

1 **Supplementary Material 1: Calculating optimal thresholds and expected payoffs**

2 We seek optimal threshold positions  $\{x_1, \dots, x_L\}$ , where the subscript denotes current reserve level,  
 3 such that the expected total payoff is maximized.

4

5 Table A1 shows the general payoff matrix for reserve level  $i$ .

6

|                 |             | Environmental condition |             |
|-----------------|-------------|-------------------------|-------------|
|                 |             | Dangerous, D            | Safe, S     |
| Action<br>taken | Run away, R | $V_{DR}(i)$             | $V_{SR}(i)$ |
|                 | Forage, F   | $V_{DF}(i)$             | $V_{SF}(i)$ |

7 Table A1: General state-dependent payoff matrix where current reserves are denoted by  $i$ .

8

9 Note that each payoff may depend on the values at other reserve levels. For instance, when dealing  
 10 with expected lifespan in Appendix B,  $V_{SR}(i) = V(i - 1) + 1$ , or with expected reproductive success in  
 11 Section 4,  $V_{SR}(i) = V(i - 1)$ . In these equations for  $V$ , the terms with subscripts denote values in a  
 12 particular position of the payoff matrix. The terms without subscripts denote the general value of  
 13 reaching that reserve level. For any reserve level  $i$ , the value  $V(i)$  can be calculated from the set  
 14  $\{V_{DR}(i), V_{SR}(i), V_{DF}(i), V_{SF}(i)\}$  and the threshold in that state,  $x_i$ , according to

15

16 
$$V(i) = p_D E(\text{payoff} \mid \text{predator present}) + (1 - p_D) E(\text{payoff} \mid \text{no predator present}).$$

17

18 i.e.,

19 
$$V(i) = p_D (\Phi_D(x_i)V_{DF}(i) + (1 - \Phi_D(x_i))V_{DR}(i)) + (1 - p_D) (\Phi_S(x_i)V_{SF}(i) + (1 - \Phi_S(x_i))V_{SR}(i))$$

20

1 where  $\Phi_D(x_i)$  and  $\Phi_S(x_i)$  denote the cumulative probabilities of a signal falling to the left of the  
2 threshold  $x_i$  under the signal distributions for predators being present and absent, respectively.

3

4 Each threshold should be positioned such that if a cue were received at that threshold position, the  
5 expected payoff would not depend on the decision. Thus, for a given set of payoffs, the optimal  
6 thresholds can be calculated using SDT according to

7

$$8 \quad \frac{P(x_i|D)}{P(x_i|S)} = \frac{(1 - p_D) (V_{SF}(i) - V_{SR}(i))}{p_D (V_{DR}(i) - V_{DF}(i))}$$

9

10 (Egan 1975).

11

12 We therefore have a system in which the expected payoffs depend on the thresholds, and the  
13 thresholds depend on the expected payoffs. We are able to resolve this circular difficulty by initially  
14 estimating each value and updating first the expected payoffs (using the thresholds) and then the  
15 thresholds using the updated payoffs. Iterating this process until all values have converged, we  
16 obtain the expected value of being in each state, the payoffs associated with each combination of  
17 situation and action, and the optimal thresholds. Note that in some systems (other than those of the  
18 main text), such an approach would not be guaranteed to find optimal values, as there could be  
19 more than one point of convergence for the various values. This is not the case for either of our  
20 models (maximizing lifespan or reproductive success), where expected payoff always increases with  
21 reserves.

22

23 Having identified the optimal thresholds (i.e., the animal's reserve-dependent strategy, and thus its  
24 behaviour), it is then possible to identify the initial effect of a rapid environmental change by  
25 applying those thresholds in the new environment. The expected payoffs can be calculated as they

1 were before, this time without subsequently adjusting the thresholds. If the effect of HIREC is to  
2 introduce a new type of animal (one which is safe but appears dangerous), the expected payoff is  
3 calculated by breaking the equation down into three parts rather than 2:

4

$$5 \quad V(i) = p_D \left( \Phi_D(x_i)V_{DC}(i) + (1 - \Phi_D(x_i))V_{DR}(i) \right) + p_N(\Phi_D(x_i)V_{SF}(i) + (1 - \Phi_D(x_i))V_{SR}(i)) \\ 6 \quad \quad \quad + (1 - p_D - p_N)(\Phi_S(x_i)V_{SF}(i) + (1 - \Phi_S(x_i))V_{SR}(i))$$

7

8 where  $p_N$  denotes the probability of the encountered animal being novel.

9

10 Reference:

11 Egan, J.P. (1975) Signal Detection Theory and ROC Analysis. Academic Press, NY.

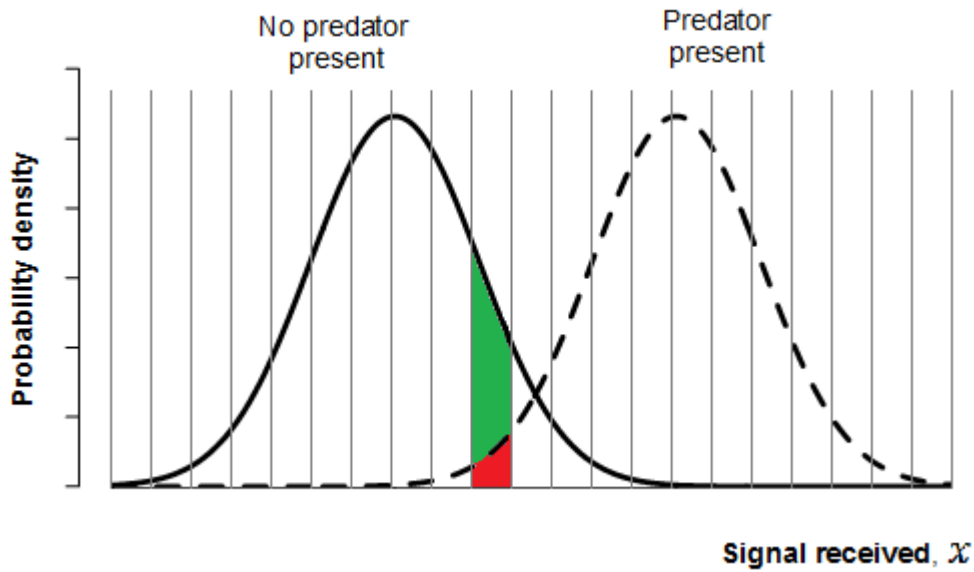
12

13 **Supplementary Material 2: Contrasting SDDT with standard state-dependent modelling (without**  
14 **the signal detection theory).**

15

16 As we mention in the main text, it is possible to approximate the SDDT result to any degree of  
17 accuracy if sufficient computational processing power is applied to the problem. This can be done  
18 by segmenting the range of possible signals into sufficiently small regions that the results are  
19 equivalent. We illustrate this in Figure B1, showing the probability density functions of signal for  
20 each scenario segmented into intervals of signal strength.

21



1

2 Figure B1: By segmenting the probability density functions into regions of signal strength, the best  
 3 decision in each region (run or forage) can be calculated (assuming the payoffs are known for each  
 4 action), along with the probability of such an occurrence. The signal distribution relating to safe (i.e.,  
 5 non-predatory) scenarios is shown as the solid normal distribution on the left; the dashed line shows  
 6 the distribution when a predatory threat is present. Taken each region in turn, the probability of  
 7 obtaining a signal in that region can be calculated as the prior expectation multiplied by the area  
 8 under the respective curve (for the region highlighted, the red area in the case of a predator, and the  
 9 red + green area in the case of no predator). By summing the multiples of these probabilities by the  
 10 expected payoff of the action associated with that region, the expected overall value of being in that  
 11 state can be calculated.

12

13

14 For any given region, the relative probability of receiving a signal in that range can be estimated  
 15 using the probability density values at the mid-point of the section (and the prior probability of each  
 16 scenario). If the payoffs of each combination of situation and action are known, the expected value  
 17 of each action can be calculated; it is best to choose the action which has the highest value. Thus, by  
 18 doing this in each segment, we find the best policy in a piece-meal manner, whereby all the sections

1 to the right of some signal strength will trigger anti-predator behavior (running away) and all to the  
2 left of that position will result in foraging. By increasing the number of segments (reducing the  
3 length of each), the approximations improve and the signal detection theory solution can be found  
4 to an arbitrarily fine accuracy. This can be carried out for each segment, and for each possible  
5 reserve level. Just as is done with the SDDT approach, the reproductive value of each reserve level  
6 can thus be calculated iteratively, along with the decision that would be made for each signal at each  
7 reserve level. The only difference is the ease of computation of the decision threshold if the signal  
8 detection equation is not used.

9

10 This seemingly small difference can affect run time and tractability, as the number of calculations  
11 required can be considerable; the number of signal intervals (e.g., 100) is multiplied by the number  
12 of possible reserve levels and again by the number of time units to a time horizon (if applying a  
13 standard state-dependent approach of a time-horizon; Houston & McNamara 1999, Clark & Mangel  
14 2000). For each of these cases, the pdf of each signal must be multiplied by the relevant prior  
15 probabilities and the expected payoffs of outcomes to determine the best action (and these must  
16 then all be summed to obtain the reproductive value associated with reaching each reserve state).  
17 In contrast, the use of the signal detection theory (equation 1 of the main text) makes this process  
18 both faster and neater, reaching the optimum solution with minimal calculation.

19

20

### 21 **Supplementary Material 3: Expected Lifespan**

22

23 In this appendix, we treat each payoff value as an expected lifespan, and identify the strategy (i.e.,  
24 the set of reserve-dependent thresholds) which maximizes the expected lifespan from any given  
25 reserve level.

26

1 We discretize time into a series of periods and assume that the environmental condition is  
 2 independent at each period. We set an upper bound on the possible reserve levels, so reserves take  
 3 an integer value,  $\{0, 1, \dots, L\}$ , where the animal dies if reserves fall to zero.

4  
 5 We assume that at each period, the animal either takes evasive action (running away), in which case  
 6 its reserves will decrease by one unit, or forages, in which case reserves increase by one unit. We  
 7 have used this movement of only 1 unit (in either direction) for illustrative purposes because it is the  
 8 most simple; many authors may prefer, for instance, to increase reserves by more than a single unit  
 9 if food is obtained; this sort of detail will depend on the specific situation being considered. We  
 10 assume that death (be it through starvation or predation) occurs at the end of a period. Setting  
 11 optimal thresholds at each reserve level depends on the payoff values of each action from the  
 12 current state,  $i$ . The resulting payoffs, which depend on the payoffs at one step higher reserves and  
 13 one step lower reserves, are shown in Table C1.

14

|                     |             | Environmental condition |                |
|---------------------|-------------|-------------------------|----------------|
|                     |             | Dangerous, D            | Safe, S        |
| Action<br><br>Taken | Run away, R | $V(i - 1)e + 1$         | $V(i - 1) + 1$ |
|                     | Forage, F   | $V(i + 1)m + 1$         | $V(i + 1) + 1$ |

15 Table C1: Payoff matrix of expected lifespan for state-dependent thresholds, starting from reserves  $i$ .  
 16  $e$  is the escape probability when running from a predator.  $m$  is the probability of surviving despite  
 17 having decided to forage (either by being missed by the predator, or escaping when attacked);  $e > m$ .  
 18  $V(0) = 0$ . When  $i = L$ ,  $V(i + 1) = V(i) = V(L)$ .

19

1 At maximum reserves, a successful foraging individual will maintain its reserve level (subject to the  
2 risk of being predated whilst foraging). At reserves of 1, the individual must forage, as it will die  
3 anyway at the end of the period if it has run. Consequently, as this aspect of the model is not  
4 stochastic, the animal will never starve to death, but the threat of doing so means that at low  
5 reserves, it will expose itself to any amount of predation risk (for a proof, see McNamara 1990). (In a  
6 simple extension to this model, where food is also stochastic, it would also be possible for the animal  
7 to starve to death.) At intermediate reserves, the optimal threshold will depend on the relative value  
8 of food compared to the risk of predation.

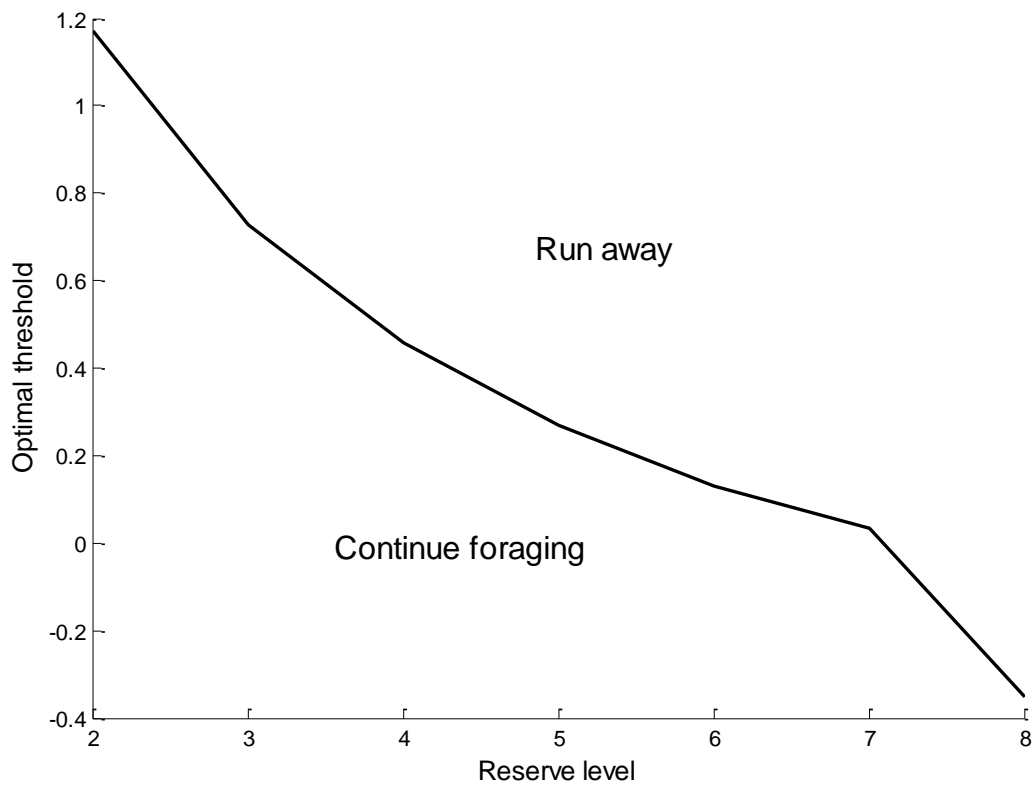
9

10 An iterative method of calculating both the payoff values (in this case, expected lifespan) and the  
11 optimal thresholds is described in Appendix 1. Throughout this paper, we shall assume that the  
12 mean signal of the safe animal is zero; the mean signal of the predator is 2. Thus, for instance,  
13 setting a threshold of 1 would place equal emphasis on detection of predators and foraging.  
14 Thresholds lower than 1 place more emphasis on the risk of predation.

15

16 Figure C1 shows how the optimal threshold varies with reserve level, for a particular set of  
17 parameters; we have calculated the thresholds such as to maximize the expected lifespan of an  
18 individual starting with reserves of 1.

19



1

2 Figure C1: The optimal signal-detection threshold varies as a function of reserves. Note that there is  
 3 no decision to be made at reserves of 1; it is best to forage regardless of the risk of predation. At  
 4 maximum reserves (of  $L = 8$ ), there is less to be gained by foraging (simply staying at maximum  
 5 reserves), so there is considerably more incentive to run away. [Parameters:  $L = 8$ ,  $p_D = 0.1$ ,  $\mu_s = 0$ ,  $\mu_D$   
 6  $= 2$ ,  $\sigma = 1$ ,  $e = 1$ ,  $m = 0$ .]

7

8

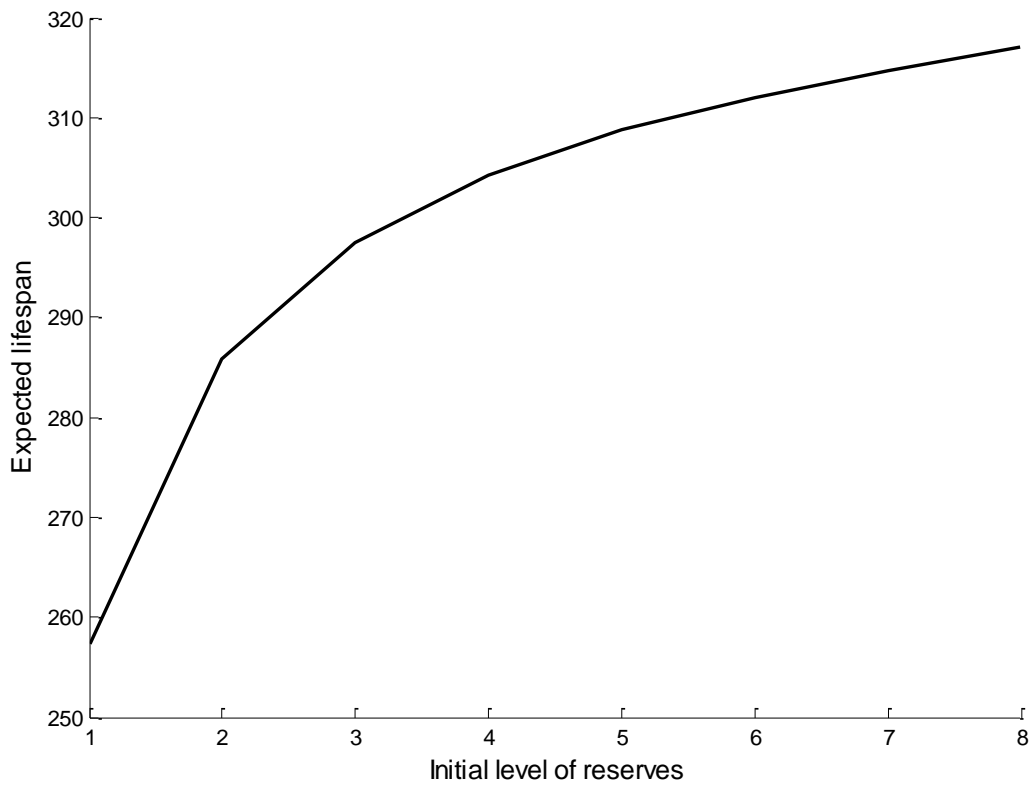
9 Note that with higher reserves, the risk of death from starvation is reduced, so the animal can afford  
 10 to be (and is) more wary of potential predators. In contrast to Figure B1, the results when  
 11 maximising reproductive success (Figure 1 of the main text) show that the threshold does not  
 12 decrease as much at high reserves; this is because rather than simply aiming to stay alive, the  
 13 reward (through the payoff matrix in the main text) of reproduction is attained by reaching high  
 14 reserves.

15



1 The expected lifespan of individuals increases with initial reserve level, as shown in Figure C2.

2



3

4 Figure C2: Expected lifespan increases with reserves. Note that in this model, at minimal reserves,  
5 the individual will always forage, and will always obtain food, so death only occurs through  
6 predation. For many animals, where food is also stochastic, there will be a much more significant  
7 reduction in expected lifespan for an individual with very low reserves. [Parameters:  $L = 8$ ,  $p_D = 0.1$ ,  
8  $\mu_S = 0$ ,  $\mu_D = 2$ ,  $\sigma = 1$ ,  $e = 1$ ,  $m = 0$ .]

9

10

11 Ref:

12 McNamara, J.M. (1990) The policy which maximizes long-term survival of an animal faced with the  
13 risks of starvation and predation. *Advances in Applied Probability* 22(2), 295-308

14

15

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15

**Supplementary Material 4: Effects of other parameters on reproductive success: probability of danger,  $p_D$ , discernability of danger,  $\mu_D - \mu_S$ , and survival probabilities  $e$  and  $m$ .**

Figure D1 shows the effect of varying the probability of danger,  $p_D$ , from the baseline values, both without any HIREC (marked pre-HIREC) and following the introduction of SBADs (such that 25% of the safe situations now appear dangerous:  $\mu_N = \mu_D = 2$ ).

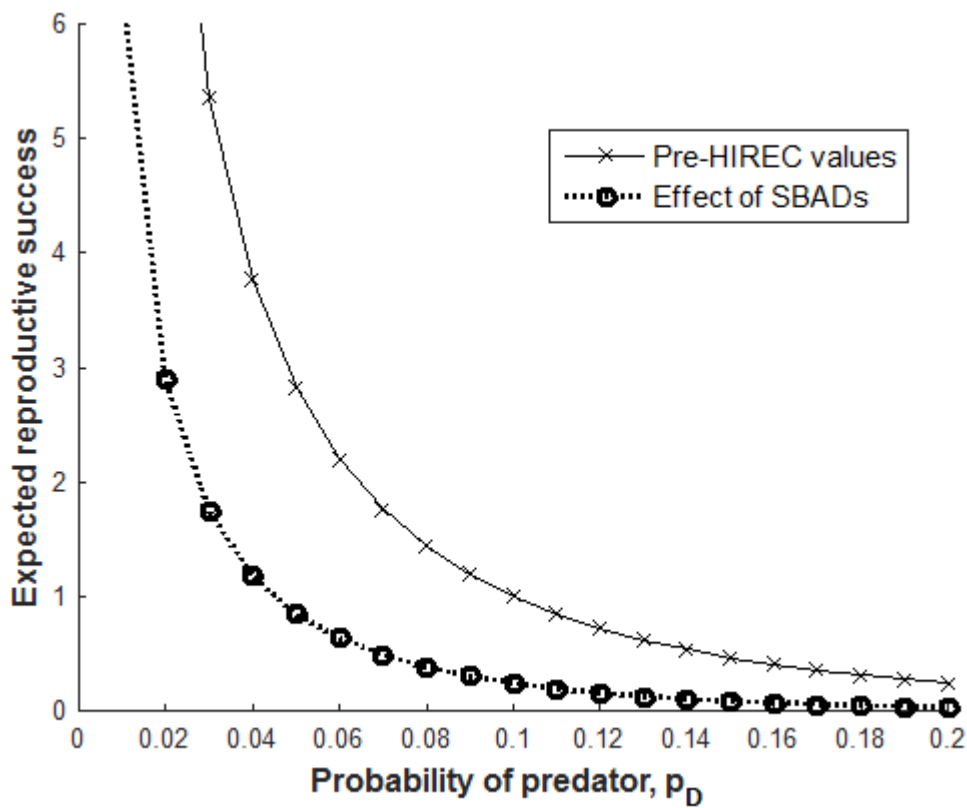
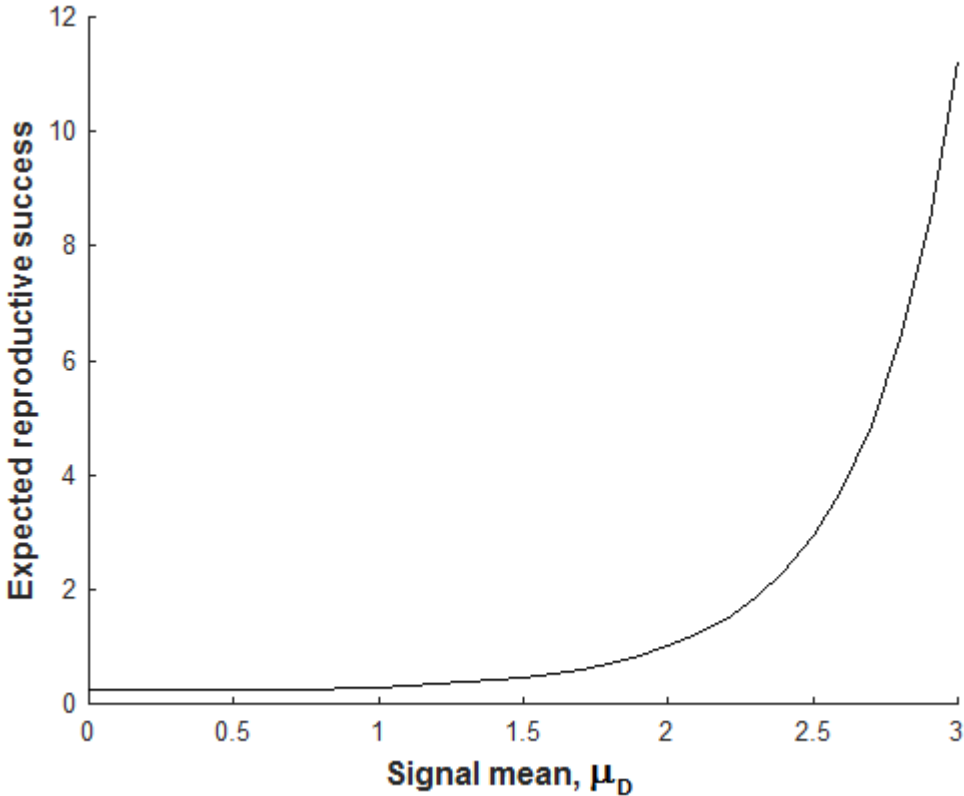


Figure D1: The effect of  $p_D$  on reproductive success: the effect of altering the pre-HIREC values (i.e., evolving to the true  $p_D$ ) is shown by the higher of the two lines. By introducing the novel species at a rate of 25% of the safe situations now appearing dangerous (in terms of signal mean), the expected reproductive success decreases due to unnecessary hiding, but the general trend of results with respect to  $p_D$  remains similar. [Parameters:  $\mu_S = 0$ ,  $\mu_D = 2$ ,  $\sigma = 1$ ,  $e = 1$ ,  $m = 0$ ,  $c = 6$ . Post-HIREC, 25% of the safe situations involve the novel species, i.e.,  $p_N = 0.225$ .]

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11

The distinguishability of the signals,  $\mu_D - \mu_S$ , also influences results (here we vary the means and keep the variance constant; holding the means constant and reducing the variance would also increase distinguishability of the signals). The effect pre-HIREC (i.e., evolved without any SBADs) is shown in Figure D2; note that  $\mu_S$  is zero, so the separation between the means of each signal distribution is summarised by  $\mu_D$ . The effect immediately following the introduction of SBADs is shown in Figure D3; note that the relationship  $\mu_N = \mu_D$  has been maintained for this graph, so that the signals from the newly introduced SBADs are indistinguishable from the dangerous signals, though the species has evolved to respond according to the old dangerous signals ( $\mu_D = 2$ ), resulting in a point of inflexion.

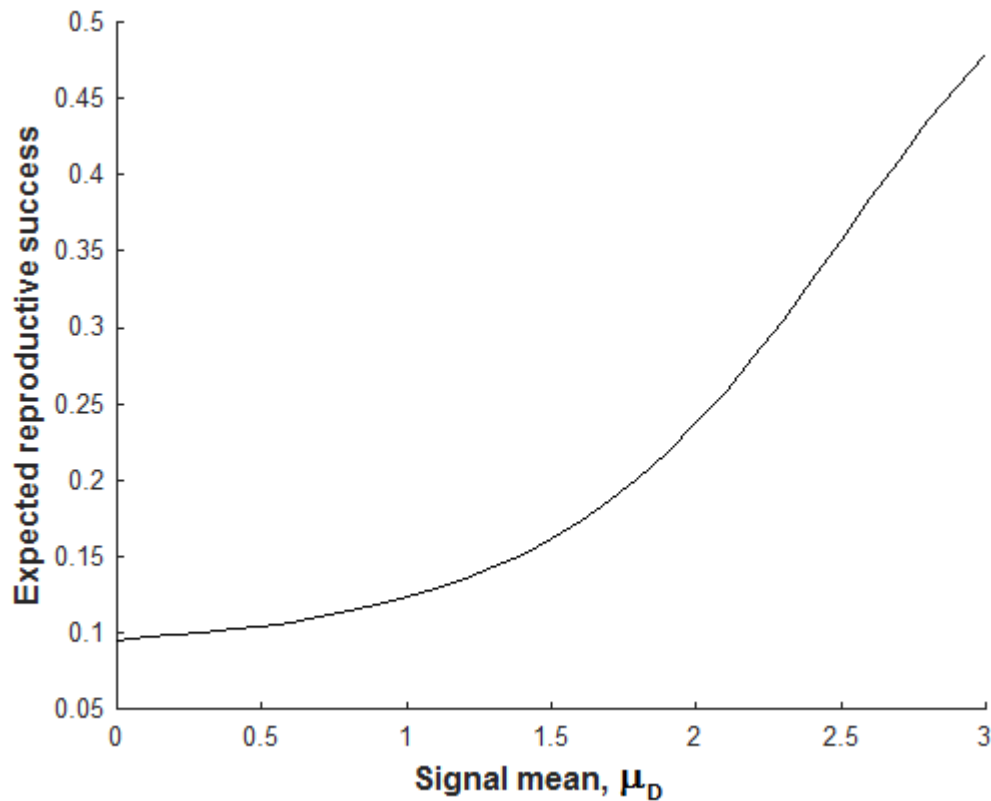


12  
13  
14  
15

Figure D2: The effect of separation between the mean signals of safe and dangerous situations has a dramatic effect on expected reproductive success (of the evolved species) as the overlap between the distributions starts to disappear, because the focal species can evolve a threshold whereby it

1 always forages when safe and runs when there is danger. [Parameters:  $p_D = 0.1$ ,  $\mu_s = 0$ ,  $\sigma = 1$ ,  $e = 1$ ,  
2  $m = 0$ ,  $c = 6$ .]

3



4

5 Figure D3: Assuming that the signal distribution of the novel species (introduced during HIREC) is  
6 always indistinguishable from the real predator, this graph shows how the separation between safe  
7 and dangerous signals, along with the introduction of the SBADs, influences the immediate  
8 reproductive success following HIREC. [Parameters:  $p_D = 0.1$ ,  $\mu_s = 0$ ,  $\mu_D = 2$  initially,  $\sigma = 1$ ,  $e = 1$ ,  $m =$   
9  $0$ ,  $c = 6$ . Post-HIREC, 25% of the safe situations involve the novel species, i.e.,  $p_N = 0.225$ .]

10

11

12 We have also looked at the effects of  $e$  (the probability of escape, given running) and  $m$  (the  
13 probability of predator missing the focal individual when they have foraged).

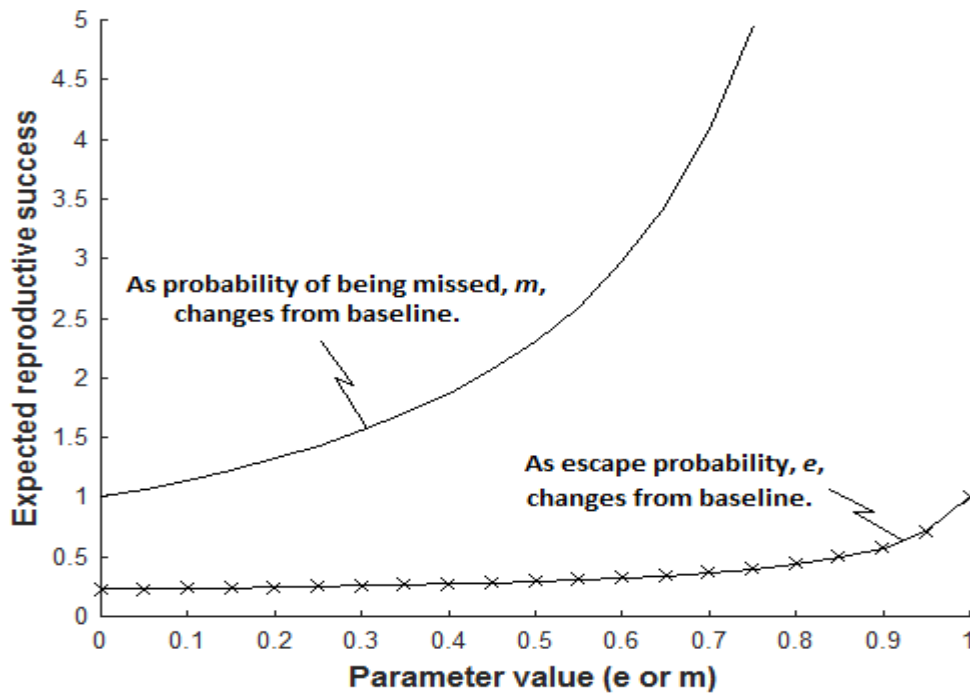
14

1 As  $e$  decreases from our baseline of 1, the worth of running away becomes decreased somewhat, so  
2 the thresholds for running increase. As  $m$  increases from our baseline of 0, the worth of foraging  
3 increases somewhat, so the thresholds for running increase. Thus, in both cases, the effect of  
4 altering from our baseline values is to increase the thresholds, corresponding to animals that are  
5 slightly less reactive than our baseline outcomes. However, the changes have opposing effects in  
6 terms of the expected reproductive value; this obviously increases as  $m$  increases, and decreases as  
7  $e$  decreases. As each alteration from baseline decreases the responsiveness of the animal to possible  
8 predation cues, the effect of this form of HIREC on animals is also reduced with alterations from the  
9 baseline, in terms of expected number of offspring.

10

11 Figure D4 shows the effects of  $e$  and  $m$  on expected reproductive success as another type of HIREC  
12 (without the introduction of any novel species, and without the probability of safe or dangerous  
13 situations being altered), for instance, through the amount of vegetative cover being altered. Note  
14 that because of the graph scaling, it is easy to be visually misled into believing that  $m$  has a stronger  
15 effect on reproductive success than  $e$ . Shifting the value of  $m$  from the baseline of 0 to 0.5 increases  
16 reproductive success from 1 to 2.3 (just over double), whereas shifting  $e$  from a baseline of 1 to 0.5  
17 reduces reproductive success from 1 to 0.29 (much less than half), so the latter parameter arguably  
18 has the larger effect.

19



1

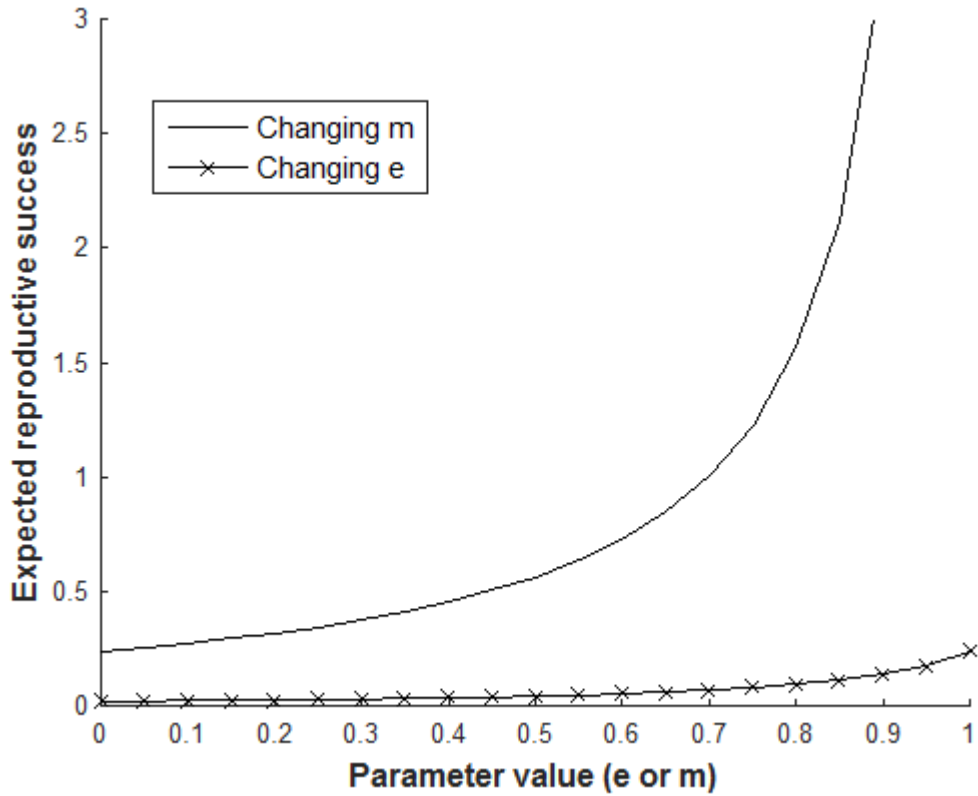
2 Figure D4: Effects of  $e$  and  $m$  on reproductive success in the baseline scenario. [Parameters:  $\mu_S = 0$ ,  
 3  $\mu_D = 2$ ,  $\mu_N = 2$ ,  $\sigma = 1$ ,  $e = 1$  (when  $m$  is being altered),  $m = 0$  (when  $e$  is being altered),  $c = 6$ ,  $p_D = 0.1$ .]

4

5

6 Figure D5 shows the immediate effect of  $e$  and  $m$  following HIREC, i.e., at the same time as the  
 7 introduction of a novel species, the probability of a predator missing an opportunity (through not  
 8 spotting its prey,  $m$ , or the prey escaping,  $e$ ) are also altered. Just like Figure D4, the visual effect of  
 9 the graph can be misleading; the reproductive success for  $m = 0$  is the same as that of  $e = 1$ , but the  
 10 latter line (relating to the effect of  $e$ ) has a larger gradient at that point, so the effect of a small  
 11 change in  $e$  is greater than a small change in  $m$  from our baseline values.

12



1

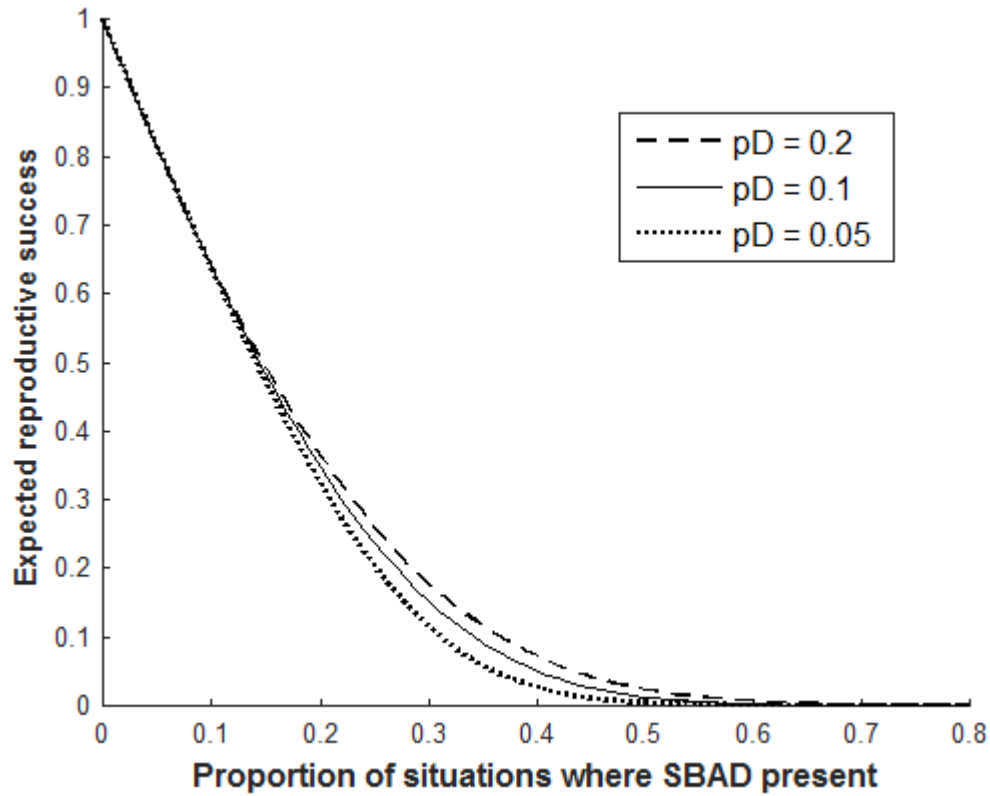
2 Figure D5: Effects of  $e$  and  $m$  on reproductive success, in conjunction with the introduction of a  
 3 novel species during HIREC. [Parameters:  $\mu_S = 0$ ,  $\mu_D = 2$ ,  $\mu_N = 2$ ,  $\sigma = 1$ ,  $e = 1$ ,  $m = 0$ ,  $c = 6$ ,  $p_D = 0.1$ .]

4

5

6 Figure D6 shows that for the baseline parameters, the effect of SBADs on reproductive rate is not  
 7 very sensitive to the probability of danger,  $p_D$ . The effect of  $m$ , the probability of a predator missing  
 8 the opportunity to kill, is even smaller (nearly undetectable by eye for values between 0 and 0.4).

9



1

2 Figure D6: Effect of probability of danger on the subsequent (immediate) effect of SBADs. Note that  
 3 each line has been 'normalised' such that expected reproductive success without SBADs is 1, so that  
 4 the population under consideration is neither growing nor shrinking prior to HIREC. [Parameters:  $\mu_s$   
 5 = 0,  $\mu_D = 2$ ,  $\mu_N = 2$ ,  $\sigma = 1$ ,  $e = 1$ ,  $m = 0$ ,  $c = 6$ .]

6

7