Electronic appendices to accompany “Territorial intrusion risk and antipredator behaviour: a mathematical model”

Appendix A: expected accumulated time that intruders spend in the territory

A.1 Time spent by other conspecifics

If the presence of a predator does not affect the entry of intruders, the expected total time that the other conspecifics accumulate within a territory in the absence of the territory owner is given by

$$E\left[\int_h^r N(t)\,\mathrm{d}t\right] = \int_h^r E\left[N(t)\right]\,\mathrm{d}t = \int_h^r \beta(t-h)\,\mathrm{d}t = \beta\frac{(r-h)^2}{2} \tag{A-1}$$

where $N(t)$ is the number of other conspecifics by time t, h is the time at which the animal hides (i.e., t_p+t_h), and r is the time at which the animal reemerges (i.e., $t_p+t_h+t_r$); the first equal sign (interchange of order of integration and expectation) follows from Fubini’s theorem (e.g., Williams, 1991 [Williams, D. 1991. “Probability with martingales”. Cambridge University Press], ch. 8) and the second results from direct substitution of the expected value of a Poisson random variable. Once intruders are present in the territory they stay until the resident reemerges.

Expression A-1 needs to be modified because no intruder can enter the territory while the predator is in the area; therefore, the starting time of the process is not h, but a random variable, z, whose pdf is the pdf of the time at which the predator leaves the area (i.e., $f_Z(z) = \rho\mathrm{e}^{-\rho(z-h)}$). Then, using conditional expectation ($E[Y] = E[E[Y|Z]] = \int E[Y|Z=z]f_Z(z)\,\mathrm{d}z$) the expected total time that the other conspecifics accumulate is given by

$$\int_h^r \beta\frac{(r-u)^2}{2}\rho\,\mathrm{e}^{-\rho(u-h)}\,\mathrm{d}u = \int_0^{t_r} \beta\frac{(t_r-s)^2}{2}\rho\,\mathrm{e}^{-\rho s}\,\mathrm{d}s = \frac{\beta}{\rho^2} - \frac{\beta}{\rho^2\mathrm{e}^{\rho t_r}} - \frac{\beta t_r}{\rho} + \frac{\beta t_r^2}{2}. \tag{A-2}$$

A.2 Time spent by the reintruder

First, suppose that, conditional on the reintruder attempting a return, the reintruder return time is fixed (i.e., the pdf of t is 1 for $t = t_i$ and 0 otherwise). Define $t_{ip} = t_i - t_p$ as the time at which the intruder returns with respect to the predator attack. Since the reintruder can only invade successfully if the resident is hiding and the predator is not present, the expected time spent by the reintruder is given by

$$(r-t_i)(1-\mathrm{e}^{-\rho(t_i-(t_p+t_h))})p = (t_r+t_h+t_{pi})(1-\mathrm{e}^{-\rho(t_{ip}-t_h)})p, \tag{A-3}$$

whenever $t_h < t_{ip} < (t_r+t_h)$, and 0 otherwise.

If time when the reintruder attempts to return, t_i, has a pdf $f_T(t_i)$, then the expected time that the reintruder spends in the territory can be found as follows. The random variable of interest is not t_i but the time that the reintruder spends in the territory, given by $r - t_i$. Define a random variable X that takes the value $r - t_i$ when the reintruder successfully reinvades, and 0 otherwise (i.e., if the reintruder never attempts to return, or if it attempts to return while the resident is hiding —between r and h— but is unsuccessful because the predator is present), so $0 \le x \le r - t_i$. We are interested in the expected value of X conditional on the reintruder not having attempted a return by $h = t_p + t_h$. The expectation can be written as

$$\begin{aligned} &E[X|\text{No attempted invasion by } h] = \\ &E[X|(\text{No attempted invasion by } h)\cap(\text{Attempted invasion})] \\ &P\text{Attempted invasion}|\text{No attempted invasion by } h\ . \end{aligned} \tag{A-4}$$

Eq. A-4 comes from the relationship

$$E[X|A] = E[X|A \cap B]\, P[B|A] + E[X|A \cap B^c]\, P[B^c|A], \tag{A-5}$$

where X is a random variable and A and B are events or sets, $\cap$ denotes intersection of events, and ^{c} denotes the complement. To derive eq. A-4 from eq. A-5 note that X takes value 0 when no attempted invasion, or

$$E[X\,|(\text{No attempted invasion by } h) \cap (\text{No attempted invasion})] = 0.$$

To evaluate eq. A-4 we will need

$$P\{\text{No invasion by } h\} = (1-p) + p(1 - F_T(h)) = 1 - pF_T(h)$$

where $F_T(t)$ is the cumulative distribution function of time to reintrusion. Thus,

$$\begin{aligned} &P\{\text{Attempted invasion}|\text{No attempted invasion by } h\} = \\ &1 - P\{\text{No attempted invasion}|\text{No attempted invasion by } h\} = \\ &\text{(from Bayes theorem)} \qquad 1 - \frac{1-p}{1-pF_T(h)} = \frac{p(1-F_T(h))}{1-pF_T(h)}. \end{aligned} \tag{A-6}$$

We need to obtain the pdf $f_{(X\,|(\text{No attempted invasion by } h) \cap (\text{Attempted invasion}))}(x)$ to compute the expectation in (A-4). In what follows I only show the pdf for $0 < x \leq r - h$, because when $x = 0$ it does not contribute to the expectation; in this interval $f_X(x) = f_T(r - x)$ (e.g., Roussas, 1997 [Roussas, G. R. 1997. "A course in mathematical statistics", Academic Press], pp. 215 & ff.). Hence, for $0 < x \leq r - h$ or, equivalently, $0 < x \leq t_r$, and using the definition of conditional pdf (e.g., Roussas, 1997, pp. 93 & ff.),

$$f_{(X\,|(\text{No attempted invasion by } h) \cap (\text{Attempted invasion}))}(x) = \frac{pf_T(r-x)}{p(1-F_T(h))}\, P\{\text{No predator at } r - x\}; \tag{A-7}$$

where

$$P\{\text{No predator at } r - x\} = 1 - \mathrm{e}^{-\rho(r-x-h)} = 1 - \mathrm{e}^{-\rho(t_r - x)}, \tag{A-8}$$

since the process of the predator leaving starts at the time the resident hides (h). Finally, substituting (A-8) into (A-7), using (A.2) in (A-4), applying the definition of expectation to the random variable in (A-7), and simplifying and showing results in terms of t_h and t_r, we obtain

$$\begin{aligned} &E[X|\text{No attempted invasion by } t_{p+}t_h] = \\ &\frac{p}{1 - pF_T(t_p + t_h)} \int_0^{t_r} x f_T(t_p + t_h + t_r - x)\,(1 - \mathrm{e}^{-\rho(t_r - x)})\,\mathrm{d}x. \end{aligned} \tag{A-9}$$

In all the figures shown in this paper, I evaluated this integral using numerical integration.

Appendix B: Results for reintruders with fixed reintrusion time

This appendix shows the results for optimal time to hide and optimal time to reemerge when the reintruder has a fixed time of return. These results are similar to those that we can obtain for a stochastic intruder with variance of return time almost zero. To make these results comparable to those of stochastic reintruders, I have set the time of return at 400. The main difference between these results and those from a stochastic intruder are that, in this case, we can appreciate the effects of the predator precluding the reintruder's return.

B.1 Optimal time to reemerge

Fig. B-1 shows optimal time to reemerge, t_r^*, as a function of t_p for different combinations of β, ρ , I, and c when $t_i = 400$. To explain the results I will refer to two points in Fig. B-1, t_1 and t_2 that divide the range of t_p into three distinct regions, and are the t_p's that correspond to the minimum and maximum t_r^*. A $t_p > 400$ means that the predator is initiating its attack after the intruder is scheduled to come and thus t_r^* is the same as if there were no reintruder. If the reintruder comes shortly after the predator attacks ($t_1 < t_p < 400$) t_r^* is large: it is very unlikely that the reintruder will invade the territory (as that can only happen if the predator is no longer present), and thus the resident can reemerge late; for example, with decreasing ρ the predator is likely to stay longer, which results in larger t_r^* at t_p close to 400 —see Fig. B-1b vs. B-1a. For $t_2 < t_p < t_1$, t_r^* decreases linearly with t_p: the resident is reemerging at t_i ($t_r^* = t_{ip} = 400 - t_p$) so that the reintruder does not accumulate any time in the territory. For $t_p < t_2$, t_r^* is not affected by changes in t_p: to prevent further increases in territorial costs from the other conspecifics' intrusions the resident is reemerging before the reintruder is scheduled to come, and t_r^* is the same as if there were no reintruder.

Increasing β increases the number of conspecifics that can intrude per unit time, and decreases the sensitivity of t_r^* to changes in t_p, because the effect of the reintruder decreases relative to other conspecifics. The largest possible difference in t_r^* (between points t_1 and t_2) is smaller because t_2 is shifted to the right; in other words, as we increase β the t_p at which the resident's behaviour is no longer affected by the reintruder is larger. Decreasing I also decreases sensitivity to the reintruder (Fig. B-1a vs. B-1c) as does increasing c (Fig. B-1c vs. B-1d): if initial assets are small or loss of reproductive success fast, the reproductive success that a resident can afford to loose to intrusion decreases; this causes the maximum t_r^* to decrease: t_2 is shifted to the right and this is not compensated by the small decrease in t_r^* at t_1. However, changes in I and c do not make the reintruder less important relative to the other conspecifics: they simply magnify the effect of any territorial losses. Finally, increasing t_p (i.e., staging a predator attack a longer time after an intruder is chased away) will decrease t_r^* whenever $t_2 < t_p < t_1$; this is counterintuitive, because the effect of a past aggressive interaction becomes stronger (t_r^* smaller compared to a situation without reintruder) as the predator attacks a longer time after the intruder was chased away. The cause of this counterintuitive result is different from the counterintuitive result for a reintruder with log-normal return time shown in Fig.2 in main text. Finally, the "intuitive" result of a wearing-off of the effects of a past aggressive interaction as t_p increases is only observed for $400 < t_p < t_1$, but this region ($400 < t_p < t_1$) might be small.

B.2 Optimal time to hide

With a reintruder that returns at a fixed time (t_i), optimal time to hide, t_h^*, can only take two values: 0 and t_{ip} (the time at which reintruder attempts to return relative to predator's attack). When t_h is 0, the resident avoids mortality risks from predation during the initial attack. When $t_h = t_{ip}$ (i.e., delayed hiding) the resident prevents the reintruder from coming back (as the reintruder can only come back if $t_h < t_{ip} < (t_r + t_h)$). No other value of t_h can be optimal; any value of t_h between 0 and t_{ip} exposes the resident to predation without preventing the reintruder from returning, and values of $t_h > t_{ip}$ result in increases in mortality risk with respect to $t_h = t_{ip}$ with no further reduction in territorial intrusion risk. Delaying hiding will also allow the resident to reemerge later than if it had hid at 0 as the re-intruder is no longer a threat and reemergence is only dictated by the rate of intrusion of other intruders.

Fig. B-2a shows t_h^* as a function of time to predator attack (t_p) when $t_i = 400$ for three different β's. In every case, when $t_p < 390$ then $t_{ip} > 10$ and thus t_h^* is always 0: delaying hiding in these cases would require delaying hiding for more than 10 time units, which results in no survivorship. When $t_p > 400$

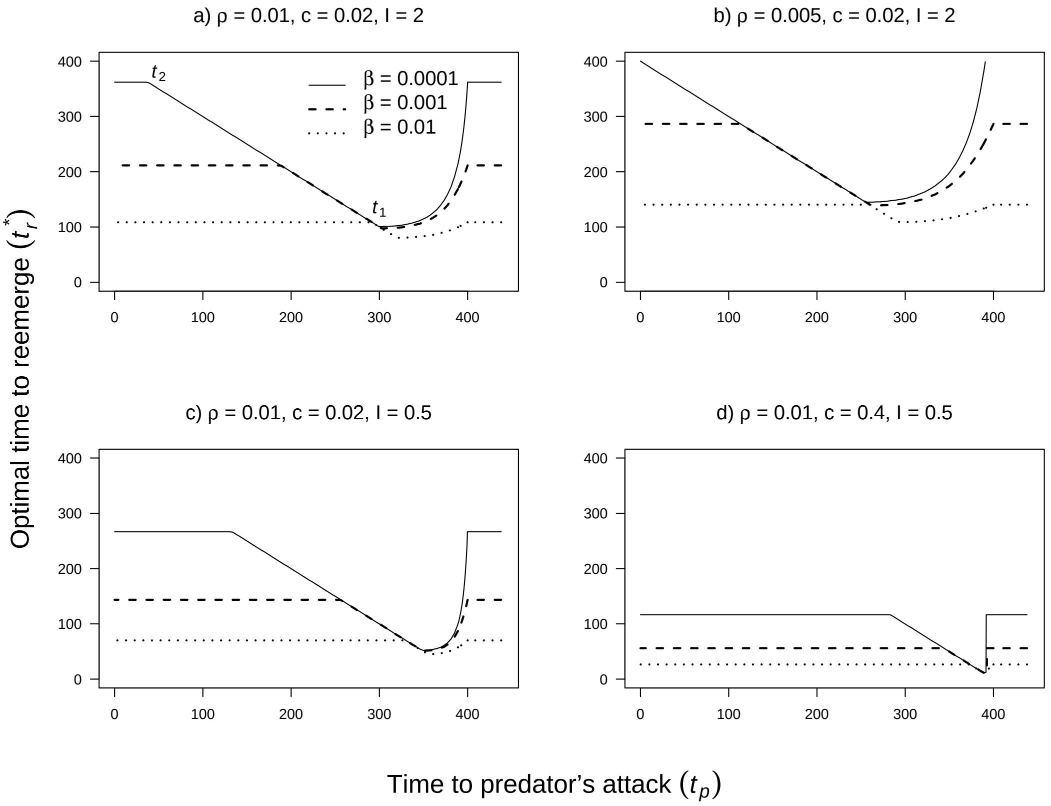

Figure B-1: Optimal time to reemerge (t_r^*) as a function of time to predator attack (t_p), when time to reintruder's return (t_i) is 400. Points t_1 and t_2 (panel c) divide the range of t_p into three regions: when $t_1 < t_p < 400$ t_r^* increases as t_p increases; for $t_2 < t_p < t_1$ $t_r^* = 400 - t_p$; for $t_p < t_2$ the behaviour of the resident is insensitive to the past aggressive interaction (t_r^* does not depend on t_p). Values of $t_p > 400$ correspond to the predator attacking after the reintruder is scheduled to come, and thus t_r^* is the same as in the absence of a reintruder (i.e., there are no effects of reintrusion).

the predator is attacking after the reintruder is scheduled to come, so the reintruder is no longer a threat and thus t_h^* is 0. For $390 < t_p < 400$ it might be optimal to delay hiding; in this region t_h^* can be either 0 (no delayed hiding) or t_{ip}; thus, the line in Fig. B-2a has a slope of -1 ($t_h^* = t_{ip} = 400 - t_p$). In general, it is more likely that delaying hiding will be optimal at small t_{ip}: here, delaying hiding does not represent a large increase in mortality, whereas for large t_{ip} the mortality risk of delaying hiding will be very large. However, delaying hiding, if at all, will only be observed in a small range of values of t_p (when the predator attacks shortly before the reintruder is scheduled to come). Fig. B-2a and b also shows the effects of β on $t_h^* = t_{ip}$. As the rate of intrusion of other conspecifics increases, the relevance of the reintruder decreases, and thus it becomes less worthy of increasing mortality risks. The optimal time to delay hiding depends also on the effect of intruders on reproductive success (c), the initial territorial assets (I), and the predator's behaviour (ρ) (Fig. B-2b).

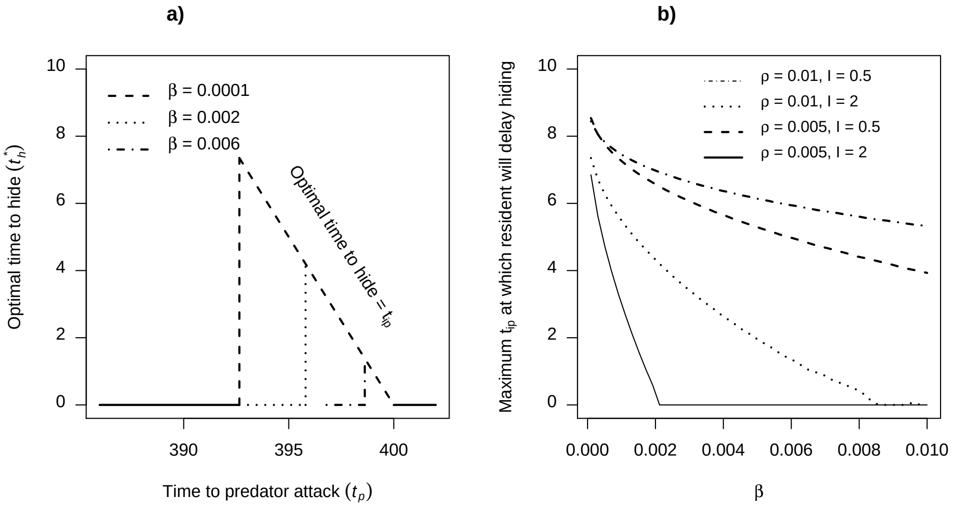

Figure B-2: Optimal time to hide, t_h^*. a) Effects of time to predator attack (t_p) on t_h^* when the reintruder is scheduled to come at $t_i = 400$. In the case represented, for instance, when $\beta = 0.002$, the resident will delay hiding if $396 < t_p < 400$ (see text for explanation), and the delay will be equal to $t_{ip} = 400 - t_i$; at any other values the resident will hide immediately ($t_h = 0$). b) Maximum t_{ip} (time or reintruder's return relative to the attack of the predator) at which a resident will delay hiding, as a function of rate of intrusion of other conspecifics (β) for different values of predator's leaving rate (ρ) and initial assets (I). The value shown in the figure is the largest t_{ip} for which fitness is larger when $t_h = t_{ip}$ compared to $t_h = 0$. For any intruder returning at a t_{ip} below the line, the resident's optimal behaviour will be to make make $t_h = t_{ip}$; for any t_{ip} above the line the optimal t_h will be zero.