

# 1 Single-predator model

## 1.1 Probability of predator presence

In the single predator model by [Taborsky \*et al.\* \(2021\)](#), the probability  $p_{\text{pred}}(\tau)$  that one of the stressors is present at  $\tau$  time steps since the last attack is given by

$$p_{\text{pred}}(\tau) = \begin{cases} 1 - \lambda_L & \tau = 1 \\ \frac{p_{\text{pred}}(\tau-1)(1-p_{\text{att}})(1-\lambda_L) + (1-p_{\text{pred}}(\tau-1))\lambda_A}{1-p_{\text{pred}}(\tau-1)p_{\text{att}}} & \tau > 1, \end{cases} \quad (1)$$

where the first line reflects the probability that one time step  $\tau = 1$  after the attack, the predator is still present, which happens with probability  $1 - \lambda_L$  reflecting that the predator is not leaving.

The second line reflects the probability that a predator is present  $\tau > 1$  time steps after the attack. Note that  $p_{\text{pred}}(\tau)$  for  $\tau > 1$  is a conditional probability, as a more extensive way to write this is

$$p_{\text{pred}}(\tau) = \Pr(\text{predator present at } t = \tau \mid \text{no attack at } \tau - 1), \quad (2)$$

because if there would have been an attack at time  $\tau - 1$ , we would be back at the first line of eq. (1). We use Bayes' theorem (e.g., see p. 519 in [Otto & Day \(2007\)](#)), which exploits the fact that the joint probability  $p(A, B)$  of two outcomes  $A, B$  can be written as products of the underlying conditional probabilities and the corresponding marginal probabilities  $p(A)$ , or

$$\begin{aligned} p(A, B) &= p(A \mid B)p(B) = p(B \mid A)p(A) \\ \Rightarrow p(A \mid B) &= \frac{p(B \mid A)p(A)}{p(B)}. \end{aligned}$$

Applying this to eq. (2), we have

$$\frac{\Pr(\text{predator present at } t = \tau \mid \text{no attack at } \tau - 1) = \Pr(\text{no attack at } \tau - 1 \mid \text{predator present at } t = \tau) \Pr(\text{predator present at } t = \tau)}{\Pr(\text{no attack at } \tau - 1)}.$$

Working out the numerator, we start with  $\Pr(\text{predator present at } t = \tau)$ . There are two cases that result in a predator being present at time  $t = \tau$ : (i) the predator was already present  $\tau - 1$  time steps since the last attack ( $p_{\text{pred}}(\tau - 1)$ ) and did not leave, so that we have  $p_{\text{pred}}(\tau - 1)(1 - \lambda_L)$ . Alternatively, (ii) the predator was not present  $\tau - 1$  time steps since the last attack ( $1 - p_{\text{pred}}(\tau - 1)$ ) but just arrived, so that we have  $(1 - p_{\text{pred}}(\tau - 1))\lambda_A$ .

Next, we work out  $\Pr(\text{no attack at } \tau - 1 \mid \text{predator present at } t = \tau)$ . For case (i), the probability of not being attacked at time  $\tau - 1$  is simply  $1 - p_{\text{att}}$  reflecting that the predator was present at time  $\tau - 1$ , but did not attack. For case (ii), the probability of not being attacked at time  $\tau - 1$  is 1 as the predator was absent at time  $\tau - 1$ .

Next we work out the numerator  $\Pr(\text{no attack at } \tau - 1)$ , which is  $1 - \Pr(\text{attack at } \tau - 1)$ , where

$$\Pr(\text{attack at } \tau - 1) = p_{\text{pred}}(\tau - 1)p_{\text{att}},$$

and we are done.

## 1.2 Fitness expression

The expected fitness  $W$  of the prey animal if it expresses hormone level  $h$  at  $\tau$  time steps since last having encountered a predator is then given by

$$W(\tau) = p_{\text{pred}}(\tau) \cdot p_{\text{att}} \cdot [1 - p_{\text{kill}}(h(\tau))] \cdot (1 - \mu) \cdot [r(h(\tau)) + W'(1)] \\ + (1 - p_{\text{pred}}(\tau) p_{\text{att}}) (1 - \mu) [r(h(\tau)) + W'(\tau + 1)]. \quad (3)$$

Here the first line reflects a scenario where  $\tau$  time steps after the previous attack of the predator, the predator is present and attacks (reflected by the probability  $p_{\text{pred}}(\tau) \cdot p_{\text{att}}$ ). In case the predator kills the prey (with probability  $p_{\text{kill}}(h(\tau))$ ), the resulting fitness is 0. By contrast, when the prey survives the attack (with probability  $1 - p_{\text{kill}}(h(\tau))$ ) and also does not succumb to background mortality (with probability  $1 - \mu$ ) it will produce  $r(h(\tau))$  offspring and have future fitness  $W'(1)$ : it has now survived an attack so the prey's time since it has last encountered a predator is now  $\tau = 1$ .

Alternatively, the predator is not present or it does not attack, with probability  $1 - p_{\text{pred}}(\tau) + p_{\text{pred}}(\tau)(1 - p_{\text{att}}) = 1 - p_{\text{pred}}(\tau) p_{\text{att}}$  and if the prey survives background mortality it will produce  $r(h(\tau))$  offspring and have future fitness  $W'(\tau + 1)$ , because it is now  $\tau + 1$  time steps ago that the prey has been attacked by a predator.

## 1.3 Forward simulation

See for more information [Mangel & Clark \(1988\)](#), pp. 76 - 79. The forward recursion relating the state distribution vector of the likelihood an individual is in state  $\tau$  before an attack  $F(\tau)$  to fitness following an attack  $F'(1)$  is given by

$$F'(1) = F(\tau) p_{\text{pred}}(\tau) p_{\text{att}} [1 - p_{\text{kill}}(h(\tau))] (1 - \mu).$$

The forward recursion relating the state distribution vector  $F(\tau)$   $\tau$  time steps since attack to the state distribution vector following an attack  $F'(1)$  is given by

$$F(\tau + 1) = F(\tau) [1 - p_{\text{pred}}(\tau) p_{\text{att}}] (1 - \mu).$$

The probability to die from predation is

$$p_{\text{pred,death}} = F(\tau) p_{\text{pred}}(\tau) p_{\text{att}} p_{\text{kill}}(h(\tau)).$$

The probability to die from damage is (note that  $\mu_0$  is mortality when  $d = 0$ )

$$p_{\text{damage,death}} = F(\tau) [1 - p_{\text{pred}}(\tau) p_{\text{att}} p_{\text{kill}}(h(\tau))] (\mu - \mu_0).$$

The probability to die from background mortality is

$$p_{\text{background,death}} = F(\tau) [1 - p_{\text{pred}}(\tau) p_{\text{att}} p_{\text{kill}}(h(\tau))] \mu_0.$$

## 2 Two-predator model

In a two-predator scenario, things get more complicated, as predators can differ in their probabilities of appearance (denoted by  $\lambda_{1,A}$  and  $\lambda_{2,A}$ ) and departure (denoted by  $\lambda_{1,L}$  and  $\lambda_{2,L}$ ). Moreover, predators can also differ in their attack probabilities, which we denote by  $p_{1,att}$  and  $p_{2,att}$ .

In a model with complete information, prey can distinguish between attacks by predator 1 vs predator 2. In that case, fitness is a function of the number of time steps a predator has been attacked by either predator, or  $W(\tau_1, \tau_2)$ . However, to fix ideas, we consider a basic model, in which the only thing that a prey can sense is the number of time steps  $\tau$  since it was attacked by *any* predator. Hence, fitness is simply a function of  $\tau$ , or

$$\begin{aligned}
 W(\tau) = & p_{pred,12}(\tau) p_{survive,12}(h(\tau)) (1 - \mu) [r(h(\tau)) + W'(1)] \\
 & + \sum_{i=1}^2 p_{pred,i}(\tau) p_{survive,i}(h(\tau)) (1 - \mu) [r(h(\tau)) + W'(1)] \\
 & + p_{pred,12}(\tau) (1 - p_{att,1}) (1 - p_{att,2}) (1 - \mu) [r(h(\tau)) + W'(\tau + 1)] \\
 & + \sum_{i=1}^2 p_{pred,i}(\tau) (1 - p_{att,i}) (1 - \mu) [r(h(\tau)) + W'(\tau + 1)] \\
 & + (1 - p_{pred,1}(\tau) - p_{pred,2}(\tau) - p_{pred,12}(\tau)) (1 - \mu) [r(h(\tau)) + W'(\tau + 1)] \quad (4)
 \end{aligned}$$

The first line reflects fitness accrued when the prey is attacked by one or both predators, given that both predators are currently present: here,  $p_{pred,12}(\tau)$  reflects the probability that  $\tau$  time steps since the last attack, both predators 1 and 2 are present in the local patch and is developed in eqns. (5-7) below. Next,  $p_{survive,12}(h(\tau))$  (see eqns. [14-16] below) reflects the probability that the prey expressing hormone level  $h(\tau)$  survives an attack by one or both predators, conditional upon both predators being present in the patch. A prey survives background mortality with probability  $1 - \mu$ , in which case the prey produces  $r(h(\tau))$  offspring. Moreover, the prey itself goes on to accrue fitness  $W'(1)$  in the next time step as  $\tau$  is now reset to 1 as the prey has just survived an attack.

The second line reflects the probability that the prey survives an attack when only a single predator of type  $i$  is present, where we sum over both possible types of predator. A single predator of type  $i$  is present at time  $\tau$  with probability  $p_{pred,i}(\tau)$  (see eqns. [8-13]) Again, after surviving the attack, the prey produces  $r(h(\tau))$  offspring and then goes on to accrue fitness  $W'(1)$  in the next time step.

Lines three and four reflect scenarios in which one or both predators are present, but do not attack the prey. In this case the prey produces  $r(h(\tau))$  offspring and will have fitness  $W'(\tau + 1)$  in the next time step. The final line reflects a scenario where the predators are absent.

### 2.1 Probabilities of predator presence/absence

In contrast to the previous problem, we now need to solve for the probabilities iteratively.

**Both predators present** When  $\tau = 1$ , necessarily minimally 1 predator was present during the previous time step, so that the probability that both predators are present in the current

time step is given by

$$\begin{aligned}
p_{\text{pred},12}(\tau) &= \Pr(\text{pred 1 and 2 present at } \tau \mid \text{attack at } \tau - 1) \\
&= \frac{\Pr(\text{attack at } \tau - 1 \mid \text{pred 1,2 present } \tau) \Pr(\text{pred 1,2 present } \tau)}{\Pr(\text{attack at } \tau - 1)} \\
&= \left[ (1 - \lambda_{1,L})(1 - \lambda_{2,L}) \sum_{\tau=2}^{\tau_{\max}} p_{\text{pred},12}(\tau - 1) (p_{\text{att},1} + p_{\text{att},2} - p_{\text{att},1} p_{\text{att},2}) \right. \\
&\quad + (1 - \lambda_{1,L}) \lambda_{2,A} \sum_{\tau=2}^{\tau_{\max}} p_{\text{att},1} p_{\text{pred},1}(\tau - 1) \\
&\quad \left. + \lambda_{1,A} (1 - \lambda_{2,L}) \sum_{\tau=2}^{\tau_{\max}} p_{\text{att},2} p_{\text{pred},2}(\tau - 1) \right] \\
&\quad / \Pr(\text{attack at } \tau - 1),
\end{aligned}$$

where

$$\begin{aligned}
\Pr(\text{attack } \tau - 1) &= \sum_{\tau=2}^{\tau_{\max}} p_{\text{pred},12}(\tau - 1) [p_{\text{att},1} + p_{\text{att},2} - p_{\text{att},1} p_{\text{att},2}] \\
&\quad + \sum_{\tau=2}^{\tau_{\max}} p_{\text{pred},1}(\tau - 1) p_{\text{att},1} \\
&\quad + \sum_{\tau=2}^{\tau_{\max}} p_{\text{pred},2}(\tau - 1) p_{\text{att},2}.
\end{aligned}$$

For the case where  $\tau > 1$ , we have

$$\begin{aligned}
p_{\text{pred},12}(\tau) &= \Pr(\text{pred 1 and 2 present at } \tau \mid \text{no attack at } \tau - 1) \\
&= \frac{\Pr(\text{no attack at } \tau - 1 \mid \text{pred 1,2 present } \tau) \Pr(\text{pred 1,2 present } \tau)}{\Pr(\text{no attack at } \tau - 1)} \tag{5}
\end{aligned}$$

which we can write out as

$$\begin{aligned}
p_{\text{pred},12}(\tau) &= [(1 - p_{\text{att},1})(1 - p_{\text{att},2}) p_{\text{pred},12}(\tau - 1) (1 - \lambda_{1,L})(1 - \lambda_{2,L}) \\
&\quad + (1 - p_{\text{att},1}) p_{\text{pred},1}(\tau - 1) (1 - \lambda_{1,L}) \lambda_{2,A} \\
&\quad + (1 - p_{\text{att},2}) p_{\text{pred},2}(\tau - 1) \lambda_{1,A} (1 - \lambda_{2,L}) \\
&\quad + (1 - p_{\text{pred},1}(\tau - 1) - p_{\text{pred},2}(\tau - 1) - p_{\text{pred},12}(\tau - 1)) \lambda_{1,A} \lambda_{2,A}] \\
&\quad / \Pr(\text{no attack at } \tau - 1) \tag{6}
\end{aligned}$$

here the first line reflects that both predators were present at time  $\tau - 1$  with probability  $p_{\text{pred},12}(\tau - 1)$ , did not attack with probability  $(1 - p_{\text{att},1})(1 - p_{\text{att},2})$  and then subsequently did not leave with probability  $(1 - \lambda_{1,L})(1 - \lambda_{2,L})$ . The second line reflects that predator 1 was present at time  $\tau - 1$  with probability  $p_{\text{pred},12}(\tau - 1)$ , did not leave with probability  $1 - \lambda_{1,L}$  and did not attack with probability  $1 - p_{\text{att},1}$  while predator 2 arrived with probability  $\lambda_{2,A}$ . The third line is similar to the second line, except that it is predator 2 who was present at time  $\tau - 1$  while predator 1 arrived, while the fourth line reflects that neither predator is present at time  $\tau - 1$ , but arrive with

probability  $\lambda_{1,A}\lambda_{2,A}$ . Finally, working out the denominator, we have

$$\begin{aligned} \Pr(\text{no attack at } \tau - 1) &= p_{\text{pred},12}(\tau - 1)(1 - p_{\text{att},1})(1 - p_{\text{att},2}) \\ &\quad + p_{\text{pred},1}(\tau - 1)(1 - p_{\text{att},1}) \\ &\quad + p_{\text{pred},2}(\tau - 1)(1 - p_{\text{att},2}) \\ &\quad + (1 - p_{\text{pred},1}(\tau - 1) - p_{\text{pred},2}(\tau - 1) - p_{\text{pred},12}(\tau - 1)). \end{aligned} \quad (7)$$

**Predator 1 present** Let us consider the recursion equation for predator 1. When  $\tau = 1$  (an attack took place during the previous time step), we have

$$p_{\text{pred},1}(1) = (1 - \lambda_{1,L})\lambda_{2,L} \sum_{\tau=2}^{\tau_{\max}} p_{\text{pred},12}(\tau - 1)(p_{\text{att},1} + p_{\text{att},2} - p_{\text{att},1}p_{\text{att},2}) \quad (8)$$

$$+ (1 - \lambda_{1,L})(1 - \lambda_{2,A}) \sum_{\tau=2}^{\tau_{\max}} p_{\text{pred},1}(\tau - 1)p_{\text{att},1} \quad (9)$$

$$+ \lambda_{1,A}\lambda_{2,L} \sum_{\tau=2}^{\tau_{\max}} p_{\text{pred},2}(\tau - 1)p_{\text{att},2} \quad (10)$$

When  $\tau > 1$ , we have according to the same logic as in eqns. (5,6 and 7)

$$\begin{aligned} p_{\text{pred},1}(\tau) &= [(1 - p_{\text{att},1})(1 - p_{\text{att},2})p_{\text{pred},12}(\tau - 1)(1 - \lambda_{1,L})\lambda_{2,L} \\ &\quad + (1 - p_{\text{att},1})p_{\text{pred},1}(\tau - 1)(1 - \lambda_{1,L})(1 - \lambda_{2,A}) \\ &\quad + (1 - p_{\text{att},2})p_{\text{pred},2}(\tau - 1)\lambda_{1,A}\lambda_{2,L} \\ &\quad + (1 - p_{\text{pred},1}(\tau - 1) - p_{\text{pred},2}(\tau - 1) - p_{\text{pred},12}(\tau - 1))\lambda_{1,A}(1 - \lambda_{2,A})] \\ &\quad / \Pr(\text{no attack at } \tau - 1), \end{aligned} \quad (11)$$

with the denominator given in eq. (7).

Obviously, similar logic applies when deriving  $p_{\text{pred},2}$ , yielding

$$\begin{aligned} p_{\text{pred},2}(1) &= \lambda_{1,L}(1 - \lambda_{2,L}) \sum_{\tau=2}^{\tau_{\max}} p_{\text{pred},12}(\tau - 1)(p_{\text{att},1} + p_{\text{att},2} - p_{\text{att},1}p_{\text{att},2}) \\ &\quad + \lambda_{1,L}\lambda_{2,A} \sum_{\tau=2}^{\tau_{\max}} p_{\text{pred},1}(\tau - 1)p_{\text{att},1} \\ &\quad + (1 - \lambda_{1,A})(1 - \lambda_{2,L}) \sum_{\tau=2}^{\tau_{\max}} p_{\text{pred},2}(\tau - 1)p_{\text{att},2} \end{aligned} \quad (12)$$

$$\begin{aligned} p_{\text{pred},2}(\tau) &= [(1 - p_{\text{att},1})(1 - p_{\text{att},2})p_{\text{pred},12}(\tau - 1)\lambda_{1,L}(1 - \lambda_{2,L}) \\ &\quad + (1 - p_{\text{att},1})p_{\text{pred},1}(\tau - 1)\lambda_{1,L}\lambda_{2,A} \\ &\quad + (1 - p_{\text{att},2})p_{\text{pred},2}(\tau - 1)(1 - \lambda_{1,A})(1 - \lambda_{2,L}) \\ &\quad + (1 - p_{\text{pred},1}(\tau - 1) - p_{\text{pred},2}(\tau - 1) - p_{\text{pred},12}(\tau - 1))(1 - \lambda_{1,A})\lambda_{2,A}] \\ &\quad / \Pr(\text{no attack at } \tau - 1). \end{aligned} \quad (13)$$

Finally, to make sure it all adds up, we also derive the probability that *no* predator is present at  $\tau = 1$ , when it was necessarily present at  $\tau = 0$

$$\begin{aligned}
p_{\text{no pred}}(1) &= \lambda_{1,L} (1 - \lambda_{2,A}) \sum_{\tau=2}^{\tau_{\max}} p_{\text{pred},1}(\tau-1) p_{\text{att},1} \\
&\quad + (1 - \lambda_{1,A}) \lambda_{2,L} \sum_{\tau=2}^{\tau_{\max}} p_{\text{pred},2}(\tau-1) p_{\text{att},2} \\
&\quad + \lambda_{1,L} \lambda_{2,L} \sum_{\tau=2}^{\tau_{\max}} p_{\text{pred},12}(\tau-1) (p_{\text{att},1} + p_{\text{att},2} - p_{\text{att},1} p_{\text{att},2})
\end{aligned}$$

Hence,  $p_{\text{pred},12}(1) + p_{\text{pred},1}(1) + p_{\text{pred},2}(1) + p_{\text{no pred}}(1)$  should sum to one.

## 2.2 Survival probabilities given one or both predators attack

We have

$$\begin{aligned}
p_{\text{survive},12}(h(\tau)) &= p_{\text{att},1} \cdot p_{\text{att},2} \cdot (1 - p_{\text{kill}}(h(\tau)))^2 \\
&\quad + [p_{\text{att},1} (1 - p_{\text{att},2}) + (1 - p_{\text{att},1}) p_{\text{att},2}] (1 - p_{\text{kill}}(h(\tau))), \tag{14}
\end{aligned}$$

$$p_{\text{survive},1}(h(\tau)) = p_{\text{att},1} \cdot (1 - p_{\text{kill}}(h(\tau))) \tag{15}$$

$$p_{\text{survive},2}(h(\tau)) = p_{\text{att},2} \cdot (1 - p_{\text{kill}}(h(\tau))) \tag{16}$$

where the first line of  $p_{\text{survive},12}(h(\tau))$  reflects the probability that both predators attack and the prey survives, while the second line reflects that only one of both predators attack. Note that in case neither predator attacks, with probability  $(1 - p_{\text{att},1})(1 - p_{\text{att},2})$   $\tau$  is not reset to 1, so it does not feature.

## 2.3 Forward simulation

More about a forward simulation can be found in [Mangel & Clark \(1988\)](#), pp. 76 - 79. The previous backward simulation algorithm is used to find the decisions that maximize fitness. Yet, what does the model then predict about actual observations on the optimal sequence of decisions taken by an individual organism? We cannot use the backward simulation for this, as that is chiefly used to calculate the optimal decision, rather than what is going on with a single individual.

In a forward simulation, we focus on the state distribution vector  $F(\tau)$  which describes the probability that an organism has been last attacked  $\tau$  time steps ago. We can then relate the state distribution vector  $F'(\tau)$  to the state distribution vector in the previous time step according to

$$\begin{aligned}
F'(1) &= F(\tau) p_{\text{pred},12}(\tau) p_{\text{att},1} p_{\text{att},2} [1 - p_{\text{kill}}(h(\tau))]^2 (1 - \mu) \\
&\quad + F(\tau) p_{\text{pred},12}(\tau) [(1 - p_{\text{att},1}) p_{\text{att},2} + p_{\text{att},1} (1 - p_{\text{att},2})] [1 - p_{\text{kill}}(h(\tau))] (1 - \mu) \\
&\quad + F(\tau) p_{\text{pred},1}(\tau) p_{\text{att},1} [1 - p_{\text{kill}}(h(\tau))] (1 - \mu) \\
&\quad + F(\tau) p_{\text{pred},2}(\tau) p_{\text{att},2} [1 - p_{\text{kill}}(h(\tau))] (1 - \mu).
\end{aligned}$$

The forward recursion relating fitness  $\tau$  time steps since attack  $W(\tau)$  to fitness following an attack  $W'(1)$  is given by

$$\begin{aligned} F'(\tau + 1) = & F(\tau) p_{\text{pred},12}(\tau) (1 - p_{\text{att},1}) (1 - p_{\text{att},2}) (1 - \mu) \\ & + F(\tau) p_{\text{pred},1}(\tau) (1 - p_{\text{att},1}) (1 - \mu) \\ & + F(\tau) p_{\text{pred},2}(\tau) (1 - p_{\text{att},2}) (1 - \mu) \\ & + F(\tau) [1 - (p_{\text{pred},12}(\tau) + p_{\text{pred},1}(\tau) + p_{\text{pred},2}(\tau))] (1 - \mu) \end{aligned}$$

The probability to die from predation is

$$\begin{aligned} p_{\text{pred},\text{death}} = & F(\tau) p_{\text{pred},12}(\tau) p_{\text{att},1} p_{\text{att},2} \{1 - [1 - p_{\text{kill}}(h(\tau))]^2\} \\ & + F(\tau) p_{\text{pred},1}(\tau) p_{\text{att},1} p_{\text{kill}}(h(\tau)) \\ & + F(\tau) p_{\text{pred},2}(\tau) p_{\text{att},2} p_{\text{kill}}(h(\tau)) \end{aligned}$$

The probability to die from damage is (note that  $\mu_0$  is mortality when  $d = 0$ )

$$p_{\text{damage},\text{death}} = F(\tau) [1 - p_{\text{pred}}(\tau) p_{\text{att}} p_{\text{kill}}(h(\tau))] (\mu - \mu_0).$$

The probability to die from background mortality is

$$p_{\text{background},\text{death}} = W(\tau) [1 - p_{\text{pred}}(\tau) p_{\text{att}} p_{\text{kill}}(h(\tau))] \mu_0.$$

## References

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