/or breached we are able to represent many different possible reproductive life histories (continuous reproduction, semelparity, etc.). We consider two particular scenarios: (A) the prey has positive residual fitness (e.g. still alive and can reproduce) when all defences are breached; (B) the prey has zero residual fitness (e.g. dies before reproducing) when all defences are breached. We wish to find the defence strategy that maximises R.

For scenario (A), when the prey still has positive residual fitness when all the defences are breached, the expression of the overall fitness R of the prey for a given investment strategy $S = (s_1, s_2, \ldots, s_n)$ is as follows.

$$R(s_1, s_2, \ldots, s_n)$$

$$= s_1(1 - C(I_A) - c_1)$$

(the fitness when the first defence is tested, but not breached)

$$+(1 - s_1)s_2(1 - C(I_A) - c_1 - c_2)$$

(the fitness when the second defence is tested, but not breached)

$$+...$$

$$+(1 - s_1)(1 - s_2)...(1 - s_{n-1})s_n(1 - C(I_A) - c_1 - c_2 - ... - c_n)$$

(the fitness when the $(n-1)$th defence is tested, but not breached)

$$+(1 - s_1)(1 - s_2)...(1 - s_n) \cdot (1 - C(I_A) - c_1 - c_2 - ... - c_n)$$

(the fitness when all the defences are breached)

$$= 1 - C(\sum_{i=1}^{n} I_i(s_i)) - c_1 - \sum_{j=2}^{n} c_j \prod_{k=1}^{j-1} (1 - s_k) \tag{3}$$

Note that we have assumed that the fitness when all the defences are breached is the same as the fitness when the $(n-1)$th defence is tested, but not breached, since no further tested costs are incurred after the nth defence is breached.

In many cases in the real world, the prey dies or effectively dies with 0 fitness left to reproduce when all the defences are breached. We therefore consider an alternative scenario (B) where the fitness when all the defences are breached is 0 instead of $(1 - C(I_A) - c_1 - c_2 - ... - c_n)$. Then the fitness function is as follows.

$$R(s_1, s_2, \ldots, s_n) = (1 - \prod_{j=1}^{n}(1-s_j))\Big(1 - C(\sum_{i=1}^{n} I_i(s_i))\Big) - c_1 - \sum_{j=2}^{n} c_j \prod_{k=1}^{j-1}(1-s_k) + (\sum_{j=1}^{n} c_j)\prod_{j=1}^{n}(1-s_j) \tag{4}$$

These two scenarios represent the two extreme possibilities for the fitness that ensues when all defences are breached: fitness is not decreased further by the *n*th defence failing in scenario (A), whereas all fitness is lost in scenario (B) if the *n*th defence fails. We expect that the results for an intermediate scenario will lie between those for these two extreme scenarios.

If the organism invests less than the maximum available resources in defences, then those resources are available for reproduction and other fitness-enhancing activities. This is represented in the model by the term $-C(\sum_{i=1}^{n} I_i(s_i))$ in both equations (3) and (4)), which tends to increase fitness if $I_A = \sum_{i=1}^{n} I_i(s_i)$ is decreased. However, due to the other terms in s_i it is not clear without analysis whether I_A is less than or equal to I_T in the optimal strategy.

When testing defences are costly, later defences receive lower investment

If the investment function is the same for all defences, $I_i(\cdot) = I(\cdot)$, we can show that the optimal solution $S = (s_1, s_2, ..., s_n)$ maximising the fitness function R in (3) and (4) always satisfies the following relation when the tested costs c_i are strictly positive ($c_i > 0 \, \forall i$).

$$s_1 \geq s_2 \geq ... \geq s_n. \tag{5}$$

This is because, for any i such that $s_i < s_{i+1}$, we can always make R larger by switching the value of s_i and s_{i+1}, which will only change the term $-c_{i+1}\prod_{k=1}^{i}(1-s_k)$ (in the term $-\sum_{j=2}^{n} c_j \prod_{k=1}^{j-1}(1-s_k)$ in R) to $-c_{i+1}\prod_{k=1}^{i-1}(1-s_k)\cdot(1-s_{i+1})$ (larger than $-c_{i+1}\prod_{k=1}^{i}(1-s_k)$), with the other terms in R unchanged.

Since the investment function $I(s_i)$ is increasing, the relation that $s_1 \geq s_2 \geq ... \geq s_n$ means that

$$I(s_1) \geq I(s_2) \geq ... \geq I(s_n). \tag{6}$$

This shows that investment in earlier defences should never be less than than investment in later defences.

Note that, if $c_{i+1} = 0$, the above argument does not show that $s_i \geq s_{i+1}$, but rather than the fitness R is unchanged by switching the values of s_i and s_{i+1}. This means that, when one of the tested costs is zero, either (i) there is a unique optimal strategy, where $s_i = s_{i+1}$; or (ii) the optimal strategy is not unique, but the optimal strategy in which $s_j \geq s_{j+1}$, for all j has equal fitness to the best strategy where $s_{j+1} > s_j$ for some j. In any biologically realistic situation there will always be a cost — however small — to having a defence tested, but this case is still interesting because it shows what might evolve when the tested costs are very small.

Investing in multiple defences or in a single defence?

The best strategy for the organism might be to invest in multiple defences, with (according to the above result) higher investment in earlier than later defences. On the other hand, the best strategy might be to invest in a single defence, which the above argument shows should be the first one. As we will see later, either of these outcomes can occur, depending on the details of the investment function I. To show this, first we find conditions that the optimal solution must satisfy. To find the maximised R constrained by variable boundaries $0 \leq s_i < 1$, and resource boundary $\sum_{i=1}^{n} I(s_i) \leq I_T$, we write a Lagrange function for the overall fitness function (3) and (4).

$$L(s_1, s_2, \ldots, s_n; \lambda_1, \lambda_2, \ldots, \lambda_n) = R(s_1, s_2, \ldots, s_n) + \sum_{i=1}^{n} \lambda_i (1 - s_i) + h(I_T - \sum_{i=1}^{n} I(s_i)) \tag{7}$$

The necessary condition to get the maximised value R is given by the Karush-Kuhn-Tucker (KKT) condition coming from the above Lagrange function,

$$\frac{\partial L}{\partial s_i} = \frac{\partial R}{\partial s_i} - \lambda_i - hI'(s_i) \leq 0, \quad s_i \geq 0, \quad s_i \frac{\partial L}{\partial s_i} = 0 \qquad i = 1, ..., n \tag{8}$$

$$\frac{\partial L}{\partial \lambda_i} = 1 - s_i \geq 0, \quad \lambda_i \geq 0, \quad \lambda_i \frac{\partial L}{\partial \lambda_i} = 0 \quad i = 1, ..., n \tag{9}$$

$$\frac{\partial L}{\partial h} = I_T - \sum_{i=1}^{n} I(s_i) \geq 0, \quad h \geq 0, \quad h \frac{\partial L}{\partial h} = 0 \quad i = 1, ..., n \tag{10}$$

The second necessary condition (9) combined with $1 - s_i > 0$, is equivalent to

$$\lambda_i = 0 \tag{11}$$

The first necessary condition (8) is equivalent to

$$\frac{\partial L}{\partial s_i} = \frac{\partial R}{\partial s_i} - hI'(s_i) \leq 0, \quad s_i \geq 0, \quad s_i \frac{\partial L}{\partial s_i} = 0 \qquad i = 1, ..., n \tag{12}$$

(a)When $s_i > 0$: we have that $\frac{\partial L}{\partial s_i} = \frac{\partial R}{\partial s_i} - hI'(s_i) = 0$.

(b)When $s_i = 0$: we have that $\frac{\partial L}{\partial s_i} = \frac{\partial R}{\partial s_i} - hI'(s_i) \leq 0$.

For the third necessary condition (10),

(a)When $I_T - \sum_{i=1}^{n} I(s_i) > 0$: we have that $\frac{\partial L}{\partial h} = I_T - \sum_{i=1}^{n} I(s_i) > 0$, so $h = 0$ since $h\frac{\partial L}{\partial h} = 0$.

(b)When $I_T - \sum_{i=1}^{n} I(s_i) = 0$: we have that $\frac{\partial L}{\partial h} = I_T - \sum_{i=1}^{n} I(s_i) = 0$; so we still have $h \geq 0$.

To put them together, the necessary condition is equivalent to the following:

(I) When $0 < s_i < 1$,

$$\frac{\partial R}{\partial s_i} - hI'(s_i) = 0, \qquad h \geq 0, \tag{13}$$

$$(\text{and } h = 0, \text{ when inside the resource boundary } I_T - \sum_{i=1}^{n} I(s_i) > 0)$$

(II) When $s_i = 0$,

$$\frac{\partial R}{\partial s_i} - hI'(s_i) \leq 0, \qquad h \geq 0 \tag{14}$$

$$(h = 0, \text{ when inside the resource boundary } I_T - \sum_{i=1}^{n} I(s_i) > 0)$$

So far, the analysis has been the same whether we assume that the fitness after all defences are breached is zero (Scenario (B), equation (4)) or not (Scenario (A), equation (3)). For the following calculation, we assume scenario (B) only; the calculation for scenario (A) follows along similar lines, and has the same conclusion, and is presented in Appendix B. Given the fitness function R in (4), the necessary condition for R is as follows,

(I) When $0 < s_i < 1$,

$$\begin{aligned}
&\frac{\partial R}{\partial s_i} - hI'(s_i) \\
&= \frac{1}{1-s_i}\prod_{j=1}^{n}(1-s_j)\big(1 - C(I_A) - \sum_{j=1}^{n} c_j\big) - \big(1 - \prod_{j=1}^{n}(1-s_j)\big)\frac{\partial C(I_A)}{\partial s_i} + \frac{1}{1-s_i}\sum_{j=i+1}^{n} c_j \prod_{k=1}^{j-1}(1-s_k) - hI'(s_i) \\
&= 0 \quad (\text{ with } h \geq 0)
\end{aligned} \tag{15}$$

(II) When $s_i = 0$,

$$\begin{aligned}
&\frac{\partial R}{\partial s_i} - hI'(s_i) \\
&= \frac{1}{1-s_i}\prod_{j=1}^{n}(1-s_j)\big(1 - C(I_A) - \sum_{j=1}^{n} c_j\big) - \big(1 - \prod_{j=1}^{n}(1-s_j)\big)\frac{\partial C(I_A)}{\partial s_i} + \frac{1}{1-s_i}\sum_{j=i+1}^{n} c_j \prod_{k=1}^{j-1}(1-s_k) - hI'(s_i) \\
&\leq 0 \quad (\text{ with } h \geq 0)
\end{aligned} \tag{16}$$

Now we have the necessary condition to maximise R— (15) and (16). Next, we are going to explore whether investment can happen in multiple defences or only in one defence.

Since the investment functions are the same for all the defences ($I_i(\cdot) = I(\cdot)$), we have that investment in earlier defences is always larger than investment in later defences (equation (5), (6)), so for some $j(< n)$,

$$1 > s_1 \geq s_2 \geq \ldots \geq s_j > s_{j+1} = \ldots = s_n = 0, \tag{17}$$

or

$$1 > s_1 \geq s_2 \geq \ldots \geq s_{n-1} \geq s_n > 0. \tag{18}$$

Note that when $j = 1$,

$$1 > s_1 > s_2 = \ldots = s_n = 0, \tag{19}$$

then the investment is concentrated only in the first defence.

We will now find the conditions that determine whether investment is concentrated only in the first defence, or in multiple defences.

Let us first assume that there are multiple defences ($2 \leq j \leq n$), then for some $i \in \{1, 2, ..., j-1\}$, we will have $s_i \geq s_{i+1} > 0$. Then from equation (15), we have (20) and (21).

$$\begin{aligned}
&\frac{\partial R}{\partial s_i} \cdot (1 - s_i) - h(1 - s_i) I'(s_i) \\
&= \prod_{j=1}^{n} (1 - s_j) \big(1 - C(I_A) - \sum_{j=1}^{n} c_j\big) - (1 - s_i)(1 - \prod_{j=1}^{n} (1 - s_j)) \frac{\partial C(I_A)}{\partial s_i} + \sum_{j=i+1}^{n} c_j \prod_{k=1}^{j-1} (1 - s_k) - h(1 - s_i) I'(s_i) \\
&= 0,
\end{aligned} \tag{20}$$

$$\begin{aligned}
&\frac{\partial R}{\partial s_{i+1}} \cdot (1 - s_{i+1}) - h(1 - s_{i+1}) I'(s_{i+1}) \\
&= \prod_{j=1}^{n} (1 - s_j) \big(1 - C(I_A) - \sum_{j=1}^{n} c_j\big) - (1 - s_{i+1})(1 - \prod_{j=1}^{n} (1 - s_j)) \frac{\partial C(I_A)}{\partial s_{i+1}} + \sum_{j=i+2}^{n} c_j \prod_{k=1}^{j-1} (1 - s_k) - h(1 - s_{i+1}) I'(s_{i+1}) \\
&= 0
\end{aligned} \tag{21}$$

The term $\prod_{j=1}^{n} (1 - s_j) \big(1 - C(I_A) - \sum_{j=1}^{n} c_j\big)$ in both (20) and (21) is the same, so that we have

$$\begin{aligned}
&- (1 - s_{i+1})(1 - \prod_{j=1}^{n} (1 - s_j)) \frac{\partial C(I_A)}{\partial s_{i+1}} + \sum_{j=i+2}^{n} c_j \prod_{k=1}^{j-1} (1 - s_k) - h(1 - s_{i+1}) I'(s_{i+1}) \\
&= -(1 - s_i)(1 - \prod_{j=1}^{n} (1 - s_j)) \frac{\partial C(I_A)}{\partial s_i} + \sum_{j=i+1}^{n} c_j \prod_{k=1}^{j-1} (1 - s_k) - h(1 - s_i) I'(s_i).
\end{aligned} \tag{22}$$

Since $I_A = \sum_{i=1}^{n} I(s_i)$, the above is equivalent to

$$\begin{aligned}
&- (1 - s_{i+1})(1 - \prod_{j=1}^{n} (1 - s_j)) C'(I_A) I'(s_{i+1}) - h(1 - s_{i+1}) I'(s_{i+1}) \\
&= -(1 - s_i)(1 - \prod_{j=1}^{n} (1 - s_j)) C'(I_A) I'(s_i) + c_{i+1} \prod_{k=1}^{i} (1 - s_k) - h(1 - s_i) I'(s_i).
\end{aligned} \tag{23}$$

$\Rightarrow$

$$-(1-s_{i+1})I'(s_{i+1})\Big((1-\prod_{j=1}^{n}(1-s_j))C'(I_A)+h\Big) = -(1-s_i)I'(s_i)\Big((1-\prod_{j=1}^{n}(1-s_j))C'(I_A)+h\Big) + c_{i+1}\prod_{k=1}^{i}(1-s_k). \tag{24}$$

Since $C'(I_A) > 0$ and also $1-\prod_{j=1}^{n}(1-s_j) > 0$ and $h \geq 0$, we have that $\Big((1-\prod_{j=1}^{n}(1-s_j))C'(I_A)+h\Big) > 0$, so that equation (24) is equivalent to

$$-(1-s_{i+1})I'(s_{i+1}) = -(1-s_i)I'(s_i) + c_{i+1}\frac{\prod_{k=1}^{i}(1-s_k)}{\Big((1-\prod_{j=1}^{n}(1-s_j))C'(I_A)+h\Big)}. \tag{25}$$

The last term in the right-hand side $c_{i+1}\frac{\prod_{k=1}^{i}(1-s_k)}{\Big((1-\prod_{j=1}^{n}(1-s_j))C'(I_A)+h\Big)}$ is positive when $c_{i+1} > 0$, therefore

$$-(1-s_{i+1})I'(s_{i+1}) > -(1-s_i)I'(s_i). \tag{26}$$

which is the same to,

$$(1-s_{i+1})I'(s_{i+1}) < (1-s_i)I'(s_i). \tag{27}$$

The analyses for the fitness function (3) (in Appendix B) are similar to the analysis for the fitness function (4) (from equation 15 to 27). As the relation between s_i and s_{i+1} for the fitness function (3) (equation B.11) is the same as the relation (27) for the fitness function (4), the following analyses hold for both (3) and (4).

If $(1-s)I'(s)$ is a monotonic decreasing function of s, (27) is inconsistent with $s_i \geq s_{i+1} > 0$, so we conclude that $s_{i+1} = 0$. That is, investment can not be in multiple defences but only in the first defence (example see in Figure 3),

$$1 > s_1 > s_2 = \ldots = s_n = 0. \tag{28}$$

However, multiple defence can occur when the function $(1-s)I'(s)$ is an increasing function, at least for some range of values of s, in which case $s_i \geq s_{i+1} > 0$ ($i \in \{1, 2, ..., j-1\}$) is consistent with (27) (we give examples in Figure 1). Note that multiple defences are impossible if $(1-s)I'(s)$ is a decreasing function, but that $(1-s)I'(s)$ being an increasing function does not guarantee that the optimal solution has investment in multiple defences (see Figure 1).

Note that, if $c_{i+1} = 0$, as mentioned before in the section ”When testing defences are costly, later defences receive lower investment”, the optimal solution either (i) has the relation $s_i = s_{i+1}$ or (ii) is not unique, with one optimal solution having $s_i > s_{i+1}$ and the other being obtained by swapping the values of s_i and s_{i+1}. When the function $(1-s)I'(s)$ is an increasing function, we can prove that only $s_i = s_{i+1}$ occurs (Appendix A (i); for an example see in Figure 2). Similarly, when $c_{i+1} = c_{i+2} = 0$, the optimal solution will have the relation that $s_i = s_{i+1} = s_{i+2}$. In biologically realistic situations, tested costs will usually be nonzero, so since the fitness function R is continuous in c_{i+1}, we will have s_i being slightly larger than s_{i+1}.

When the function $(1-s)I'(s)$ is a decreasing function, we can prove that only $c_2 = 0$ changes the relation (28), and that $s_i = s_{i+1}$ is not possible in the optimal solution, and that the same amount investment will be concentrated only in the first or only in the second defence ($1 > s_1 > s_2 = s_3 = s_4 = ... = s_n = 0$ or $1 > s_2 > s_1 = s_3 = s_4 = ... = s_n = 0$) (Appendix A (ii)(iii)). Similarly, when $c_2 = c_3 = 0$, investment will only be in one of the first three defences. However, a small tested cost will drive the investment to be only in the first defence (For example see in Figure 3, 4).

Examples of investment in defences

We will give numerical examples for the cases when (1) investment happens in multiple defences, (2) only in one defences, and also (3) the investment functions are different, so that the investment in earlier defences can be either higher or lower than in later defences. The investment functions for all the three cases are given in the examples below. To show a numerical result of the optimal defence strategy, we further specify the expression for the cost function $C(I_A)$ as follows,

$$C(I_A) = {I_A}^a, \quad a \geq 1 \tag{29}$$

We assume that $a \geq 1$, since we expect that the marginal investment cost in defences is non-decreasing in respect to the defence investment (no less additional investment cost for additional amount of investment when the total amount of investment becomes larger). For simplicity, we consider scenario (B) (where the fitness is zero if all defences are breached), and assume that I_T is large enough that, in the optimal strategy, the organism does not need to invest all of its resources in defences ($I_A < I_T$), so that we do not need to consider I_T when maximising the fitness function (4).

We use a heuristic search algorithm to find the optimal investment strategy. The search starts at an initial point $S_0 = (s_{10}, s_{20}, s_{30}, s_{40})$. First, we calculate the value of R at this point, and then search whether there exists higher value of R in the positive direction of the first axis, through calculating the value of R at $(s_{10} + \delta_0, s_{20}, s_{30}, s_{40})$, where δ_0 is initial search step. If the value is higher, then we double the search step value and and do the search again, and repeat it until we find the maximum value of R and the corresponding value $S_1 = (s_{11}, s_{20}, s_{30}, s_{40})$; If however the value is not higher, we do the same procedure in the negative direction of the first axis to find the the maximum value of R and the corresponding value $(s_{11}, s_{20}, s_{30}, s_{40})$. We then do the same process in all the axes, and after that we get the corresponding value $S_1 = (s_{11}, s_{21}, s_{31}, s_{41})$. Second, we do the same as the first to find $S_2 = (s_{12}, s_{22}, s_{32}, s_{42})$ except that we shorten the initial search step to be $\frac{\delta}{u}$ (where $u > 1$). Third, we let the initial search step to be $\frac{\delta}{u^2}$ and do the same. We repeat this process until (e.g. at the n-th time, we find $S_n = (s_{1n}, s_{2n}, s_{3n}, s_{4n})$) the initial search step is less than a threshold ϵ_1 and the distance between the last two corresponding points $d(S_{n-1}, S_n)$ is less than a threshold ϵ_2, then stop.

Note that the above process might only find a local, rather than global, maximum. To solve this problem, we divide each of the interval $(0, 1]$ (note that each probability $s_i \in (0, 1]$) in each axis into m equal subintervals, and since we have four levels of defences, altogether, we have m^4 subareas. Then we do the same process as above to find all the m^4 local maxima. Theoretically, if m were large enough, we would have the global maximum in one of our searched results, and the largest local maximum is the global maximum. Due to computational limitations, we only devide into $3^4 = 81$ subareas. However, in all cases we found that, the 80 out of 81 subregions did not hold the largest local maximum, because those local maxima were on the boundaries of the subregions. This suggests that R does not have multiple stationary values, and that the largest local maximum we found is indeed the global maximum.

In our example specifically, the initial start point S_0 is given by $s_{1i} = 0.3, 0.6, 0.9$ in the three subintervals respectively ($i = 1, 2, 3, 4$) ($3^4 = 81$ start points for the 81 subareas in total), and $\delta_0 = 0.35$, $u = 1.5$, $\epsilon_1 = \epsilon_2 = 0.0001$.

Example of investment in multiple defences

As described above, when $(1 - s)I'(s)$ is an increasing function, investment could happen in multiple defences. As an example for this relation, we use the investment function of the form

$$I(s) = k(\frac{1}{1-s} - 1)^b, \quad i = 1, ..., n, \qquad k > 0, b > 1. \tag{30}$$

For this function, $(1 - s)I'(s) = kb(\frac{1}{1-s} - 1)^{b-1}\frac{1}{1-s}$, which can easily be shown to be an increasing function, when $k > 0$, $b > 1$.

Specifically we let $a = 2$, $b = 2$, $k = 0.2$, and the total number of defences be four.

Figure 1 gives that the optimal investment is concentrated in the only the first defence/ the first two defences/ the first three defences/ in all the four defences.

Figure 2 gives that for a specific i ($i = 1, 2..., N - 1$), if $c_{i+1} = 0$, then the investments in the i-th and $(i + 1)$-th defence are the same ($s_i = s_{i+1}$).

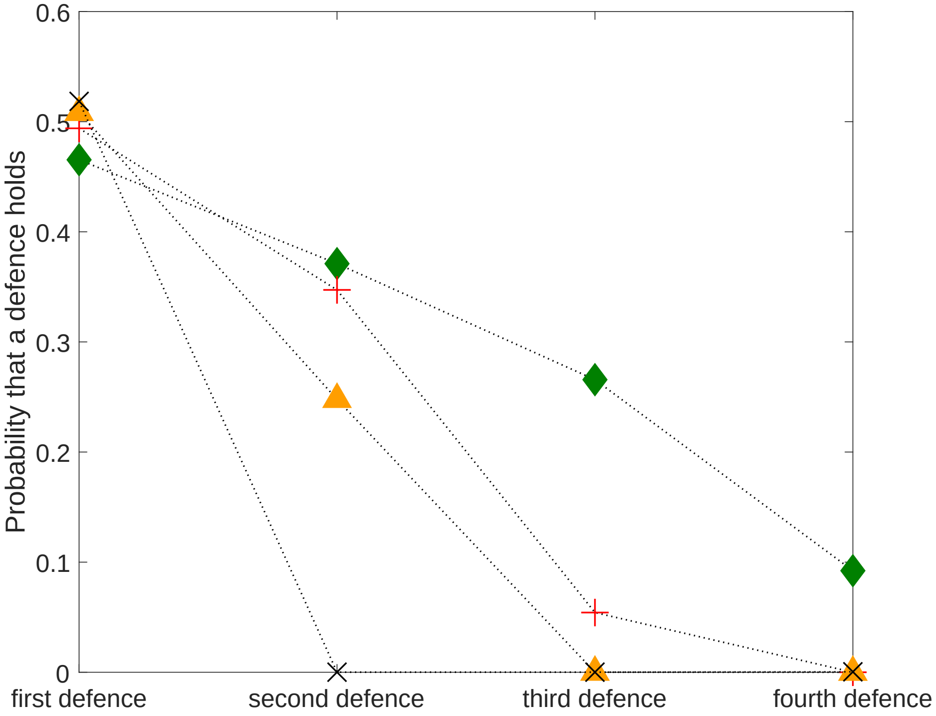

Figure 1: For investment functions I where $(1-s)I'(s)$ is an increasing function, prey can invest in multiple defences but always invest more in earlier defences. Here, the investment function is given in (30) and the cost function is given in (29). The vertical axis is s, the probability that a defence is not breached when tested, and is zero when investment in that defence is zero. Depending on the tested costs, the prey can invest in: all defences ($c_i = 0.2 \forall i$, green rhombus); the first three defences only ($c_i = 0.3 \forall i$, red cross); the first two defences only ($c_i = 0.4 \forall i$, yellow triangle); or only the first defence ($c_i = 0.5 \forall i$, black cross). Other parameter values: number of defences=4; $a = 2$, $b = 2$, $k = 0.2$.

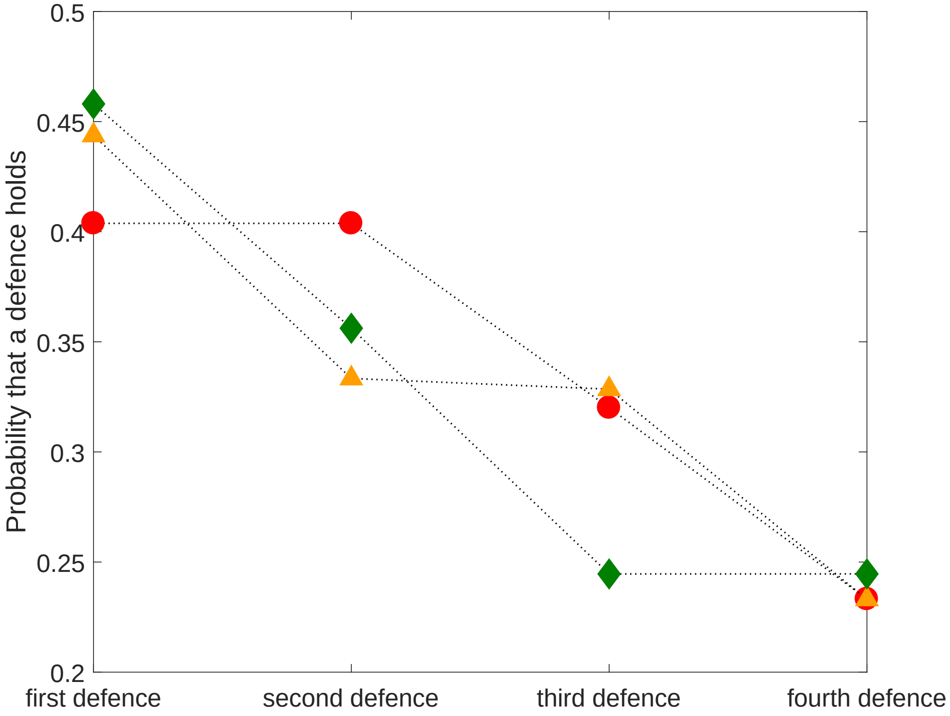

Figure 2: For investment functions I where $(1-s)I'(s)$ is an increasing function, prey can invest the same amount in two successive defences if the later defence has tested cost zero. Here, the investment function is given in (30) and the cost function is given in (29), and the tested costs are $c_i = 0.2$ for all values of i except one. Optimal strategy is to invest the same in: first and second defences when $c_2 = 0$ (red circles); second and third defences when $c_3 = 0$ (orange triangles); third and fourth defences when $c_4 = 0$ (green diamonds). Other parameters: number of defences=4; $a = 2$, $b = 2$, $k = 0.2$.

Example of investment only in the first defence

As described above, if $(1-s)I'(s)$ is a decreasing function, then investment only happen in the first defence (when $c_2 > 0$). As an example for this relation, we use the investment function

$$I(s) = -k(\ln(1-s) + ds \qquad k > 0, d > 0. \tag{31}$$

For this function, $(1-s)I'(s) = k + d(1-s)$, which is a decreasing function. Then we set the parameter values $a = 2$ to do the simulations as in the above example. Figure 3 shows that the optimal investment is concentrated only in the first defence. Figure 4 shows that, when $c_2 = 0$, there are two optimal solutions with one optimal solution having $s_1 > s_2 = s_3 = s_4 = 0$ (investment concenrated only in the first defence), and the other being the swapped values of s_1 and s_2 (investment concenrated only in the second defence).

Example of different investment functions among defences

When the investment functions are different among defences (e.g. the value of k might be different in the investment function (30), which correponding to the efficiency to make resources into defences might be different among defences),

$$I_i(s) = k_i(\frac{1}{1-s} - 1)^b, \quad i = 1, ..., n, \qquad k > 0, b > 1, \tag{32}$$

it is possible that investment in the later defences are higher than in the earlier defences. When the investment is more efficient to make resources into defences, in the later defences than in the earlier defences ($k_i > k_{i+1}$), the investment in later defences might or might not be higher than in the earlier defences (see the black cross or the red cross in Figure 5). However, when the investment in earlier defences is more efficient or equally efficient to make resources into defences than in the later defences ($k_i < k_{i+1}$), investment will be higher in the earlier than in the later defences (see the yellow triangle or the green rhombus in Figure 5).

Discussion

Endler (1991) argued that prey should generally invest preferentially in defences that act early in the predation sequence, in part because defences met earlier in a sequence will on average be deployed more frequently and in part because he expects late acting defences to be less efficient (higher k_i values in (32)). We have shown however that the skew will occur when the investment function is the same for all the

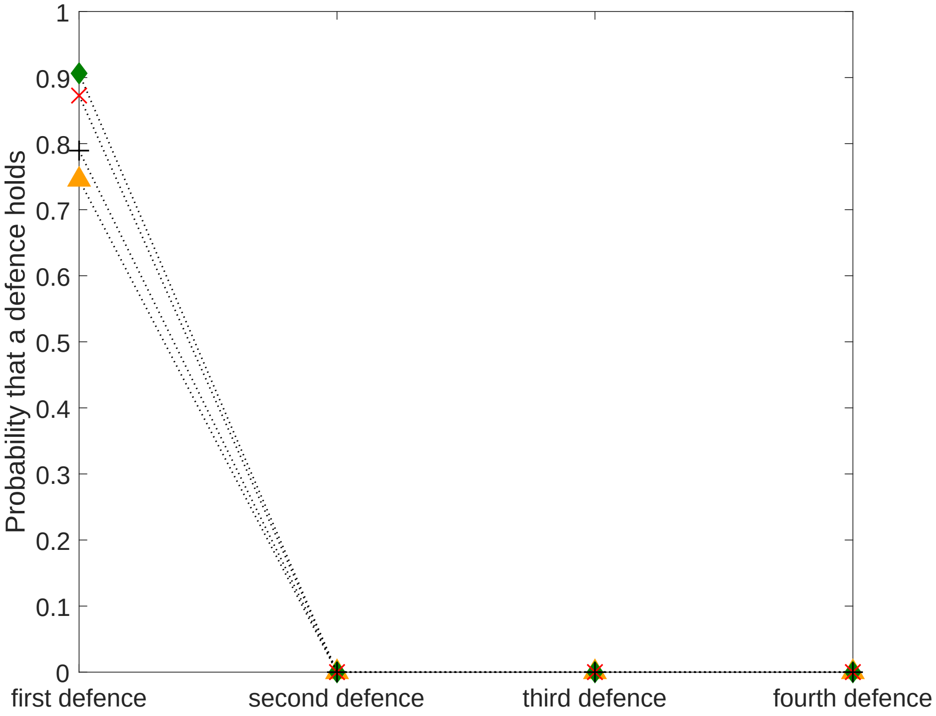

Figure 3: For investment functions I where $(1-s)I'(s)$ is a decreasing function, the optimal strategy is to invest in one defence only; this will be the first defence when the second defence has nonzero tested cost, $c_2 \neq 0$. Here, the investment function is given in (31), the cost function is given in (29), and the tested costs are $c_i = 0.2 \forall i$. Different symbols correspond to different values of parameters d and k: $(d,k) = (0.1, 0.1)$ (green rhombus); $(d,k) = (0.2, 0.1)$ (red cross); $(d,k) = (0.1, 0.2)$ (black cross); $(d,k) = (0.2, 0.2)$ (yellow triangle). Other parameters: number of defences=4; $a = 2$.

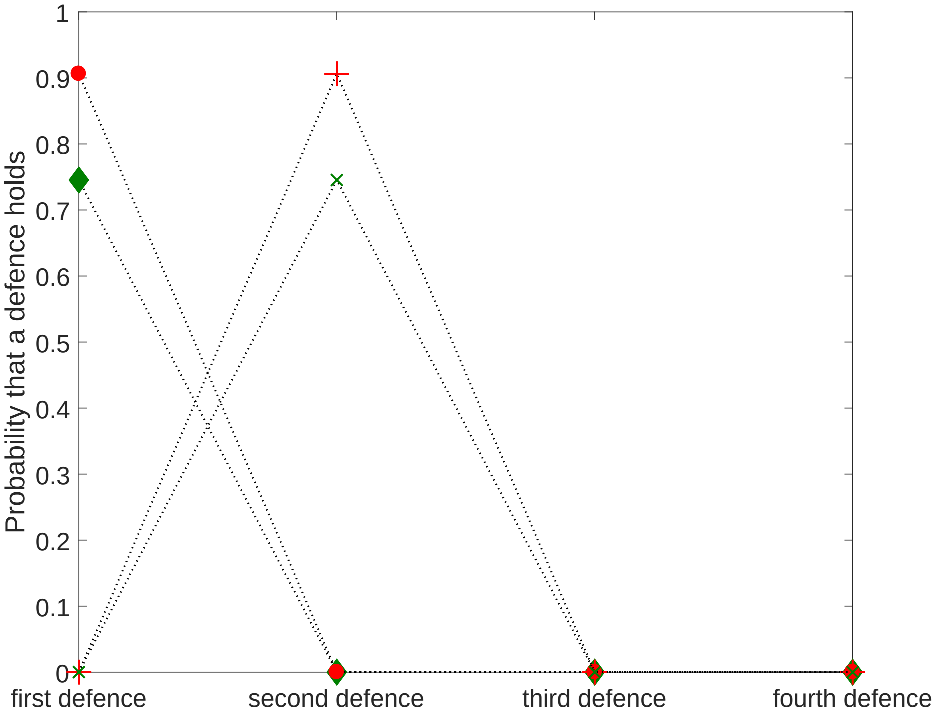

Figure 4: For investment functions I where $(1-s)I'(s)$ is a decreasing function, the optimal strategy is to invest in one defence only, but is degenerate when the second defence has tested cost zero ($c_2 = 0$): the fitness is the same whether the prey invests in the first defence only, or invests the same resources in the second defence only. Here, the investment function is given in (31), the cost function is given in (29), and tested costs are $c_2 = 0$, $c_i = 0.2$ for $i \neq 2$. Different colours correspond to different different values of parameters d and k: $d = k = 0.1$ (red); $d = k = 0.2$ (green). Different symbols distinguish the two optimal solutions: investment in first defence (red circle and green diamond); investment in second defence only (red cross and green cross). Other parameter values: number of defences=4, $a = 2$.

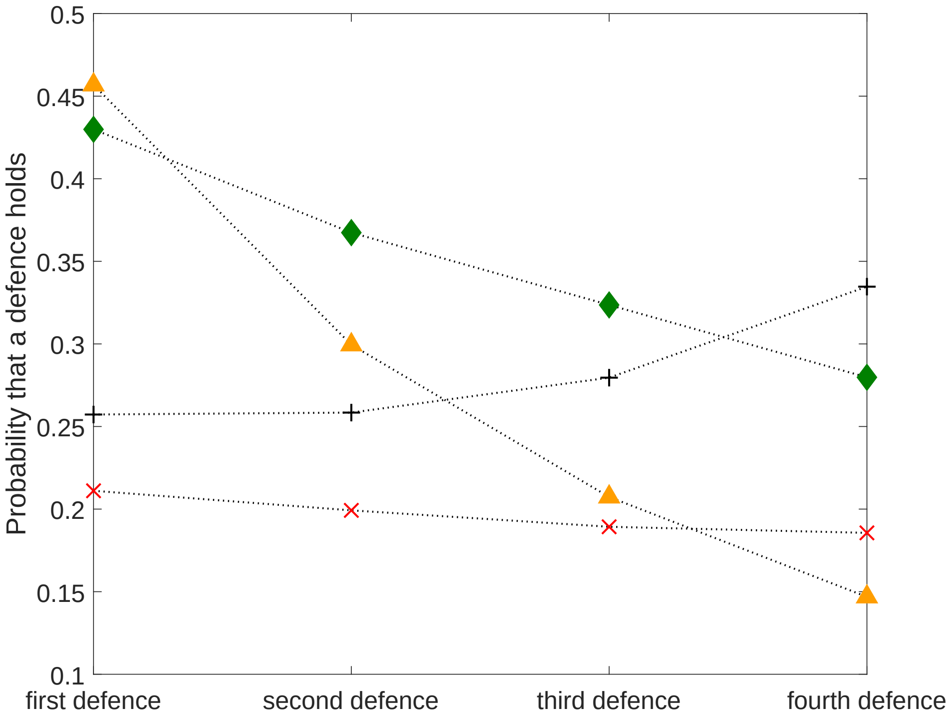

Figure 5: The optimum strategy might be to invest more in later defences, if the different defences do not have the same investment functions. Here, the investment function is given in (30) and the cost function is given in (29). The prey should invest more in earlier defences when defences have the same cost functions ($k_i = 0.2 \forall i$, green rhombus) or when later defences are more costly ($(k_1, k_2, k_3, k_4) = (0.2, 0.4, 0.6, 0.8)$, yellow triangle). However, when later defences are less costly, the optimal strategy might be to invest more in earlier defences ($(k_1, k_2, k_3, k_4) = (1.6, 1.4, 1.2, 1.0)$, red cross) or more in later defences ($(k_1, k_2, k_3, k_4) = (0.8, 0.6, 0.4, 0.2)$, black cross). Other parameters: number of defences=4; $a = 2$, $b = 2$, $c_i = 0.2 \forall i$.

defences (so the efficiency k_i is equal across defences) provided there is a risk-of-injury (c_i) and other cost ($C(I_A)$) associated with implementing each in a set of sequentially organised defences. Also, we found that under some conditions defence investment will concentrated only in the first defence, while, under other conditions, investment can be distributed in several defences with more investment in earlier than in later defences. We suspect such costs will be common. We also suspect that Endler (1991)'s assumption that later-acting defences will be inherently more expensive for a given level of effectiveness (k_i increases with i) might hold generally (though it needs to be demonstrated), and this would more likely to further exaggerate the skew towards earlier-acting defences (yellow triangle in Figure 5). However, if the effectiveness of later defences is much higher, investment in later defences could be higher than in earlier defences. Our general theory and predictions allow us to synthesize previous more system-specific work on multi-component defences, and we now consider its application in specific biological and theoretical contexts, starting with plant defence against insect herbivores.

Application to Plant Defences

It is common, when a victim is an animal prey, that it is killed and eaten (so has zero fitness, if it has not already reproduced) if the predator overcomes all of its defences (scenario (B)). Our model can also apply to many plant-herbivore interactions in which a small insect damages, but does not kill, the plant on which it is feeding (Speed et al. 2015 also described a related model for these). In scenario (A), breaching the final defence does not cause further fitness cost on the prey, so the fitness keeps the same between when the final defence is tested but not breached and when the final defence is breached. We have done the analyses for both this extreme case and the the other extreme case –scenario (B), when all the remaining fitness are gone when the final defence is breached. The results are the same for these two extreme cases, so can be extended to the other intermediate cases when the prey still can reproduce (positive remaining fitness) but the remaining fitness is diminished when the final defence is breached.

If plant defences do offer sequential barriers to herbivores, what can our model tell us about variation in investment in these defences? Some insight is possible here from the notable meta-analysis of studies in herbivore damage reported by Carmona et al. (2011). They report that variation in concentrations of plant secondary metabolites is a poor predictor of herbivore damage overall. In contrast, variation in physical defences, such as hairs and spines, provided better overall prediction of damage. The most consistent predictor of herbivore damage was however in life history traits, such as varied phenology which allow growth and flowering at times that enemies are rare - effectively hiding in time. One interpretation of these results is that it supports the sequential nature of plant defences, with the earlier acting defences (hiding, then physical defences) having much stronger influence on vulnerability than the last line of defence, of plant tissues by toxic secondary metabolites. If this interpretation has general validity, then it suggests that our framework can have widespread application in plant-animal interactions. Several items need to be measured for parameterised evaluation of the model's predictions including; costs of generating and deploying defences, survival benefits of each defence. In principle however, the model is open to empirical testing, and in the right systems may even be open to testing through experimental evolution. Key predictions could then be tested, for example that chemical defences never have more investment than earlier acting physical defences. We note the complexity of ontogenetic choice by plants makes the area all the more interesting (see Barton and Boege 2017), and suggests developments of our approach to incorporate developmental plasticity.

Relation to Other Theoretical Work on Sequential Defences

We present here a general model to predict the optimal investment in sequential defences. We now consider our model's relevance to other, often more specialised models of defence. Our work here can be seen as a generalisation of the work of Broom et al. (2010), who presented a simple model of investment across two sequentially encountered anti-predatory defences. A predator must overcome both defences to capture the prey, and probability of overcoming a defence declines linearly with increasing investment in defences. However there are costs every time a defence is used and these increase linearly with investment in a particular defence. On top of that there is an initial outlay in the construction of a defence, with the fecundity of the prey being a decreasing decelerating function of investment across both defences.

Broom et al. (2010) provide predictions for circumstances where there is investment in only one defence or investment spread across both defences. When the ratio of the constitutive costs to the effectiveness of defences is generally similar and low for both defences, then investment across both defences can be optimal. Increasing rate of attack also increases the likelihood of investment across both defences. However investment in both defences was only predicted for relatively narrow combinations of circumstances, where investing heavily to produce one very effective defence was prohibitively expensive and the best solution was to offer two modestly effective defences that must be overcome. Our model further solves the problem where there are more than two defences, and gives the conditions under which investment are applied in multiple defences or only one defences, and the relation between investment in the sequential defences.

Strategy Blocking

The host reed warbler *Acrocephalus scirpaceus* is often found to have an egg-rejection defence strategy but not a chick-rejection defence strategy against the parasite cuckoo *Cuculus canorus*. Britton et al. (2007) uses a concept called "strategy blocking" to explain this phenomenon. Strategy blocking describes the situation in which a strategy which would be adaptive in isolation ceases to be adaptive in the presence of a second strategy. Strategy blocking explains this phenomenon in terms of the different pay-offs for each defence, but it is not framed as a sequential defences scenario, so it does not explain the effect of the sequence on defence strategy. Our sequential defences model provides an alternative explanation for why the reed warblers are found more likely to have defences in the earlier stage (rejecting the eggs) than in the later stage (rejecting the chicks). We particularly consider the condition under which the investment will be concentrated only in the first defence (egg-rejection). The rate that the warblers fail or succeed in rejecting the cuckoos' eggs (which corresponds to s_1 in our model) is dependant on the investment in the egg-rejection defence, which could explain why warblers are sometimes found not to reject eggs.

Although the concept of strategy blocking is raised in a population dynamics model (Britton et al. (2007)), its idea that one defence will often reduce the benefits of a second defence can be explained otherwise through probabilities. Let us assume that if a predator encounters a prey then it is repelled with probability a if defence A only is expressed by the prey, with probability b if defence B only is expressed and with probability $1 - (1 - a)(1 - b)$ if both are expressed. This implies that the two defences work independently and the predator must overcome all defences expressed in order to be successful. The benefit of defence B is the increase in the probability of an predator being repelled when defence B is expressed relative to when B is not expressed. This is a function of a, the higher the value of a (the more predators would have been repelled without B being expressed by defence A), the less often investing in B makes a difference to the prey and so the less the benefit of investment in B. This was a situation where the two defences worked independently, but it may also be the case that expression of one defence reduces the effectiveness of another, in our case that increasing a causes a decrease in b. As an example, if an animal invests in a heavy armoured shell, then its ability to outrun predators is compromised. The work of Britton et al. (2007) can be seen as a more general examination of earlier modelling by Brodie et al. (1991) that reached essentially similar conclusions in a more restricted setting.

In contrast Kilner and Langmore (2011) introduce the concept of *strategy-facilitation* as the complement to the concept of *strategy-blocking*. Here they imagine that the evolution of one defence makes the evolution of another defence easier. As an example of this they cite the modelling work of Svennungsen and Holen (2010) who demonstrated that in avian brood parasite systems it can sometimes be advantageous for hosts to reject a randomly-selected egg if they know that they have been parasitised but are unable to identify the parasitic egg. Kilner and Langmore (2011) argue that if the strategy of such random rejection evolves then this will allow subsequent evolution of egg recognition to facilitate non-random targeting of the alien egg. As well as facilitating cognitive changes in the host it could trigger physiological change in egg appearance to improve such recognition.

This means that sometimes an inefficient defence is worth employing/investing in; in our model example (equation (32)) this is a defence with a high value of k_i. Given this defence is invested in, its cost has an effect on the fitness function R, which if it was not invested in ($s_i = 0$) would be absent. There is thus evolutionary pressure to improve the efficiency (lower k_i) if this were possible, which there would not be in the absence of investment.

Kilner and Langmore (2011) also argue that defences can operate at levels of organisation greater than the individual that are often overlooked. They give as an example workers of the ant genus *Temnothorax* that can be enslaved by the species *Protomognathus americanus*, but which selectively destroy the slave-making pupae in their care. As a result *P. americanus* colonies are unusually small for a slavemaker and are less effective at conducting slave raids on neighbouring *Temnothorax* colonies. Since *Temnothorax* populations are highly kin-structured then there is a kin-selected benefit to this defence. Kilner and Langmore (2011) speculate that as a generality kin-structuring in a host population will select for a more extensive portfolio of defences. They also predict that a high parasitic virulence will also select for more extensive portfolios. The last of their predictions is that where a parasite exploits more than one host, competition between the hosts to shift their parasite's attention toward the others should again select for complexity of defensive portfolio.

Coevolutionary Considerations in Sequential Defence Suites

Jongepier et al. (2014) argue that for sequential lines of defence, later lines will be more expensive. Thus arms races between prey and predators would have started with the prey using a cheap defence acting early in the predation sequence, but as the predator evolved to overcome this defence there would then have been selection pressure for investment in later-acting more costly defences. Thus over evolutionary time there will have been a shift towards investment in more costly defence that act later in the sequence of the interaction between prey and predator. To put this a different way, the temporal order in which defences are employed will reflect the order in which they evolved. Gilman et al. (2012) argue theoretically that there are co-evolutionary advantages to a multi-dimensional defence against any type of antagonist (parasite, predator or pathogen). Using a modelling framework, they argue that a prey is more likely to evolve a way to neutralise the predator as the number of defences increases or as the correlation between values across traits increases. Essentially each additional trait provides the prey with an additional opportunity to evolve an effective escape mechanism. A key point here is that sequential layering of defences is not necessary for these general conclusions, rather it is the use of multiple defences per se that matters. This is illustrated in the Gilman et al. (2012) model itself, and in a subsequent extension modelling plant toxicity by Speed and Ruxton (2014). Sasaki (2000) considers the multiplicative interaction among the effect of defence genes, and finds that the cost of resistance and virulence values can influence the coexistence of multiple defences in static equilibria or coevolutionary cycle.

In contrast, Bateman et al. (2014) introduce population dynamics into the discussion of investment across defences. They use a two-prey, one-predator Rosenzweig-McArthur model of predator-prey interaction. Prey can invest in each of two defences, one of which acts before the other in the predation sequence, and defences have costs as well as anti-predatory benefits. The system is allowed to come to equilibrium with only a single prey before a different prey with a different investment strategy across defences is introduced at low population density. Bateman et al. (2014) then explore whether this second prey increases in population size. They conclude that the invasion of a given defence strategy is dependent on the fine detail of traits of the predator and the existing prey type, and the nature of the costs and benefits of the different defences; and so general conclusions are difficult to draw. However they do conclude that on the basis of their simulations "there exists no exclusive ecological or evolutionary advantage to defending early in the predation sequence". The word "exclusive" seems important here they mean there is nothing fundamentally beneficial about easy disruption of attacks per se from a population dynamic perspective. We agree with this, but there are mechanisms (like risk of injury or time lost to other beneficial activities) that may be correlated with early disruption, are not considered in their model, and bring benefits.

Conclusions

In our view the sequential organisation of defences has received relatively little rigorous examination in the literature. This is explained in part by expertise focusing on the mechanisms of individual defensive types (e.g. camouflage or chemical defence), rather than their integration into suites of defences. A valuable predictive aspect of our model, is to make a general argument that explains why earlier defences may gain higher investment than later acting defences. Suppose that a victim could biologically generate a suite of ten equally effective sequential defences, but it is optimal to only invest in five, then which five should it invest in, and how much in each? Our model predicts that the solution is to concentrate in earliest five defences rather than in the other five defences. Moreover, regarding the trade-off of the investments among each defence, a victim will invest no less in earlier defences than later defences, given that the investment functions among defences are the same (e.g. converting resources into defences is equally efficient across the sequential defences). In our Discussion section, we have shown that the model can be applied to animal, plant and other defensive systems. Our model can replicate and add quantitative rigor to the question of strategy-blocking, in which the effectiveness of early-acting defences makes the deployment of later acting defences redundant. In relating it to other theoretical works in the field, we note that coevolutionary approaches to the general question we examine here would add predictive sophistication.

References

Barton, K. E., and K. Boege. 2017. Future directions in the ontogeny of plant defence: understanding the evolutionary causes and consequences. Ecology Letters.

Bateman, A. W., M. Vos, and B. Anholt. 2014. When to Defend: Antipredator Defenses and the Predation Sequence. The American Naturalist 183:847-855.

Britton, N., R. Planqué, and N. Franks. 2007. Evolution of Defence Portfolios in Exploiter–Victim Systems. Bulletin of Mathematical Biology 69:957-988.

Brodie, E., D. Formanowicz, and E. Brodie. 1991. Predator avoidance and antipredator mechanisms: distinct pathways to survival. Ethology Ecology & Evolution 3:73-77.

Broom, M., A. Higginson, and G. Ruxton. 2010. Optimal investment across different aspects of anti-predator defences. Journal of Theoretical Biology 263:579-586.

Carmona, D., M. Lajeunesse, and M. Johnson. 2011. Plant traits that predict resistance to herbivores. Functional Ecology 25:358-367.

Caro, T. 2005. Antipredator defences in birds and mammals (1st ed.). Chicago University Press, Chicago.

Endler, J. A. 1991. Interactions between predators and prey. Behavioural ecology: an evolutionary approach 3:169-196.

Gilman, R. T., S. L. Nuismer, and D. Jhwueng. 2012. Coevolution in multidimensional trait space favours escape from parasites and pathogens. Nature 483:328-330.

Jongepier, E., I. Kleeberg, S. Job, and S. Foitzik. 2014. Collective defence portfolios of ant hosts shift with social parasite pressure. Proceedings of the Royal Society B: Biological Sciences 281:20140225-20140225.

Kilner, R. M. and N. E. Langmore. 2011. Cuckoos versus hosts in insects and birds: adaptations, counter-adaptations and outcomes. Biological Reviews 86:836-852.

Ruxton, G. D., T. N. Sherratt, and M. P. Speed. 2004. Avoiding attack (1st ed.). Oxford University Press, Oxford.

Sasaki, A. 2000 Host-parasite coevolution in a multilocus gene-for-gene system. Proceedings of the Royal Society of London B: Biological Sciences, 267(1458), 2183-2188.

Speed, M. P. and G. D. Ruxton. 2014. Ecological pharmacodynamics: prey toxin evolution depends on the physiological characteristics of predators. Animal Behaviour 98:53-67.

Speed, M. P., A. Fenton, M. G. Jones, G. D. Ruxton, and M. A. Brockhurst. 2015. Coevolution can explain defensive secondary metabolite diversity in plants. New Phytologist 208:1251-1263.

Svennungsen, T. O. and Ø. H. Holen. 2010. Avian Brood Parasitism: Information Use and Variation in Egg-Rejection Behavior. Evolution 64:1459-1469.

Vermeij, G.J. 1987. Evolution and escalation (1st ed.). Princeton University Press, Princeton.

Wilkening, D.A. 1999. A simple model for calculating ballistic missile defense effectiveness. Science & Global Security 8:183-215.

A Appendix

The relation between s_i and s_{i+1} when $c_{i+1} = 0$

(i) We will prove that when $c_{i+1} = 0$, and when $(1-s)I'(s)$ is an increasing function, only $s_i = s_{i+1}$ can happen.

(a) When both $s_i > 0$ and $s_{i+1} > 0$, and from (25) and $c_{i+1} = 0$ we would have $(1-s_{i+1})I'(s_{i+1}) = (1-s_i)I'(s_i)$ and so $s_i = s_{i+1}$.

(b) and when both $s_i = 0$ and $s_{i+1} = 0$, we have $s_i = s_{i+1}$.

(c) If $s_i > s_{i+1} = 0$, from the necessary condition (15) and (16), we have

$$\begin{aligned}
&\frac{\partial R}{\partial s_i}\cdot(1-s_i) - h(1-s_i)I'(s_i)\\
&= \prod_{j=1}^{n}(1-s_j)\big(1-C(I_A)-\sum_{j=1}^{n}c_j\big) - (1-s_i)(1-\prod_{j=1}^{n}(1-s_j))\frac{\partial C(I_A)}{\partial s_i} + \sum_{j=i+1}^{n}c_j\prod_{k=1}^{j-1}(1-s_k) - h(1-s_i)I'(s_i)\\
&= 0,
\end{aligned} \tag{A.1}$$

$$\begin{aligned}
&\frac{\partial R}{\partial s_{i+1}}\cdot(1-s_{i+1}) - h(1-s_{i+1})I'(s_{i+1})\\
&= \prod_{j=1}^{n}(1-s_j)\big(1-C(I_A)-\sum_{j=1}^{n}c_j\big) - (1-s_{i+1})(1-\prod_{j=1}^{n}(1-s_j))\frac{\partial C(I_A)}{\partial s_{i+1}} + \sum_{j=i+2}^{n}c_j\prod_{k=1}^{j-1}(1-s_k) - h(1-s_{i+1})I'(s_{i+1})\\
&\leq 0
\end{aligned} \tag{A.2}$$

Then following are the similar deduction as (22)-(27), we have

$$\begin{aligned}
&-(1-s_{i+1})(1-\prod_{j=1}^{n}(1-s_j))\frac{\partial C(I_A)}{\partial s_{i+1}} + \sum_{j=i+2}^{n}c_j\prod_{k=1}^{j-1}(1-s_k) - h(1-s_{i+1})I'(s_{i+1})\\
&\leq -(1-s_i)(1-\prod_{j=1}^{n}(1-s_j))\frac{\partial C(I_A)}{\partial s_i} + \sum_{j=i+1}^{n}c_j\prod_{k=1}^{j-1}(1-s_k) - h(1-s_i)I'(s_i).
\end{aligned} \tag{A.3}$$

Since $I_A = \sum_{i=1}^{n} I(s_i)$, the above is equivalent to

$$\begin{aligned}
&-(1-s_{i+1})(1-\prod_{j=1}^{n}(1-s_j))C'(I_A)I'(s_{i+1}) - h(1-s_{i+1})I'(s_{i+1})\\
&\leq -(1-s_i)(1-\prod_{j=1}^{n}(1-s_j))C'(I_A)I'(s_i) + c_{i+1}\prod_{k=1}^{i}(1-s_k) - h(1-s_i)I'(s_i).
\end{aligned} \tag{A.4}$$

$\Rightarrow$

$$
\begin{aligned}
&-(1-s_{i+1})I'(s_{i+1})\Big((1-\prod_{j=1}^{n}(1-s_j))C'(I_A)+h\Big)\\
&\le -(1-s_i)I'(s_i)\Big((1-\prod_{j=1}^{n}(1-s_j))C'(I_A)+h\Big)+c_{i+1}\prod_{k=1}^{i}(1-s_k). \qquad \text{(A.5)}
\end{aligned}
$$

Since $C'(I_A) > 0$ and also $1-\prod_{j=1}^{n}(1-s_j) > 0$ and $h \geq 0$, we have that $\Big((1-\prod_{j=1}^{n}(1-s_j))C'(I_A)+h\Big) > 0$, so that equation (24) is equivalent to

$$
-(1-s_{i+1})I'(s_{i+1}) \le -(1-s_i)I'(s_i)+c_{i+1}\frac{\prod_{k=1}^{i}s_k}{\Big((1-\prod_{j=1}^{n}(1-s_j))C'(I_A)+h\Big)}. \qquad \text{(A.6)}
$$

The last term in the right-hand side $c_{i+1}\frac{\prod_{k=1}^{i}s_k}{\Big((1-\prod_{j=1}^{n}(1-s_j))C'(I_A)+h\Big)}$ is positive when $c_{i+1} > 0$, therefore

$$
-(1-s_{i+1})I'(s_{i+1}) \le -(1-s_i)I'(s_i). \qquad \text{(A.7)}
$$

which is the same to,

$$
(1-s_{i+1})I'(s_{i+1}) \ge (1-s_i)I'(s_i). \qquad \text{(A.8)}
$$

(35) together with that the function $(1-s)I'(s)$ is increasing violate that $s_i > s_{i+1} = 0$. So $s_i > s_{i+1} = 0$ is not possible.

(d) $s_{i+1} > s_i = 0$ is not possible either for the same reason as (c).

Therefore, when $c_{i+1} = 0$ and when $(1-s)I'(s)$ is an increasing function, we have $s_i = s_{i+1}$ (Example see in Figure 2).

(ii) We will prove that when $c_2 = 0$, and when $(1-s)I'(s)$ is a decreasing function, only $s_1 > s_2 = 0$ or $s_2 > s_1 = 0$ can happen.

(a) When both $s_1 > 0$ and $s_2 > 0$, and when $c_2 = 0$, from (25),

$$
(1-s_{i+1})I'(s_{i+1}) = (1-s_i)I'(s_i). \qquad \text{(A.9)}
$$

so we have $s_i = s_{i+1}$.

However, when $s_1 = s_2 = 1-m$, for some specific $m \in (0,1)$, we can always increase the value of R by decreasing the value of s_1 and increasing the value of s_2, given that $(1-s_1)(1-s_2) = m^2$ and the values of the other s_j $(j > 2)$ fixed (e.g. let $s_1 = 1-m^{\frac{1}{2}}$ and $s_2 = 1-m^{\frac{3}{2}}$). This is because, the solution that $s_1 = s_2 = 1-m < 1$ is the maximum solution of $I(s_1)+I(s_2)$ given that $(1-s_1)(1-s_2) = m^2$ and therefore the minimum solution of R (see in (4)) given that $(1-s_1)(1-s_2) = m^2$ and the values of the other s_j ($j > 2$) fixed.

To prove this, we only need to see the necessary and sufficient condition for the question

$$Max \quad I(s_1) + I(s_2) \quad s.t.(1-s_1)(1-s_2) = m^2 \tag{A.10}$$

that is

$$Max \quad F(s_1) = I(s_1) + I(1 - \frac{m^2}{1-s_1}), \tag{A.11}$$

where m^2 is a constant value.

The necessary condition (the first derivative of $F(s_1)$ equals 0) is that

$$\begin{aligned} F'(s_1) &= I'(s_1) + I'(1 - \frac{m^2}{1-s_1})(-\frac{m^2}{(1-s_1)^2}) \\ &= I'(s_1) + I'(s_2)(-\frac{1-s_2}{1-s_1}) \\ &= 0 \end{aligned} \tag{A.12}$$

which is equilalent to

$$(1-s_1)I(s_1) = (1-s_2)I(s_2), \tag{A.13}$$

so when $(1-s)I'(s)$ is decreasing,

$$s_1 = s_2 \tag{A.14}$$

The sufficient condition (the second derivative of $F(s_1)$ larger than 0) is that

$$\begin{aligned} F''(s_1) &= I''(s_1) + I''(1 - \frac{m^2}{1-s_1})\frac{m^4}{(1-s_1)^4} - 2I'(1 - \frac{m^2}{1-s_1})\frac{m^2}{(1-s_1)^3} \\ &= \frac{1}{(1-s_1)^2}\Big((1-s_1)^2 I''(s_1) + (1-s_2)^2 I''(s_2) - 2(1-s_2)I'(s_2)\Big) \\ &= \frac{1}{(1-s_1)^2}\Big(2(1-s_2)^2 I''(s_2) - 2(1-s_2)I'(s_2)\Big) \quad \text{(since } s_1 = s_2\text{)} \\ &< 0 \quad \text{(since } (1-s)I'(s) \text{ is decreasing function)} \end{aligned} \tag{A.15}$$

So $s_1 = s_2 > 0$ is the local maximum solution of $I(s_1) + I(s_2)$ and therefore the local minimum solution of R.

(b) When both $s_1 = 0$ and $s_2 = 0$, we can follow the proof below in (iii)(b)(c), and then all rest $s_i = 0$ ($i > 2$), which is not the optimal solution for R.

Therefore, when $c_2 = 0$, and when $(1-s)I'(s)$ is a decreasing function, only $s_1 > s_2 = 0$ or $s_2 > s_1 = 0$ can be the optimal (Example see in Figure 4).

(iii) We will prove that when $(1-s)I'(s)$ is a decreasing function, for any $i \neq 2$, $c_i = 0$ but $c_2 > 0$ does not change the relation $1 > s_1 > s_2 = ... = s_n = 0$ (equation (28)).

(a) $c_1 = 0$ does not change the relation in (25), therefore the relation (28) still holds.

(b) If $c_3 = 0$ but $c_2 > 0$, we would have $s_1 > 0$ and $s_2 = 0$ since $c_2 > 0$. If however $s_3 = m > 0$, since the symmetric relation between s_2 and s_3 in R when $c_3 = 0$, we would have $s_2 = m > 0$ and $s_3 = 0$ to be another optimal solution, which violates the fact that $s_2 = 0$. So s_3 can only be 0.

If $c_3 > 0$, s_3 can still only be 0 due to the asymmetric relation between s_2 and s_3 in the R function and that we can only have $s_2 \geq s_3$.

Therefore, no matter $c_3 > 0$ or $c_3 = 0$, we can only have $s_3 = 0$

(c) For the same reason, no matter $c_4 > 0$ or $c_4 = 0$, we can only have $s_4 = 0$; and so is for any $c_i = 0$ $(i > 2)$.

Therefore when for any $i \neq 2$, $c_i = 0$ but $c_2 > 0$ and when $(1-s)I'(s)$ is a decreasing function, the relation (28) still holds.

B Appendix

When the residual fitness when all the defences are breached is positive (scenario (A)), the fitness function is (3) as follows.

$$R(s_1, s_2, \ldots, s_n) = 1 - C(\sum_{i=1}^{n} I_i(s_i)) - c_1 - \sum_{j=2}^{n} c_j \prod_{k=1}^{j-1} (1 - s_k). \tag{B.1}$$

The analysis for (3) is similar to when the fitness function is (4) (scenario (B)– when the residual fitness is zero when all the defences are breached). The necessary conditions to maximise R– (15) and (16) in this case can be written as follows,

(I) When $0 < s_i < 1$,

$$\frac{\partial R}{\partial s_i} - hI'(s_i) = -\frac{\partial C(I_A)}{\partial s_i} + \frac{1}{1-s_i} \sum_{j=i+1}^{n} c_j \prod_{k=1}^{j-1} (1 - s_k) - hI'(s_i) = 0$$

$$(\text{with } h \geq 0) \tag{B.2}$$

(II) When $s_i = 1$,

$$\frac{\partial R}{\partial s_i} - hI'(s_i) = -\frac{\partial C(I_A)}{\partial s_i} - \frac{1}{1-s_i}\sum_{j=i+1}^{n} c_j \prod_{k=1}^{j-1}(1-s_k) - hI'(s_i) \le 0$$

$$(\text{with } h \ge 0) \tag{B.3}$$

Now (B.2) and (B.3) together is the necessary condition. The following analyses are similar to the scenario (B). Similar to the equations (20) and (21),

$$\frac{\partial R}{\partial s_i}\cdot(1-s_i) - h(1-s_i)I'(s_i) = -(1-s_i)\frac{\partial C(I_A)}{\partial s_i} + \sum_{j=i+1}^{n} c_j \prod_{k=1}^{j-1}(1-s_k) - h(1-s_i)I'(s_i) = 0, \tag{B.4}$$

$$\frac{\partial R}{\partial s_{i+1}}\cdot(1-s_{i+1}) - h(1-s_{i+1})I'(s_{i+1}) = -(1-s_{i+1})\frac{\partial C(I_A)}{\partial s_{i+1}} + \sum_{j=i+2}^{n} c_j \prod_{k=1}^{j-1}(1-s_k) - h(1-s_{i+1})I'(s_{i+1}) = 0 \tag{B.5}$$

Then we have

$$-(1-s_{i+1})\frac{\partial C(I_A)}{\partial s_{i+1}} + \sum_{j=i+2}^{n} c_j \prod_{k=1}^{j-1}(1-s_k) - h(1-s_{i+1})I'(s_{i+1}) = -(1-s_i)\frac{\partial C(I_A)}{\partial s_i} + \sum_{j=i+1}^{n} c_j \prod_{k=1}^{j-1}(1-s_k) - h(1-s_i)I'(s_i). \tag{B.6}$$

Since $I_A = \sum_{i=1}^{n} I(s_i)$, the above is equivalent to

$$-(1-s_{i+1})C'(I_A)I'(s_{i+1}) - h(1-s_{i+1})I'(s_{i+1}) = -(1-s_i)C'(I_A)I'(s_i) + c_{i+1}\prod_{k=1}^{i}(1-s_k) - h(1-s_i)I'(s_i). \tag{B.7}$$

$\Rightarrow$

$$-(1-s_{i+1})I'(s_{i+1})\Big(C'(I_A)+h\Big) = -(1-s_i)I'(s_i)\Big(C'(I_A)+h\Big) + c_{i+1}\prod_{k=1}^{i}(1-s_k). \tag{B.8}$$

Since $C'(I_A) > 0$, we have that $\Big(C'(I_A)+h\Big) > 0$, so that equation (B.8) is equivalent to

$$-(1-s_{i+1})I'(s_{i+1}) = -(1-s_i)I'(s_i) + c_{i+1}\frac{\prod_{k=1}^{i}(1-s_k)}{\Big(C'(I_A)+h\Big)}. \tag{B.9}$$

The last term in the right-hand side $c_{i+1}\frac{\prod_{k=1}^{i}(1-s_k)}{\Big(C'(I_A)+h\Big)}$ is negative since $c_{i+1} > 0$, $C'(I_A) > 0$ and $h \ge 0$, therefore

$$-(1-s_{i+1})I'(s_{i+1}) > -(1-s_i)I'(s_i). \tag{B.10}$$

which is equivalent to,

$$(1 - s_{i+1})I'(s_{i+1}) < (1 - s_i)I'(s_i). \tag{B.11}$$

Therefore we have the same relation between s_i and s_{i+1} as (27). The later analyses are the same as in the section ”Investing in multiple defences or in a single defence?”.