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Territorial intrusion risk and antipredator behaviour: a mathematical model

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In territorial animals that hide to avoid predators, a predatory attack creates a conflict because a hiding animal cannot defend its territory from conspecific intruders. When intruders are persistent, a past conspecific intrusion informs a territorial resident that future intrusions by the same animal are likely. Using a mathematical model, I examine the effects that past territorial intrusions can have on antipredator behaviour. Past territorial intrusions rarely affect a resident animal's time to hide (the optimal behaviour is to hide as soon as the predator initiates its attack). In contrast, past intrusions should shorten the length of time during which territory holders remain in hiding, with the magnitude of this effect depending on the time of the predator's attack, the re-intruder's pattern of return, and the intrusion rates of other conspecifics. The results of the model show that we need more information on patterns of re-intruders' behaviour, and emphasize that a similar functional explanation could underlie other behavioural changes following territorial and/or aggressive encounters (such as winner/loser effects or changes in display frequency and territorial vigilance). Differences between my findings and those from previous studies suggest that the trade-off between antipredator behaviour and territorial defence can involve different costs from the trade-off between antipredator behaviour and foraging.

Keywords: antipredator behaviour; predation risk; territoriality; aggressive behaviour; trade-off; mathematical model

1. INTRODUCTION

The antipredator strategy of territorial animals should be affected by the need to defend a territory. Theoretical and empirical work on the trade-off between predator avoidance and foraging has shown that antipredator behaviour will change when there are alterations in the terms of the trade-off between mortality risk from predation and costs of hiding/escaping from predators (see Clark 1994; Ydenberg & Dill 1986; reviews in Lima & Dill 1990; Lima 1998). For instance, animals adopt behavioural strategies that lead to an increase in exposure to predation (e.g. delaying escape from a predator) when the costs of interrupting foraging increase (e.g. when foraging at a better patch).

In contrast to the wealth of studies on the trade-off between antipredator and foraging behaviour, there is little research on the trade-off between antipredator behaviour and territorial defence, even though the reproductive success of territorial animals can be strongly affected by successful territorial defence. The approach of a predator creates conflicting demands on a territorial animal: hiding minimizes mortality from predation but decreases the chances of detecting and chasing away conspecific intruders (i.e. increases the territorial costs of hiding). There is evidence that increases in predation risk tend to result in a decrease in the number or intensity of aggressive interactions (e.g. Baker *et al.* 1999; Brick 1999; Helfman 1989; Krupa & Sih 1998; Martel 1996; Whitehouse 1997; Wisenden & Sargent 1997), but the effects of aggressive interactions and territorial intrusions on antipredator behaviour have been rarely examined (but see Brick 1998; Cooper 1999; Díaz-Uriarte 1999; Jakobsson *et al.* 1995). The trade-off between territorial defence and predator avoidance can be particularly interesting if there are short-term changes in the territorial costs of hiding that are caused by local changes in the social environment. In fact, in some territorial species intruders enlarge or obtain territories by intruding persistently into the territories of settled animals (see reviews in Stamps & Krishnan 1995, 1998). Thus, there is an increased probability of re-intrusion following a conspecific intrusion because some of the intruders that have been chased away might return. If some of the intruders tend to return, the territorial costs of hiding could be very high following a conspecific intrusion; thus, antipredator behaviour should change to decrease the chances of territorial intrusions at the cost of increased predation risks.

There is recent empirical evidence (Díaz-Uriarte 1999; Díaz-Uriarte & Marler, 2001) that territorial males of the lizard *Tropidurus hispidus* increase their exposure to predation when a predator approaches shortly after the territorial male has chased away a conspecific intruder male, consistent with the arguments above. In these experiments, male lizards fought with a conspecific intruder male, and 5 min later were subject to a simulated predatory attack by a human. Antipredator behaviour was characterized using two types of variables: (i) the time when the lizard initiated escape from the predator; and (ii) the time when the lizard re-emerged from the refuge after hiding. In both studies male lizards re-emerged sooner from the refuge after a territorial intrusion; however, initiation of hiding was affected by a past territorial intrusion only in the second study (see § 4(a)).

The conditions that give rise to a trade-off between antipredator behaviour and territorial defence in males of the lizard *Tropidurus hispidus* are likely to be common to many other species that are both territorial and prey of other animals. Thus, effects of past territorial intrusions

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Table 1. *Main variables and parameters of the model*

symbol	meaning	range
t_h	time to hide (relative to initiation of predator attack)	optimized variable
t_r	time to re-emerge (relative to initiation of hiding)	optimized variable
t_p	time to predator attack (relative to time when intruder is chased away)	0–7000
p	probability of re-intruder's return	0.4–0.99
t_i	time of re-intruder's return (relative to time when intruder is chased away)	400 or random
μ	for re-intruder with log-normal return PDF: mean of log(return time)	log(400)
σ	for re-intruder with log-normal return PDF: standard deviation of log(return time)	0.001–1
λ	for re-intruder with exponential return PDF: mean of the exponential distribution	2–800
β	rate of intrusion of other conspecifics	0.00009–0.012
ρ	rate of predator leaving the area after resident hides; mean time to leave $= 1/\rho$	0.005–0.05
I	initial territorial assets	0.1–4
c	rate of decrease of reproductive success with time intruders spend in territory	0.02–0.9
	variables derived from the above	
t_{ip}	time of re-intruder's return relative to time of predator's attack ($t_{ip} = t_i - t_p$)	
h	time of hiding ($h = t_p + t_h$)	
r	time of re-emergence ($r = t_p + t_h + t_r$)	

on antipredator behaviour are likely to be widespread, but factors that vary both within and among species, such as population density and behaviour of intruders, could affect this trade-off. The purpose of this paper is to investigate how past conspecific territorial intrusions should affect antipredator behaviour in territorial animals that need to defend their territories against conspecifics and are also potential prey that use refuges to avoid predation. The model focuses on the effects of the re-intruder's behaviour, the probability of intrusion of other conspecifics, and the timing of predator attack relative to the end of the conspecific territorial intrusion.

2. THE MODEL

(a) *The basic problem*

Suppose that a territorial male is defending an area that overlaps the home ranges of several females. If other males invade the territory while the resident is hiding then they could mate with the females in the territory, and the number of females that can be fertilized by the invading males increases with the time these invading males spend in the territory before being evicted (this model also applies to a more general scenario; see § 2(c)). The territorial male chases away a conspecific intruder at time zero. Some time later (t_p), a predator initiates an attack (the predator is detected as soon as it initiates attack). The resident needs to decide (i) when to escape (time to hide, t_h), and (2) when to re-emerge (time to re-emerge, t_r). The longer the resident waits to hide or the shorter the time to re-emerge, the more likely it becomes that it will be killed by the predator. However, the longer the animal remains in hiding the more likely it becomes that intruders can invade the territory. After an intruder enters the territory, it stays there until the resident re-emerges, and the reproductive success of the resident decreases with time that intruders spend in its territory. There are two types of intruders: the re-intruder that was chased away at time zero, and other conspecifics from the overall population (see § 2(c)(ii) for justification). The effects of the prior territorial intrusion (by the intruder chased away at time zero) are only related to the probability that the re-intruder returns, but do not affect the rate of intrusion of other conspecifics. Conspecific intruders cannot successfully invade the territory if the predator is in the area or if the territorial resident is not hiding (i.e. there are never any intruders in the territory if the resident is not hiding), but they can attempt to re-invade during these periods.

I assume that the resident maximizes fitness, the product of its probability of surviving the attack of the predator times its expected reproductive success, by choosing optimal values of time to hide (t_h) and time to re-emerge (t_r). In the next sections, I give details about each component of the model (see also table 1 for a summary of variables). In the model, I make many simplifying assumptions, with function selection dictated by the desire to have simple functions that are, nonetheless, biologically plausible.

(b) *Surviving the predator's attack*

I assume that the predator is attacking. Furthermore, the probability of surviving the initial attack of the predator decreases linearly with time to hide, t_h, so that at $t_h \geqslant 10$ the probability of surviving is zero. Thus, I assume that the probability of surviving the initial attack is

$$1 - \frac{t_h}{10}, \tag{1}$$

for all $0 \leqslant t_h \leqslant 10$, and zero otherwise. (Differences in predators' speed can be accommodated by changing the value of the denominator or the shape of the function.) Once the resident hides in the refuge, the predator stays around the area but has a constant rate of leaving ρ; thus, the predator's time of leaving is an exponential distribution with mean $1/\rho$. I assume that the resident is killed if it re-emerges from the refuge while the predator is in the area. Thus, the probability that the resident survives re-emergence is the probability that the predator has left the area by the time to re-emerge, t_r, or

$$1 - e^{-\rho t_r}. \tag{2}$$

The probability of surviving the attack is therefore the product of expressions (1) and (2). There is no mortality while the resident is hiding.

(c) *Time that intruders spend in the territory*

(i) *Effects of intruders on reproductive success*

I assume that the decrease in reproductive success of the resident is a linear function of the time that intruders spend in its territory. Final reproductive success is

$$I - c \times \text{total time intruders spend in territory}, \qquad (3)$$

where I represents the initial territorial assets (i.e. the reproductive success yielded by a territory before any intruder spends any time there at all, or before any intruder causes any decrease) and c is a scaling factor for the rate of decrease of reproductive success with time that intruders spend in the territory (c is equivalent to the decrease in reproductive success per unit of time spent by intruders in the territory); the larger the value of c, the greater the decrease in reproductive success per unit time that intruders spend in the territory while the resident is hiding.

I assume that the only variable that affects reproductive success is the total accumulated time that intruders spend in the territory while the resident is hiding (e.g. one intruder spending 20 time-units in the territory results in the same decrease in reproductive success as four intruders each spending 5 time-units). The model assumes that the resident detects and chases away all intruding males (i.e. both other conspecifics and the re-intruder all disappear immediately when the resident re-emerges from the refuge). However, the qualitative results do not require small territories with high visibility. If a non-hiding resident cannot detect all intruders, its final reproductive success will also decrease while it is out of the refuge, due to the undetected intruders. But we can still evaluate the effects of a territorial intrusion while hiding; the difference would be that the relative effect of hiding while an intruder is in the territory would be comparatively smaller in relation to an identical situation where the resident detects and chases all intruders.

Both other conspecifics and re-intruder can only successfully invade if the predator has left the area. Why would intruders invade rather than hide while the resident is hiding? The resident is forced to hide when the predator attacks, but neither the other conspecifics nor the (potential) re-intruder were in the area when the predator initiated attack (i.e. they were not forced to hide) and thus both other conspecifics and the re-intruder can observe that the predator is no longer in the area, because they are invading from outside the territory.

The model applies not only to males defending areas that overlap females' territories, but to situations where an animal that avoids predators by hiding can defend a resource (mates, food, nesting sites, etc.) that can be depleted by conspecifics. Thus, I have made no attempt to model the females' behaviour. For the case of a male defending an area that overlaps the home ranges of several females, the model does not require that all females be out of the refuge when the territorial male is hiding; the model only assumes that there is some probability that one or more females do not hide. The larger the proportion of females that are not hiding, the larger the potential costs of an intrusion, and this is accounted for by the constant c in expression (3). It is biologically plausible that some females might not be hiding if the female is sufficiently far away from the predator, or if the female has not detected the predator.

(ii) *Time spent by other conspecifics*

I model the entry of the other conspecifics (as opposed to the re-intruder) as a Poisson process, where β is the rate of entry of intruders. I assume that β does not change over time or with the number of intruders already in the territory, except that no conspecific can intrude into the territory if the predator is still present. It is shown in electronic Appendix A (available on The Royal Society's Web site) that the expected total time that the other conspecifics accumulate in the territory before the territory holder re-emerges at time t_r is given by

$$\int_0^{t_\mathrm{r}} \beta \frac{(t_\mathrm{r} - s)^2}{2} \rho\, \mathrm{e}^{-\rho s}\, \mathrm{d}s = \frac{\beta}{\rho^2} - \frac{\beta}{\rho^2 \mathrm{e}^{\rho t_\mathrm{r}}} - \frac{\beta t_\mathrm{r}}{\rho} + \frac{\beta t_\mathrm{r}^2}{2}. \qquad (4)$$

Instead of modelling the entry of other conspecifics, we could have used a cost to hiding without specifying how this cost arises (e.g. this unspecified cost could include foraging or thermoregulatory costs of hiding). However, because we are modelling trade-offs between defending a territory and avoiding predation, I examine only territorial costs of antipredator behaviour to avoid confounding them with other potential costs. Given that most natural situations will include other conspecifics in addition to the re-intruder, all territorial costs of hiding in this model will arise from intruders (either re-intruder or other conspecifics). This also allows us to incorporate in a consistent way the costs that arise from hiding (see equation (3)) using a simple mechanistic model.

(iii) *Time spent by the re-intruder*

In contrast to the other conspecifics, the re-intruder is the individual that was chased away at time zero. The re-intruder can either attempt to re-invade the territory or not; if it attempts a re-invasion (i.e. conditional on it attempting a re-invasion), the re-intruder's attempted return time has a certain probability density function (PDF), such as those represented in figure 1. However, the re-intruder can only re-invade successfully if the resident is hiding and the predator has left the area. I show in electronic Appendix A that if the time of return t_i is distributed according to the PDF $f_T(t_\mathrm{i})$, the expected time that the re-intruder spends in the territory (x), conditional on the re-intruder not having attempted an invasion by time $h = t_\mathrm{p} + t_\mathrm{h}$, is given by

$$E[X|\text{No attempted invasion by } \mathrm{t_p} + \mathrm{t_h}] = \frac{p}{1 - pF_T(t_\mathrm{p} + t_\mathrm{h})} \int_0^{t_\mathrm{r}} x f_T(t_\mathrm{p} + t_\mathrm{h} + t_\mathrm{r} - x)\,(1 - \mathrm{e}^{-\rho(t_\mathrm{r} - x)})\,\mathrm{d}x, \qquad (5)$$

where $F_T(t_\mathrm{i})$ is the cumulative distribution function of $f_T(t_\mathrm{i})$. I evaluated this integral numerically.

Note that the lack of attempted re-invasion by the re-intruder before the resident hides can provide the resident with information on the probability of a re-invasion in the future. Suppose that the re-intruder, conditional on it

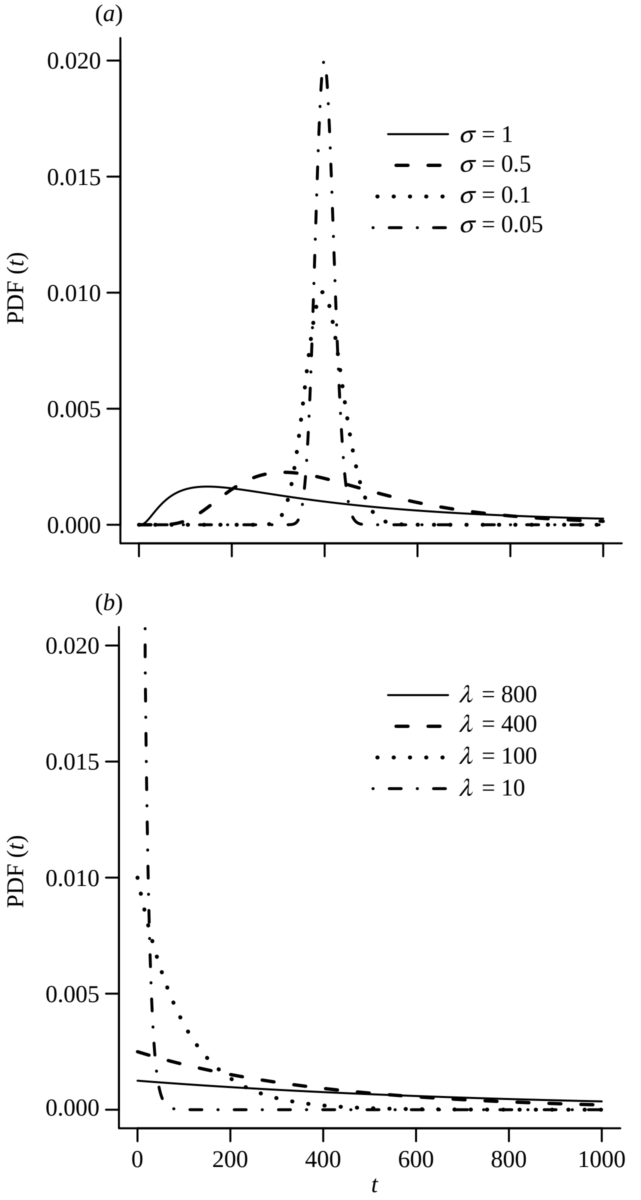

Figure 1. Examples of the probability density functions (PDFs) used for the re-intruder's return time, conditional on the intruder attempting a re-invasion. (*a*) For the log-normal distribution, σ is the standard deviation of log(return time); (*b*) for the exponential distribution, λ is the mean of the return time.

attempting a re-invasion, has a high probability of having returned by a certain time (such as time-unit 100 for an exponential distribution with $\lambda = 10$ in figure 1); if there has been no attempted re-invasion by that time it is very unlikely that the re-intruder will ever attempt a re-invasion because it should have already returned if it were to attempt a re-invasion. This is formally included in the model using Bayes' theorem (see equation (A6) in electronic Appendix A). In general, the smaller the variance of the re-intruder's attempted return time, the more information is gained by a lack of attempted re-invasion.

(d) *Parameter values and robustness of results*

The ranges of values for the different parameters are shown in table 1. Changes in the values of the parameters do not alter the qualitative patterns (see also § 4); for instance, the different panels within figures 2–4 are scaled versions of each other. The only exception to this are very small values for the variance of the re-intruder's return time (see below). All results shown in the figures correspond to a probability of re-intrusion (p) of 0.9; changes in this parameter alter the effects of the re-intruder, but in most cases the effects of a past re-intrusion are observable with $p = 0.4$.

To examine the effects of variation in the intruder's behaviour, I have modelled return times (conditional on attempted return) using two different distributions, an exponential and a log-normal, and have generated additional variability in the re-intruder's behaviour by modifying the parameters of these PDFs (figure 1). I have chosen these two distributions because they represent two different, biologically plausible, behaviours that cover a wide range of re-intrusion patterns. Both distributions have a single maximum, a biologically reasonable assumption. The two distributions differ in the location of that maximum: the exponential distribution has a maximum at zero (thus, if the intruder attempts a re-intrusion, the probability that the intruder returns during an interval of fixed length is largest immediately after it has been evicted by the resident), whereas the log-normal distribution has a maximum at some positive (non-zero) time. Other distributions meet these criteria, but the above two are mathematically tractable; nevertheless, the qualitative results of the model do not depend on the details of the distribution but on where the maximum of the PDF is located and on the variance of the PDF. With the log-normal PDF, the first parameter (the mean of the log(return time)) has been set equal to log(400), and I have varied the second parameter, the standard deviation of log (return time) (note that the mean of t_i is not exactly 400). Choosing a different value for the mean makes no qualitative difference, because the relevant variable is not the mean but t_{ip}, the time at which the re-intruder returns with respect to the predator attack. For the exponential, I have changed its mean, which also changes its variance (because for an exponential distribution the variance is the square of the mean). Several examples of the PDF of return times, conditional on the intruder attempting a re-invasion, are shown in figure 1.

3. RESULTS

The focus of this work is the effect of a past intrusion, which can be evaluated by comparing the optimal values of time to hide (t_h) and time to re-emerge (t_r) with the optimal values for an identical situation without the re-intruder (i.e. when only other conspecifics can invade). Thus, I first examine the effects of having only other conspecifics on optimal time to hide and time to re-emerge. Next, I show the results when a re-intruder is added. Because the most relevant results are those from a re-intruder with stochastic behaviour, I concentrate on those; the results for a re-intruder with fixed return time are shown in electronic Appendix B (available on The Royal Society's Web site).

(a) *Effects of other conspecifics*

When there are no re-intruders, but only other conspecifics, nothing is gained by delaying hiding from an

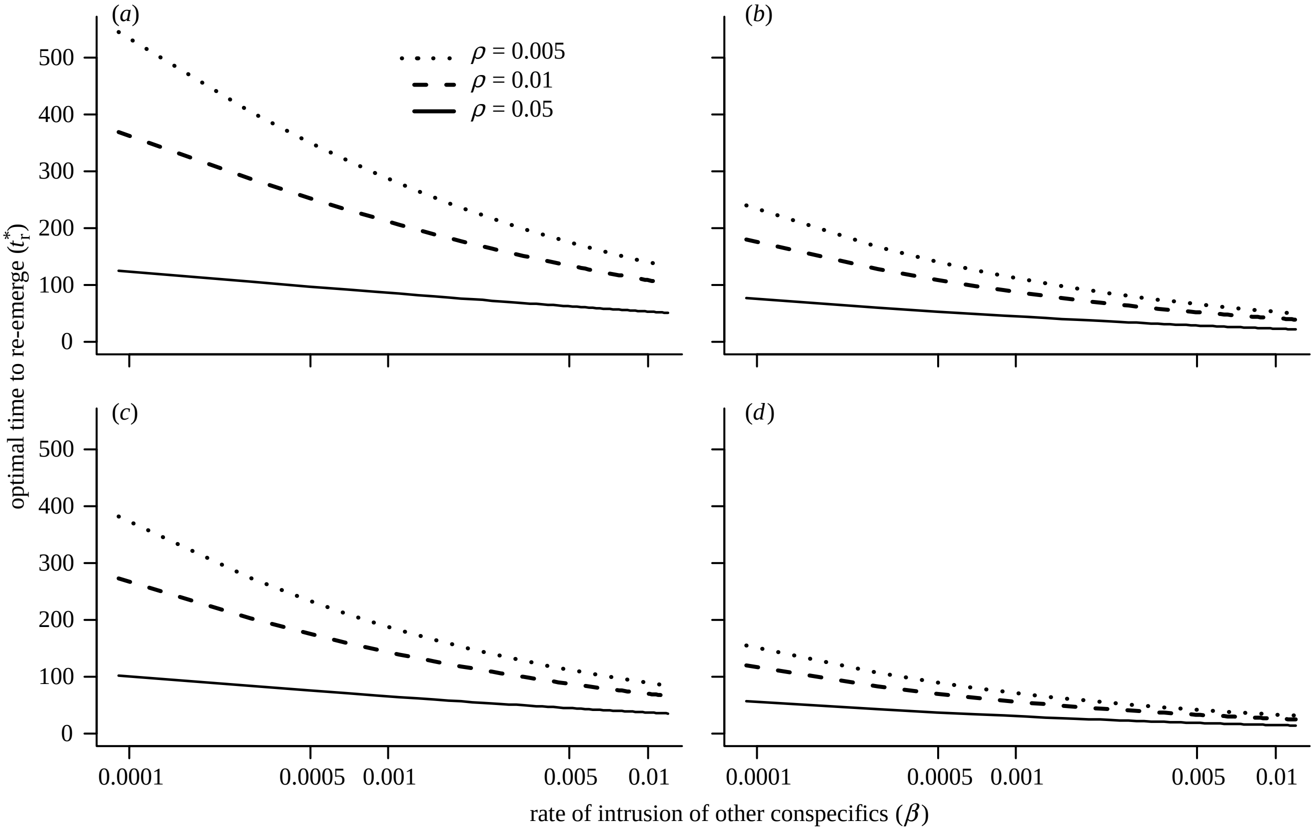

Figure 2. Optimal time to re-emerge (t_r^*) when there is no re-intruder, as a function of rate of intrusion of other conspecifics (β), for different values of predator's leaving rate (ρ), initial assets (I), and effects of intruder's time on reproductive success (c). The x-axis is in logarithmic scale to facilitate comparisons. (a) $I = 2$, $c = 0.02$, (b) $I = 2$, $c = 0.4$, (c) $I = 0.5$, $c = 0.02$ and (d) $I = 0.5$, $c = 0.4$.

attacking predator. Because the rate of intrusion of other conspecifics is constant over time, the loss in reproductive success due to territorial intrusions is only affected by the time spent in hiding (i.e. t_r; see expression (4)), and not by when the animal hides. Delaying hiding ($t_h > 0$) only results in increased mortality risk. Therefore, an animal can increase survival by hiding at time zero (i.e. $t_h = 0$) while keeping the territorial costs of hiding fixed, and thus the optimal time to hide is zero. (Note that, in contrast to the re-intruder case (see § 2(c)(iii)), for the other conspecifics no information can be gained by delaying hiding.)

In contrast to time to hide, other conspecifics do influence time to re-emerge (see figure 2). Increases in the rate of intrusion of other conspecifics (β) and the rate of the predator leaving the area (ρ) decrease the optimal time to re-emerge (t_r^*): if the rate of intrusion is higher, the resident ought to re-emerge sooner at the expense of risk of predation; if the predator is likely to leave the area sooner, the resident can re-emerge sooner without incurring increased predation risks. If intruders have a large depressive effect on reproductive success (large c) or if initial assets (I) are small, the resident will re-emerge sooner.

(b) *Effects of the re-intruder*

We now add a re-intruder and examine how optimal time to hide and optimal time to re-emerge change relative to the optimal time to hide and time to re-emerge when there are only other conspecifics (§ 3(a)).

(c) *Optimal time to hide*

When the re-intruder has a stochastic re-intrusion time, delaying hiding is never optimal, except for extremely small (and biologically unrealistic) variances in re-intruder return time and low rates of intrusion of other conspecifics; even then, the effects only occur over a very small range of times to predator attack. To make delaying hiding optimal, the decrease in territorial costs and the gain of information about the re-intruder's likely return have to be large enough to compensate for the fast increase in the risk of mortality from delaying hiding. This can only be achieved if, (i) there is almost certainty about the re-intruder's return (variance close to zero: in such cases, delaying hiding can provide a lot of information about the future probability of the re-intruder's return; see § 2(c)(iii)), and (ii) the loss of reproductive success from the re-intruder has a major effect on fitness (when the rate of intrusion of other conspecifics is very low and initial territorial assets are small).

(d) *Optimal time to re-emerge*

Optimal time to re-emerge, t_r^*, as a function of time of predator attack (t_p) is shown in figures 3 and 4 for an intruder with exponential and log-normal return times, respectively. The plot for the exponential case is like the plot for the log-normal case starting at $t_p \simeq 400$ (i.e. to the right of the maximum value of the PDF of the log normal). The major difference between the exponential and the log-normal cases is that in the log-normal case there is an initial decrease in optimal time to re-emerge,

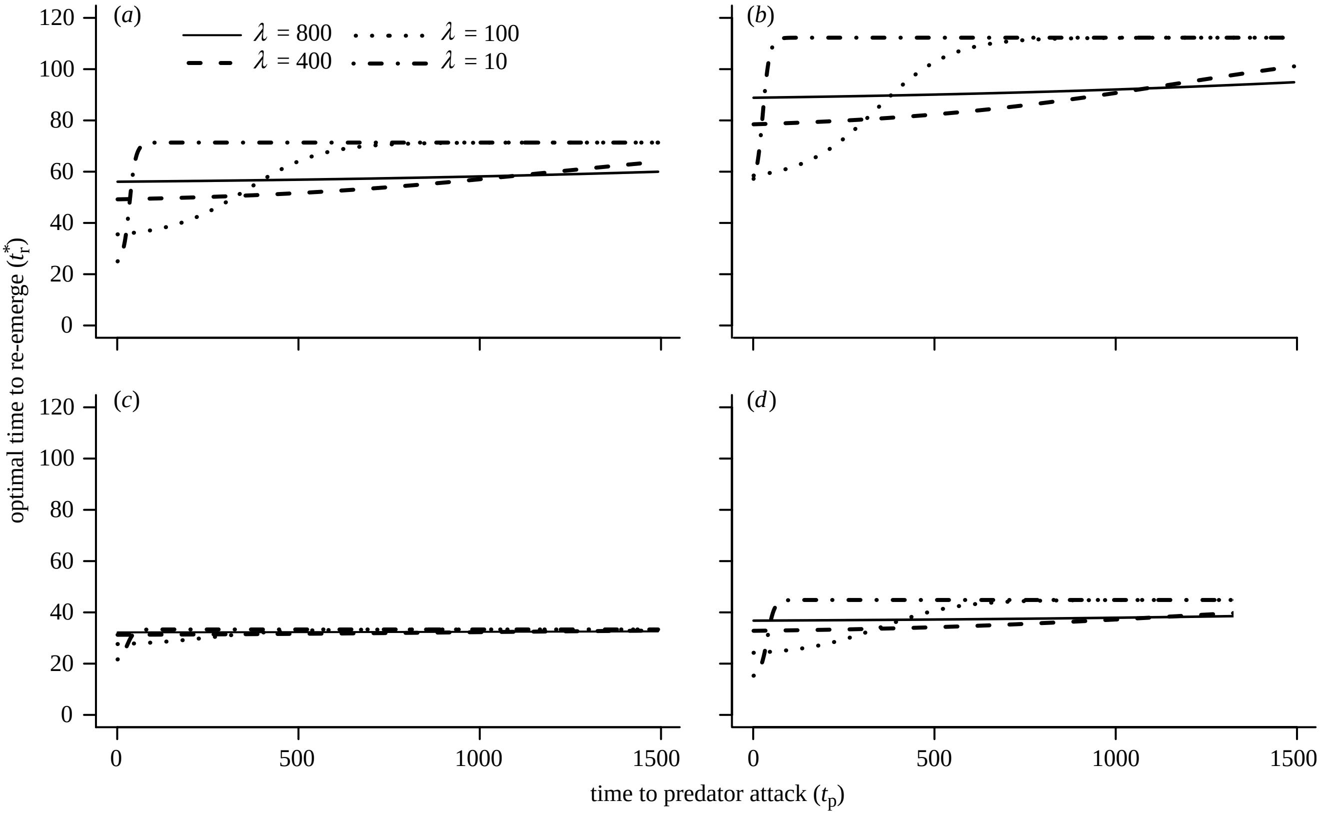

Figure 3. Optimal time to re-emerge (t_r^*) as a function of time to predator attack (t_p), when time to intruder's return (conditional on re-intruder attempting return) is exponentially distributed (with mean λ). For explanation of other parameters see table 1. (*a*) $\beta = 0.001$, $\rho = 0.005$, $I = 0.5$, $c = 0.4$, (*b*) $\beta = 0.001$, $\rho = 0.005$, $I = 2$, $c = 0.4$, (*c*) $\beta = 0.01$, $\rho = 0.005$, $I = 0.5$, $c = 0.4$ and (*d*) $\beta = 0.001$, $\rho = 0.05$, $I = 2$, $c = 0.4$.

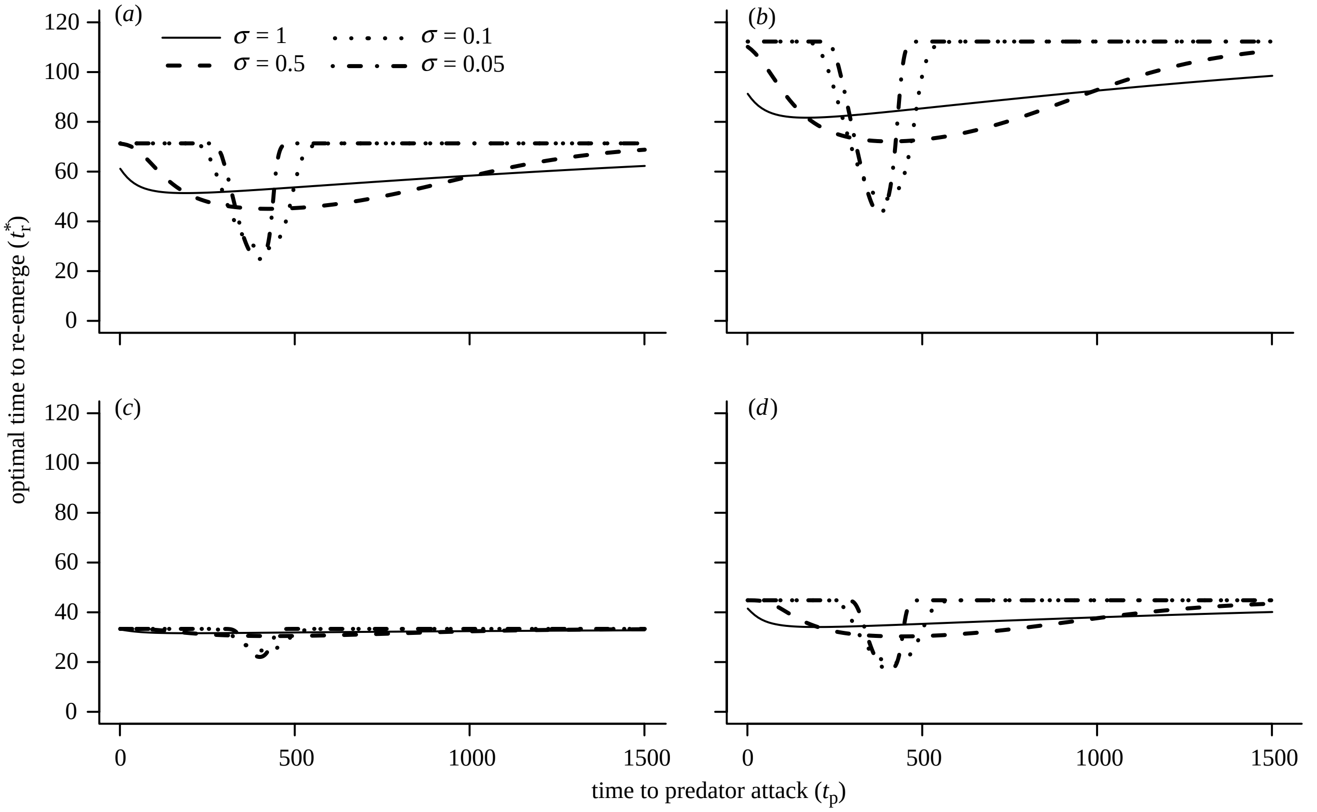

Figure 4. Optimal time to re-emerge (t_r^*) as a function of time to predator attack (t_p), when time to intruder's return (conditional on re-intruder attempting return) is log-normally distributed (with mean of log(return time) = 400). For explanation of other parameters see table 1. (*a*) $\beta = 0.001$, $\rho = 0.005$, $I = 0.5$, $c = 0.4$, (*b*) $\beta = 0.001$, $\rho = 0.005$, $I = 2$, $c = 0.4$, (*c*) $\beta = 0.01$, $\rho = 0.005$, $I = 0.5$, $c = 0.4$ and (*d*) $\beta = 0.001$, $\rho = 0.05$, $I = 2$, $c = 0.4$.

t_r^*, as the time between the end of the territorial intrusion and the predator's attack, t_p, increases. In other words, with a log-normal distribution of return times we can obtain a counter-intuitive intensification of the effects of a past territorial intrusion with time: t_r^* decreases with increasing t_p for values of t_p smaller than for the maximum of the PDF (about 400). In contrast, if intruders' return time follows an exponential distribution (or, more generally, a PDF with maximum value at zero and monotonically decreasing thereafter), we cannot observe a counter-intuitive intensification of the effects of a past territorial intrusion with increasing time to predator attack. This pattern is caused by changes in the probability of re-intrusion in the near future. In the log-normal case, the maximum of the PDF is located at some $t > 0$. If the time at which the predator initiates its attack, t_p, happens a long time after the maximum of the PDF, then the risk of a re-intrusion in the near future is small; this is also what happens for the exponential distribution when $t_p \gg 0$. But, for the log-normal distribution (and, in general, PDFs with a maximum at some value larger than zero), the risk of a re-intrusion in the near future can also be small at times that are smaller than for the maximum of the PDF. For example, in figure 4, with $\sigma = 0.05$, if the predator initiates its attack at time-unit 100, the risk of a re-intrusion in the near future is very small (most of that risk is concentrated around the 350–450 time-units; see figure 1). In other words, if the predator attacks a long time before the maximum of that PDF, the resident need not worry about a particularly high risk of re-intrusion for some time. Thus, in general, with PDFs whose maximum is not at zero, it might be possible that the risk of re-intrusion in the near future be very small both if the predator attacks a long time before that maximum (i.e. $t_p \ll$ time at which PDF is maximum) and if the predator attacks a long time after that maximum (i.e. $t_p \gg$ time at which PDF is maximum). The latter is also a feature of PDFs with a maximum at zero (such as the exponential), but the former is unique to PDFs that have a maximum at some value larger than zero. Therefore, it is necessary to understand, at least qualitatively, the pattern of re-intruder's return in order to make predictions about changes in re-emergence time with variation in time to predator attack.

Increasing the rate of intrusion of other conspecifics, β, decreases the effects of the re-intruder: the relative importance of the re-intrusion becomes smaller as the number of other intruders increases. Decreasing the probability of re-intrusion also decreases the effects of the re-intruder. Likewise, increasing the speed at which reproductive success decreases with intruders' time in the territory (i.e. increasing c) or decreasing initial assets (i.e. decreasing I) decreases the effect of the re-intruder.

The variance of the return time of the re-intruder has a strong effect on optimal time to re-emerge, t_r^*. With small variances, the risk of a re-intrusion is very high around a small set of times; outside those times, the risk of a re-intrusion in the near future is small. Thus, t_r^* can show an acute decrease if the predator initiates attack when the risk of a re-intrusion in the near future is high, whereas, outside this set of times when the risk of re-intrusion is very high, the effects of a past territorial intrusion are almost negligible. In contrast, with high variance, the probability of the re-intruder coming in any particular interval is smaller, but this probability is spread over a larger time-period. Thus, with high variances the effects of a past territorial intrusion are less intense, but can be observed over a larger range of times.

4. DISCUSSION

This paper shows that the risk of territorial intrusion of conspecifics can have large effects on some components of the antipredator strategy: increased intrusion risk results in a decrease in time until re-emergence from a refuge. When there is no threat from a re-intruder but only risk of intrusion from other conspecifics, the optimal strategy is to hide as soon as the predator attacks (i.e. not to delay hiding) and to modify time to re-emerge as a function of the threat of invasion (larger numbers of intruders result in shorter re-emergence time) and initial resources [the higher the value of initial resources, the later an animal can afford to re-emerge, as predicted from the asset-protection principle (Clark 1994; see an example in Martín & López 1999); high initial resources imply that even if an animal delays hiding, it will still have high reproductive value (the asset), and increasing exposure to predation puts the entire asset at risk; in contrast, with low initial resources the greater the predation risks that must be accepted to prevent any further decreases in the asset]. The main focus of this paper is the effects of a past territorial intrusion when intruders are persistent. In the presence of a re-intruder, as was the case in the absence of a re-intruder, the optimal strategy almost always involves hiding as soon as the predator attacks. However, re-emergence time can be strongly affected by the possibility of a conspecific re-intrusion. The extent of these effects will be modified by the time of the predator's attack (relative to the initial territorial intrusion of the potential re-intruder) and the behaviour of the re-intruder (figures 3 and 4). Timing of attack of the predator and behaviour of the re-intruder play a key role because the increase in territorial costs of intrusion is a consequence of a transient increase in the probability of re-intrusion. As this probability increases, earlier re-emergence is favoured at the expense of increased mortality risk.

(a) *Why not to delay hiding*

Flight initiation behaviour (measured either as time to hide or approach/flight distance) has been shown empirically to respond to variation in predation risk (e.g. Bauwens & Thoen 1981; Bulova 1994; Cooper 1997; see reviews in Lima & Dill 1990; Lima 1998), but few studies have examined the effects of non-predatory factors such as increased cost of flight (Lima 1998). Most evidence of delayed hiding with higher costs of hiding is limited to a few cases related to foraging costs of flight (see Lima 1998, p. 237; Ydenberg & Dill 1986, pp. 237–239). Recent empirical work has documented delayed hiding in mate guarding males (Cooper 1997, 1999) and animals involved in *ongoing* territorial intrusions (Brick 1998; Cooper 1999; Díaz-Uriarte 1999, experiment 2; Jakobsson *et al.* 1995). In addition, the model of Ydenberg & Dill (1986) predicts that time to initiate flight should increase with increasing cost of flight.

However, delaying hiding is rarely optimal in this model, which agrees with the empirical results of Díaz-Uriarte (1999) where male *Tropidurus hispidus* do not increase time to initiate escape if a predator attacks 5 min after an intruder is evicted from their territory; the predictions of this model, however, do not agree with the results of Díaz-Uriarte & Marler (2001) where there is also an increase in the delay to hide. This model's result that delayed hiding is rarely optimal does not depend on specific parameters or functions but only requires (i) that survivorship be a monotonically decreasing function of time to hide, and (ii) that the attack of the predator be a fast enough process so that the small decrease in intrusion costs and/or the added information about the re-intruder's likely behaviour cannot compensate for the fast increase in mortality risk that results from delaying hiding. Both conditions are likely to hold in most biological systems.

What, then, explains the differences between the predictions of my model and those from the model of Ydenberg & Dill (1986) and the empirical findings of Brick (1998), Cooper (1999), Díaz-Uriarte (1999; experiment 2), Díaz-Uriarte & Marler (2001) and Jakobsson *et al.* (1995)? On the one hand, in Ydenberg & Dill's (1986) model there is always a cost to fleeing from predators (for example, losing a very profitable prey item); in my model, the cost does not arise from fleeing itself but from hiding (which also explains why, in my model, when there is no re-intruder delaying hiding can never be optimal). On the other hand, all the empirical evidence (except for Díaz-Uriarte & Marler (2001)), deals with animals actively engaged in a fight. In those situations the animals are facing an actual intrusion, and not just the risk of a probable intrusion sometime in the future; when the animal is engaged in an ongoing fight, fleeing itself (and not just hiding time) has a cost, as in the model of Ydenberg & Dill (1986), and this cost could be much higher if the approaching predator is not an attacking one (Díaz-Uriarte 1999; see also Lima & Dill 1990).

Nevertheless, even for animals that are not actively engaged in foraging or fights, hiding soon could entail costs arising from interrupting sampling (such as learning and information acquisition about foraging resources; e.g. Dall *et al.* 1999) that have not been considered in this model (and these costs could be higher if the predator is not attacking). In addition, in this model (and implicitly in the model of Ydenberg & Dill (1986)) the predator is always attacking, but when there is uncertainty about the predator's intentions (attacking versus non-attacking), delaying hiding could provide valuable information about the probability that the approaching predator is an attacking one (and modify, for example, re-emergence time). These two types of effects (interrupting learning and information acquisition about both the foraging environment and the predator's likely threat) are currently under investigation. But the main conclusion from my model regarding flight behaviour is that the risk of a potential intrusion, *per se*, will very rarely justify delaying hiding from an attacking predator. Interestingly, in the experiments in Díaz-Uriarte & Marler (2001), the predator's approach speed was about half of the predator's approach speed in Díaz-Uriarte (1999); the predator's slower approach speed makes it more likely that those additional costs of hiding (interrupting information acquisition about foraging and predator's threat) could be detected. In summary, the differences from the model of Ydenberg & Dill (1986) suggest that trade-offs between predation and foraging could be very different from those between predation and territorial defence. Whereas in the former it is interrupting foraging that is most costly, in the latter, costs arising from hiding and interruption of information acquisition could be the most relevant.

(b) *Using multiple responses to characterize antipredator behaviour, and applying and testing the model*

The above results have been obtained because we have characterized antipredator behaviour using two variables, time to hide and time to re-emerge, instead of a single one (such as proportion of time hiding). As emphasized by Lima & Dill (1990), in the study of conflicting demands of antipredator behaviour it is necessary to identify the key behavioural decisions involved in predator avoidance; this context specificity is a necessary step to guide further empirical work and generate testable predictions.

The results of this paper also show that applying and extending this model requires a better understanding of re-intrusion patterns in nature. The re-invasion behaviour of the re-intruder strongly affects how detectable the changes in antipredator behaviour will be; the re-intrusion pattern also modifies the effect of time to predator attack on time to re-emerge. Unfortunately, there is no information about re-intrusion patterns in nature. A PDF of return times with a maximum not at zero (e.g. the log-normal distribution used here) creates two potential problems for empirical work. First, there will be a window of times to predator attack during which increasing the time between the end of the eviction of the intruder and the predator attack results in a counter-intuitive increase in the effects of the past territorial intrusion (figure 4). Second, and more importantly, the largest effects will be detected around the (generally unknown) maximum of the PDF, but might be negligible shortly after the intruder is evicted (figure 4). This is not a problem if the re-intruders return follows an exponential distribution (or, more generally, a PDF with maximum value at zero and monotonically decreasing thereafter); in this case, the best way to detect an effect of past territorial intrusions is to expose the resident to a simulated predator attack shortly after the resident has evicted a re-intruder (figure 3).

An increase in predation exposure following a territorial intrusion emphasizes that a similar functional explanation, adaptive response by a territorial resident to a transient increase in the probability of intrusion, could underlie different behavioural phenomena: past territorial intrusions are known to increase the time invested in territorial vigilance (e.g. great tits: Ydenberg & Krebs 1987; Kacelnick *et al.* 1981) and the frequency of territorial displays (e.g. the lizards *Sceloporus jarrovi* and *Urosaurus ornatus*; Moore 1987; Thompson & Moore 1992), and, in a wide range of taxa, past experiences of victory make winning future encounters more likely (e.g. Adamo & Hoy 1995; Chase *et al.* 1994). In addition, the consequences of past aggressive interactions are receiving increased theoretical attention (e.g. Johnstone & Dugatkin 2000), but this is, to my knowledge, the first theoretical work to relate past territorial intrusions with antipredator behaviour. Given the potentially far-reaching consequences of these effects, and their connections to other behavioural and ecological phenomena, it is hoped that the present paper will suggest further theoretical and empirical work.

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