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Prey scan at random to evade observant predators

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Anti-predator scans by animals occur with very irregular timing, so that the initiation of scans resembles a random, Poisson-like, process. At first sight, this seems both dangerous (predators could exploit the long intervals) and wasteful (scans after very short intervals are relatively uninformative). We explored vigilance timing using a new model that allows both predators and prey to vary their behaviour. Given predators that attack at random with respect to prey behaviour, constant inter-scan intervals minimize predation risk. However, if prey scan regularly to minimize their risk from randomly attacking predators, they become more vulnerable to predators that initiate attacks when the inter-scan intervals begin. If, in order to defeat this tactic, prey choose extremely variable inter-scan intervals, they become more vulnerable to predators who wait for long intervals before launching attacks. Only if predators can monitor the variability of inter-scan intervals and either attack immediately (if variability is too low) or wait for long intervals to attack (if variability is too high) does the empirically observed pattern of Poisson-like scanning become the optimal prey strategy.

Keywords: vigilance; scanning; predators; prey; random inter-scan intervals; exponential distribution

1. INTRODUCTION

Research on anti-predator vigilance represents one of the most successful combinations of theoretical and empirical work in behavioural ecology. A particular focus of attention has been the role of vigilance behaviour in explaining grouping. However, the theory on which much of the work relating vigilance and group size rests (Pulliam 1973) is based on a number of assumptions (see Bednekoff & Lima 1998*a*). First, predators are assumed to rush from cover at random times. Second, attacking predators that remain undetected for a certain critical time are assumed to be certain of catching their prey. Third, anti-predator scanning by individual prey is presumed to follow a Poisson process, so the frequency distribution of inter-scan intervals follows a negative exponential. As argued by Bednekoff & Lima (1998*a*), the validity of these assumptions requires further investigation. The first and second assumptions appear at best insufficiently general and at worst unrealistic (FitzGibbon 1989). The third assumption, while supported by considerable empirical evidence, is puzzling and is the focus of this paper. We develop a model of the relationship between the pattern of anti-predator scans and predation risk. This allows us to determine how prey should scan to minimize their predation risk, how the optimal solution depends on predator behaviour and how predator strategy, in turn, should respond to prey scanning patterns. This arms-race approach simulates the evolutionary game played between predator and prey (e.g. Stewart-Oaten 1982).

2. THE NEGATIVE EXPONENTIAL DISTRIBUTION OF INTER-SCAN INTERVALS: THEORY AND EVIDENCE

Most of the work on vigilance focuses on adaptive variation in vigilance with factors such as group size (see Elgar 1989; Roberts 1996*a* for reviews). Such work typically uses summary measures such as mean scanning rate. However, the way in which any given scanning rate is achieved is also important. Pulliam's (1973) assumption that scanning should be a Poisson process is at first sight surprising. Safety-critical vigilance by humans tends to be systematic, with the inspection schedule optimized for the risk profile between inspections and the relative cost of inspection versus failure to detect adverse events. When instantaneous risk increases with time (or use), long intervals are disproportionately dangerous and inspections should be regular (e.g. maintenance inspections of aircraft engines). When instantaneous risk decreases with time (e.g. in a patient recovering from heart surgery), examinations become progressively less frequent.

Randomly timed anti-predator vigilance gives a mixture of long and short intervals. Long intervals may be disproportionately dangerous (Desportes *et al.* 1989), while during short intervals, risk is unlikely to change and there may be little opportunity for other useful activity. The assumption of a negative exponential distribution of inter-scan intervals was originally made simply for mathematical convenience (Pulliam 1973); it has only later been given a functional justification on the grounds that a random distribution will make scanning unpredictable (Bertram 1980). According to this theory, predators will be unable to predict when randomly scanning prey will next raise their heads, and will therefore be unable to exploit this information in timing their attacks.

The theory appears to be borne out by evidence that inter-scan intervals do approximate a negative exponential. A number of authors have tested inter-scan interval distributions against a negative exponential and failed to detect a significant difference (Bertram 1980; Caraco 1982; Studd *et al.* 1983). Later work demonstrated that while inter-scan intervals did approximate a negative exponential, there was a time-dependent element, such that the probability of scanning increases with the time since the previous scan (Lendrem *et al.* 1986). The consequence of this is a distribution in which there are fewer

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very long and very short intervals (see also Hart & Lendrem 1984). Nevertheless, the evidence is that vigilance scans are closer to being initiated at random (resembling a Poisson process), than to being initiated at regular intervals (Lendrem 1983; Sullivan 1985).

Examining the frequency distribution of inter-scan intervals informs us about instantaneous randomness. However, a separate problem is whether there are any predictabilities in the sequencing of intervals. The question of whether scanning is a sequentially random process has been considered elsewhere (Desportes *et al.* 1989, 1994; Roberts 1994, 1996*b*; Suter & Forrest 1994; Ferriere *et al.* 1996; Ruxton & Roberts 1999).

3. MODELS

Here we develop models of the relationship between the pattern of anti-predator scans and predation risk. The models apply to individuals that can reduce their predation risk by scanning, whether they be solitary or in groups. We let predators initiate attacks at random or time their attacks in relation to the prey's inter-scan intervals. The probability of an attack by a predator succeeding given a time t between the start of the attack and the end of the inter-scan interval (i.e. the next anti-predator scan) is the interval-dependent risk function, $r(t)$. In general, the less time between the start of the attack and the end of the inter-scan interval, the lower the risk to the prey. For consistency with the vigilance literature (Pulliam 1973), we start by considering a step function for $r(t)$, termed $r_s(t)$. Here, risk increases from 0 to 1 when the time between the start of the attack and the end of the inter-scan interval exceeds the threshold t_s (figure 1*a*; equation (1)).

$$r_s(t) = \begin{cases} 1 \text{ when } t > t_s \\ 0 \text{ when } t < t_s. \end{cases} \tag{1}$$

Later, we represent the risk function as an exponential $r_e(t)$, that rises steeply at first and then asymptotes (figure 1*a*; equation (2)):

$$r_e(t) = 1 - e^{-t}. \tag{2}$$

We have also explored sigmoidal risk functions such as function $r_1(t)$, where t_i is the point of inflection and parameter k governs the slope (figure 1*a*; equation (3)):

$$r_1(t) = \frac{1}{1 + e^{k(t_i - t)}}. \tag{3}$$

Sigmoid and exponential functions are likely to be more realistic than the step function because the risk of prey capture is likely to be a smooth and continuous function of time. Nevertheless, the precise form of the risk function does not substantially alter any of the results presented in this paper.

To vary the pattern and rate of vigilance, we represent the inter-scan interval as a gamma-distributed random variable with a mean of μ and a variance of σ^2. We call this distribution T. Intervals lasting time t are drawn from the distribution of intervals, T. The probability density of an interval lasting time t is

$$f(t) = \frac{1}{(\sigma^2/\mu)^{(\mu^2/\sigma^2)}\Gamma(\mu^2/\sigma^2)} t^{(\mu^2/\sigma^2)-1} e^{-t/(\sigma^2/\mu)}. \tag{4}$$

The gamma distribution has a number of attractive properties. First, the exponential distribution, assumed for inter-scan intervals by classical vigilance models, is a gamma distribution in which $\mu^2 = \sigma^2$. Second, empirical data on inter-scan intervals, with the property that scanning probability increases with time since the last scan (see above) resemble a gamma distribution in which μ^2 is slightly greater than σ^2. Figure 1*b* shows probability density functions for T, using a range of values of σ^2 with μ fixed at 1.

The details of the model vary with the tactics of prey and predator. However, in general, if we know $r(t)$ and $f(t)$, we can compute an instantaneous risk function, $I(t)$, the probability that an attack will succeed at time t after its launch (figure 1*c*,*d*):

$$I(t) = r(t) \times f(t). \tag{5}$$

We can integrate $I(t)$ over time to compute Ψ, the expected or average risk from an attack:

$$\Psi = \int_0^\infty I(t)\mathrm{d}t. \tag{6}$$

Predators should maximize Ψ by adjusting their tactics and/or by identifying and attacking prey with the least effective vigilance behaviour. Prey should minimize Ψ for any mean inter-scan interval by adjusting the variance of their intervals.

We first consider predators that behave like those in the classical model. They attack at random times and succeed in capturing their prey if the interval persists longer than a critical time, t_s (i.e. the risk function is the step function $r_s(t)$, equation (1)). However, unlike the classical model we let prey vary the mean and variance of their inter-scan interval, to see how this influences predation risk. The probability density function for inter-scan intervals, $f(t)$, can be used to compute $F_r(t)$, the probability density function for interval survival times encountered by predators that arrive at random times t_r (figure 2*a*):

$$F_r(t) = \int_0^\infty f(t + t_r)\mathrm{d}t_r. \tag{7}$$

The expected risk from randomly timed attacks, Ψ_r, is computed by integrating equation (6) over all times greater than the critical time t_s at which the risk function $r_s(t)$ steps from 0 to 1:

$$\Psi_r = \int_{t_s}^\infty F_r(t)\mathrm{d}t. \tag{8}$$

Figure 2*b* shows that risk Ψ_r decreases with decreasing interval variance. In fact, Ψ_r declines monotonically with interval variance to the limiting case when $\sigma^2 = 0$:

$$\Psi_r = \begin{cases} \dfrac{\mu - t_s}{\mu} \text{ when } \mu > t_s \text{ and } \sigma^2 = 0 \\ 0 \text{ when } \mu < t_s \text{ and } \sigma^2 = 0. \end{cases} \tag{9}$$

Therefore, prey should choose regular inter-scan intervals when faced with predators whose attacks are not correlated with the timing of scanning behaviour. This result highlights an internal inconsistency in the classical model. The exponential distribution of inter-scan intervals that the classical model assumes is a bad prey strategy when

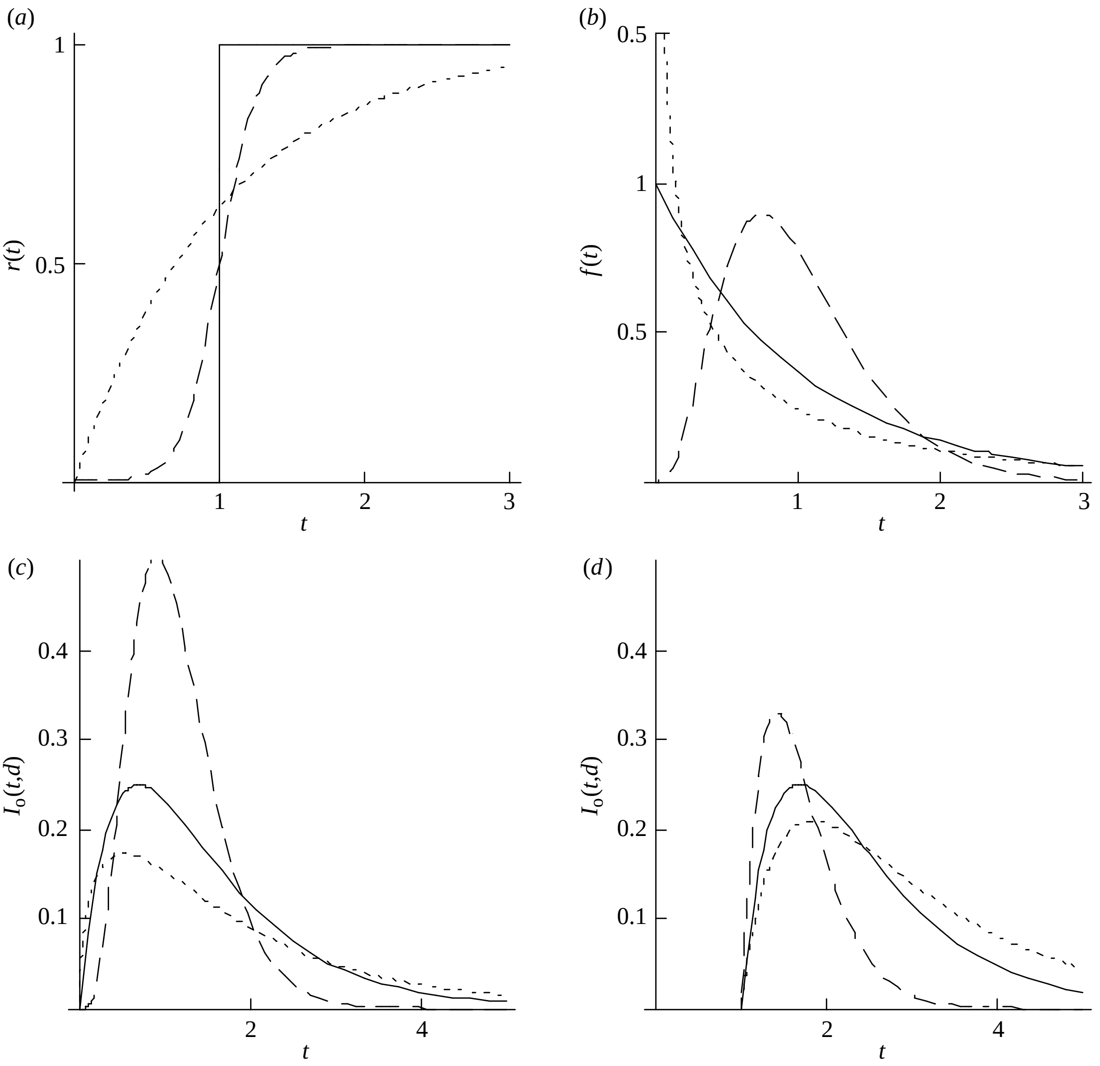

Figure 1. The basic model: (*a*) shows how the interval-dependent risk functions vary with the time, *t*, that the inter-scan interval persists after the attack is launched. We show three risk functions, $r_s(t)$ (step function, where $t_s = 1$; solid line), $r_e(t)$ (exponential, dotted line), and $r_s(t)$ (sigmoid, dashed line). (*b*) Probability density functions from which inter-scan intervals are randomly drawn. The *y*-axis shows $f(t)$ and the *x*-axis shows time, *t*. All lines represent gamma distributions with a mean inter-scan interval of $\mu = 1$. The solid line shows $\sigma^2 = \mu^2 = 1$, which is an exponential distribution; a special case of the gamma distribution. The dashed line shows a distribution with a variance of $\sigma^2 = 0.25$, and the dotted line shows a distribution with a variance of $\sigma^2 = 2$. (*c*) The instantaneous risk function, $I_o(t, d)$ (*y*-axis) at time *t* after the launch of an attack (*x*-axis) when the attack is launched at the start of the inter-scan interval ($d = 0$). The variances of inter-scan intervals are 2 (dots), 1 (solid), or 0.25 (dashes), with $\mu = 1$ and the risk function $r_e(t)$. (*d*) The instantaneous risk function, $I_o(t, d)$ at time *t* after the start of the interval when $d = 1$. The attack is launched only if the inter-scan interval persists for more than one time unit. The variances of inter-scan intervals are 2 (dots), 1 (solid), or 0.25 (dashes), with $\mu = 1$ and the risk function $r_e(t)$.

faced with predators that attack at random. However, prey that adopt regular scanning to beat random predators become vulnerable to predators that can monitor prey vigilance and launch attacks at the start of intervals (figure 2*c*). Conversely, prey that adopt highly irregular scanning to beat predators that launch attacks at the start of inter-scan intervals become vulnerable to predators that wait for long intervals before attacking (figure 2*c*). The relationship between prey and such observant predators is considered in more detail below.

What if predators can watch the prey, monitor their vigilance behaviour and use this information to time their attacks? The predator's flexible tactics are described by parameter *d*, the delay between the start of the inter-scan interval and the start of the attack. We illustrate this argument with the analytically convenient exponential risk function, $r_e(t)$ (see equation (2)), although almost identical results were obtained with the step and sigmoidal risk functions (equations (1) and (3), respectively). The instantaneous risk from an 'observant' predator, $I_o(t,d)$ is

$$I_o(t,d) = \frac{r_e(t) \times f(t+d)}{1 - \displaystyle\int_0^d f(t)\mathrm{d}t}. \tag{10}$$

The denominator in equation (10), $1 - \int_0^d f(t)\mathrm{d}t$, corrects $I_o(t,d)$ so that we only consider inter-scan intervals that survive until the attack is launched after the delay, *d*. This normalizes the results to the number of attacks launched,

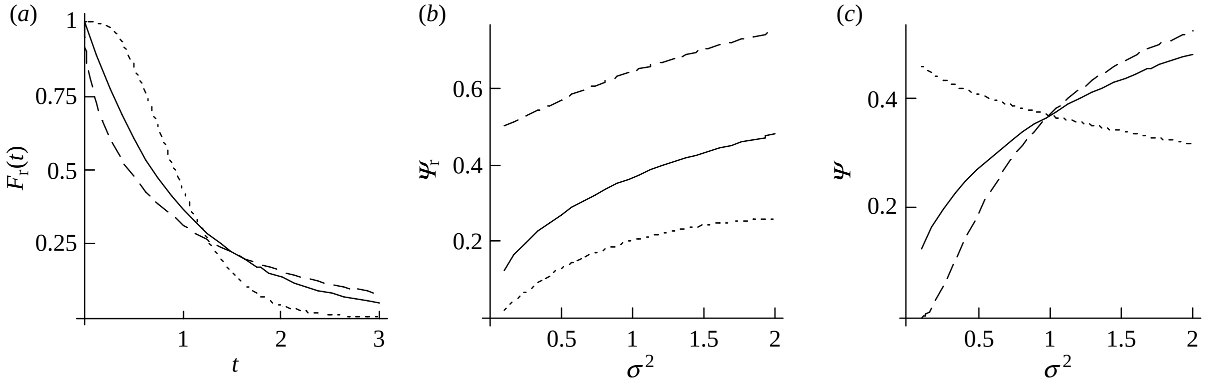

Figure 2. Risk when predators attack at random with respect to prey scanning. (*a*) Probability density $F_r(t)$ of interval survival times, t, encountered by a predator that initiates attacks at random times. Interval variance is $\sigma^2 = 1$ (solid line), 2 (dashes), or 0.25 (dots). Mean interval is $\mu = 1$ for all three curves. (*b*) Expected risk Ψ_r to randomly timed attacks as the variance, σ^2, of the inter-scan interval varies, while $t_s = 1$. Mean intervals are $\mu = 1$ (solid line), 2 (dashes) and 0.5 (dots). For any mean inter-scan interval, risk increases monotonically with variance. Therefore, prey should adopt regular scanning when faced with randomly attacking predators. (*c*) Predator fails to maximize success by attacking at random. The solid line shows expected risk to randomly timed attacks Ψ_r. When interval variance is low ($\sigma^2 < \mu^2$), this is less than the expected risk from attacks launched at the start of inter-scan intervals (Ψ with $d = 0$, dots). When variance is high ($\sigma^2 > \mu^2$), random attacks are less effective than attacks launched after a delay (Ψ with $d = 2$, dashes). In all cases, mean interval is $\mu = 1$, and the classical step risk function, $r_s(t)$, is used.

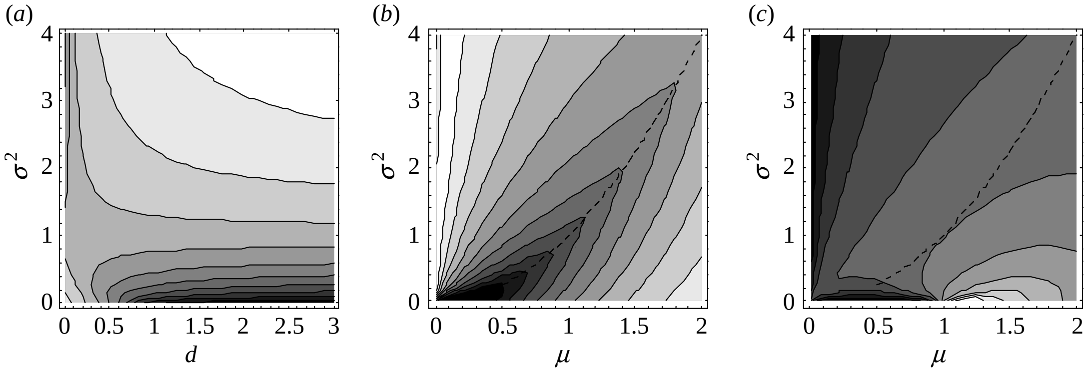

Figure 3. Risk when predators time their attacks. Lighter shades indicate higher risk. (*a*)–(*c*) were computed with the risk function $r_e(t)$, but virtually identical results were obtained with $r_s(t)$ and $r_l(t)$. (*a*) The expected risk, $\Psi_o(d)$, from an attack as inter-scan interval variance (σ^2, y-axis) and predator delay (d, x-axis) vary. The mean inter-scan interval is $\mu = 1$. When $\sigma^2 = 1$ (since $\sigma^2 = 1 = \mu^2$, this corresponds to an exponential distribution of inter-scan intervals) the predator cannot improve its success by adjusting d, the timing of its attacks. However, an exponential distribution of inter-scan intervals is not optimal for any single attack timing strategy, d. (*b*) The expected risk from attacks, $\Psi_o(d)$, by a predator that adjusts its timing to maximize its success as mean, μ (x-axis), and variance, σ^2 (y-axis), of inter-scan interval vary (equation (12)). When $\mu^2 > \sigma^2$ the predator chooses to attack immediately the interval starts. When $\mu^2 < \sigma^2$ the predator chooses to wait for an interval that persists for $d = 2$ time units before attacking. For any given mean scanning rate μ, the prey is safest when $\mu^2 = \sigma^2$, corresponding to an exponential distribution of inter-scan intervals (dotted line). (*c*) Risk per unit time, Γ_o, when the predator can adjust its timing to maximize its success, as mean, μ (x-axis), and variance, σ^2 (y-axis), of inter-scan interval vary (equation (13)). It is always best for the predator to attack at the start of intervals ($d = 0$). When intervals are short, the prey should scan regularly ($\sigma^2 = 0$). When intervals are long, the prey should use highly variable scanning ($\sigma^2 > \mu^2$). An exponential distribution of inter-scan intervals (dotted line) is not an effective prey strategy against a predator maximizing risk per unit time.

and not the time that a predator must wait before launching an attack (which is considered later). From equation (10), we can calculate the expected, or average, risk from an attack by an observant predator, $\Psi_o(d)$:

$$\Psi_o(d) = \int_0^\infty I_o(t,d)\,\mathrm{d}t. \tag{11}$$

Figure 1*c*,*d* shows the instantaneous probability of attack success, $I_o(t,d)$, when the predator attacks immediately an interval begins ($d = 0$) and when the predator attacks after a delay of $d = 1$. Waiting before attacking reduces the chance of prey capture when the variance of inter-scan intervals is low ($\sigma^2 < \mu^2$), increases the chance of prey capture when the variance is high ($\sigma^2 > \mu^2$), but has no effect when inter-scan intervals are drawn randomly from an exponential distribution ($\sigma^2 = \mu^2$; figures 1*c*,*d* and 3*a*).

Figure 3*a* shows the expected risk, $\Psi_o(d)$, as the timing of the attack, d, and the variance of the inter-scan intervals vary. Suppose that this represents a system inhabited by a predator (or predators) that can use only a single timing strategy but that can learn or evolve to optimally time attacks. Furthermore, suppose that the predator encounters prey that have evolved with randomly attacking predators, so have consequently evolved regular inter-scan intervals in which $\sigma^2 = 0$; see figure 3*a*. Over time, the predator will optimize its success by attacking at the start of intervals ($d = 0$, $\sigma^2 = 0$; figure 3*a*). However, the prey will respond to this strategy by increasing the variability of their intervals ($d = 0$, $\sigma^2 = 4$; figure 3*a*). In turn, the predator will improve its success by attacking after a delay ($d = 3$, $\sigma^2 = 4$; figure 3*a*), prompting the prey to adopt regular scanning ($d = 3$, $\sigma^2 = 0$; figure 3*a*) and bringing us back to the starting conditions. In such a system, predator behaviour will 'pursue' prey behaviour around the surface shown in figure 3*a*. The exponential distribution of intervals ($\sigma^2 = 1$), observed in a wide variety of real systems (or, indeed, any single prey strategy) does not appear to be stable when faced with predators that adopt a single timing strategy.

Now consider a more sophisticated predator that can observe prey, can measure the mean and variance of their inter-vigilance intervals, and can choose to attack immediately or after a delay. If this predator encountered prey that scanned at regular intervals, it would choose to attack at the start of intervals ($d = 0$, $\sigma^2 = 0$). Prey should then adjust their behaviour to increase variability and reduce risk. However, if variability moves beyond an exponential distribution of intervals ($\sigma^2 = 1$, $d = 0$), then the predator can switch behaviour and attack after a delay ($d \gg 0$). The ability of the predator to switch tactics forces the prey to adopt scanning intervals drawn from the empirically observed exponential distribution (although such intervals are suboptimal for any single predator strategy).

Figure 3*b* shows the risk to prey when a predator can select its timing (either $d = 0$ or $d = 2$) to optimize risk, for a range of σ^2 and μ (equation (12)).

$$\Psi_o(d) = \begin{cases} \Psi_o(0) \text{ when } \Psi_o(0) > \Psi_o(2) \\ \Psi_o(2) \text{ when } \Psi_o(2) > \Psi_o(0). \end{cases} \tag{12}$$

This illustrates the principle that risk to prey is minimum when $\sigma^2 = \mu^2$ (corresponding to intervals selected from an exponential distribution) provided that predators can adapt the timing of their attacks depending on the behaviour of the prey.

The discussion has considered risk per attack, but the waiting strategy ($d > 0$) leads predators to avoid attacks in intervals with a lifetime of less than d, so such a strategy leads to a lower overall attack rate. When prey scans are more variable than the exponential ($\sigma^2 > \mu^2$), the theoretically optimal predator maximizes risk per attack by waiting an infinitely long time before attacking. Clearly, this is unrealistic. Therefore, we have used more modest delays of $d = 1$ or 2 (figures 1–3), which would yield attack rates of one attack per e (2.7) and e^2 (7.4) time units, respectively, given prey with mean scanning rate and variance of $\mu = 1$ and $\sigma^2 = 1$ (where e is the exponential constant). However, we were interested to see if prey should behave differently given predators that maximize the chance of prey capture per unit time, rather than prey capture per attack. Risk per unit time, Γ_o, is given by equation (13):

$$\Gamma_o(d) = \frac{\int_0^{\infty} r_e(t) \times f(t + d)\mathrm{d}t}{\mu}. \tag{13}$$

Figure 3*c* shows risk per unit time, Γ_o, to predators that can adjust their timing to maximize Γ_o. It was computed with the same parameters as figure 3*b*. The figure shows that optimal interval variance, σ^2, depends on mean interval, μ. When μ is small, prey minimize risk with low variability scans. When μ is large, prey minimize risk with high variability scans. Against both prey tactics, predators maximize success by attacking immediately ($d = 0$). However, an exponential distribution of intervals (dotted line, where $\mu^2 = \sigma^2$) is not optimal for any mean interval length.

4. DIVERGENCE FROM THE EXPONENTIAL DISTRIBUTION

Our models suggest that the best response by prey to an observant predator is to select inter-scan intervals randomly from an exponential distribution. However, empirical data on the distribution of inter-scan intervals tend to show fewer very short and fewer very long intervals than the exponential (Lendrem *et al.* 1986). In other words, they resemble a gamma distribution where μ^2 is slightly larger than σ^2. There are several possible explanations for this discrepancy.

First, prey could face a mixture of timed attacks and random attacks. However, when faced with a proportion k timed attacks and $(1-k)$ random attacks whose expected outcomes are Ψ_o and Ψ_r respectively, the optimum interval variance σ^2 will minimize $k\Psi_o + (1-k)\Psi_r$. A minimum in $k\Psi_o + (1-k)\Psi_r$ when $0 < \sigma^2 < \mu^2$ is possible, but such a minimum only occurs within a narrow range of k. Therefore, in almost all mixtures of random and timed attacks, the safest variance σ^2 will be either 0 or μ^2.

Second, our model assumes an exponential risk function, $r_e(t)$, a step risk function, $r_s(t)$, or a sigmoid risk function, $r_l(t)$. However, many other risk functions could, in principle, apply, and the function may vary with both predator species and habitat features. The sigmoid risk function seems particularly realistic; risk is small initially, rises steeply and then asymptotes. Compared with the exponential risk function $r_e(t)$, where risk decelerates with t, the sigmoidal risk function shows 'risk acceleration' when $t < t_i$, and 'risk deceleration' when $t > t_i$ (figure 1*a*). This could produce a switch in optimum prey strategy as the mean inter-scan interval μ changes with respect to t_i. When μ is less than t_i, prey should adopt more regular scanning to keep all intervals below t_i (just as regular scanning is best with the step risk function when $\mu < t_s$), since in the risk acceleration phase, reducing t causes a greater than proportional reduction in risk. However, when μ is greater than t_i, the effect of the early 'low risk' phase becomes negligible, and so, as with the exponential risk function $r_e(t)$, the prey should adopt an exponential distribution of intervals. At some scanning rate between the extremes (i.e. $\mu \ll t_i$ and $\mu \gg t_i$), an optimal scanning pattern may exist that is neither regular nor exponential. However, this is unlikely to account for the empirically observed behaviour, because the optimum is likely to be unstable and will shift to the regular or exponential pattern given very small changes in mean scanning rate.

Third, in real environments, predators can only sample prey behaviour for a finite time, and so have sample mean interval, $\bar{x}$, and sample interval variance s^2 on which to base their decisions. Therefore, the 'signal' given out by prey is not their true mean and variance, but rather the joint probability density of sample mean and sample variances, $p(\bar{x}, s^2)$. This is a function G of μ, σ^2 and the length of time, t_s, for which the predator samples the prey's behaviour.

$$p(\bar{x}, s^2) = G(\mu, \sigma^2, t_s). \qquad (14)$$

Prey should minimize Ψ_s, the expected risk over the entire joint sampling probability density function, $p(\bar{x}, s^2)$.

$$\Psi_s = \int_0^\infty \int_0^\infty [p(\bar{x}, s^2) \times \Psi_o(\bar{x}, s^2)] \mathrm{d}\bar{x} \mathrm{d}s^2. \qquad (15)$$

Analytical integration of functions such as equation 15 is difficult, so we have examined the effect of finite sampling by the predator using an extensive series of Monte Carlo simulations. The simulations show that sampling error is unlikely to 'push' prey towards distributions of inter-scan intervals that are less variable than an exponential. In fact, sampling error may slightly increase interval variance. Therefore, finite sampling by the predator does not explain the difference between an exponential distribution of intervals, predicted by the model, and the empirical data.

Fourth, perhaps the empirical distribution of intervals reflects sampling from a distribution that is exponential in the short term, but in which the mean rate varies with time? However, the sum of any set of negative exponentials produces a distribution that declines monotonically with time. Therefore, this cannot be the explanation for the observed pattern.

Two likely reasons remain for the difference between the empirical data and the predictions of our model. First, very short inter-scan intervals may provide the prey with very little opportunity to do anything useful. Second, vigilance is necessary both to detect predators and to see if the overall risk level has changed (for example, by the arrival of a number of predators or a reduction in group size). By reducing the number of very long intervals, prey reduce their chance of 'undersampling' changes in risk that could trigger a change in vigilance rate.

5. DISCUSSION

Our results have a number of implications for the study of vigilance. First, they highlight an internal inconsistency in the classical model in which predators attack at random times and prey scan randomly (Pulliam 1973). Second, our model shows that inter-scan intervals that are randomly selected from an exponential distribution are an effective prey strategy when faced with observant predators that maximize their success per attack by measuring vigilance behaviour and using that information either to wait for a long interval before attacking (if prey scans are too variable) or to attack at the start of intervals (if prey scans are too regular). This finding comes from treating vigilance as an arms race between predators and prey, with prey vigilance being determined by the best response to flexible predator behaviour (see equation (12)). Third, our results suggest that an exponential (or near exponential) distribution of intervals will arise when predators seek to maximize success per attack, and not success per unit time. This suggests that in real systems with exponential (or near exponential) distributions of intervals, success per attack and not success per unit time is the primary driver of predator behaviour. This may be a consequence of the costly nature of attacks: if a predator can only launch a limited number of attacks per day, it needs to maximize its success on each attack.

We suppose that predator–prey interactions will drive prey to produce overt vigilance scans that are a signal to potential predators. Predators that detect the signal will avoid attacking vigilant prey, and prey whose signals are detected will deter attacks. That predators are responsive to prey vigilance has been shown by FitzGibbon (1989), who observed that cheetahs biased their attacks towards less vigilant gazelles. Given predators that cannot time their attacks or cannot recognize prey vigilance, regular scanning is more effective for prey. This might occur, for example, for raptors attacking nocturnal, or partly hidden, rodents, or for fish prey, whose vigilance behaviour is difficult to detect. We therefore predict that inter-scan interval distributions will vary between predator–prey systems (see also Hart & Lendrem 1984) and our results illustrate the need to know more about such systems (see also Bednekoff & Lima 1998*b*).

Different assumptions may affect the predictions of the models. We assume scanning is entirely for predator detection, whereas it may serve other functions. We also assume that inter-scan interval duration is determined solely by maximizing predator detection, whereas there may be important foraging or other constraints (e.g. there may be a minimum inter-scan interval representing a constraint on how rapidly the bird can raise or lower its head: Elcavage & Caraco 1983; Lendrem 1983; Sullivan 1985). Also, we do not consider the consequences of grouping: if group members did not scan independently, this could either increase or decrease the probability of detection by the group (Lazarus 1979; Ruxton & Roberts 1999; Ward 1985).

The assumption that animals feeding with their heads down (i.e. in a non-vigilant state) cannot detect approaching predators is too simplistic. Birds are not blind to other stimuli while feeding (Davis 1975), and have a considerable ability to detect approaching predators even when not overtly vigilant (Lima & Bednekoff 1999). Furthermore, they may increase attention to predator stimuli towards the end of an inter-scan interval, as known for motivational changes preceding other behavioural switches (Culshaw & Broom 1980; Broom 1981). As a result, prey will have an increased probability of surviving even if they do not scan within the predator's attack time.

We have shown that the exponential, or near exponential, distribution of inter-scan intervals found in prey animals in nature minimizes risk from observant predators that flexibly and adaptively time their attacks. Further work on flexible predator tactics of the kind pioneered by FitzGibbon (1989), and comparative work on the vigilance patterns of prey with flexibly and randomly attacking predators, will be required if we are to understand the adaptive nature of vigilance scheduling.

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REFERENCES

Bednekoff, P. A. & Lima, S. L. 1998*a* Randomness, chaos and confusion in the study of antipredator vigilance. *Trends Ecol. Evol.* **13**, 284–287.

Bednekoff, P. A. & Lima, S. L. 1998*b* Re-examining safety in numbers: interactions between risk dilution and collective detection depend upon predator targeting behaviour. *Proc. R. Soc. Lond.* B **265**, 2021–2026.

Bertram, B. C. R. 1980 Vigilance and group size in ostriches. *Anim. Behav.* **28**, 278–286.

Broom, D. M. 1981 *Biology of behaviour: mechanisms, functions and applications.* Cambridge University Press.

Caraco, T. 1982 Flock size and the organization of behavioural sequences in juncos. *Condor* **84**, 101–105.

Culshaw, A. D. & Broom, D. M. 1980 The imminence of behavioural change and startle responses of chicks. *Behaviour* **73**, 64–76.

Davis, J. M. 1975 Socially induced flight reactions in pigeons. *Anim. Behav.* **23**, 597–601.

Desportes, J.-P., Metcalfe, N. B., Cézilly, F., Lauvergeon, G. & Kervalla, C. 1989 Tests of the sequential randomness of vigilant behaviour using spectral analysis. *Anim. Behav.* **38**, 771–777.

Desportes, J.-P., Cézilly, F. & Metcalfe, N. B. 1994 Vigilance patterns in birds: randomness or predictability? *Anim. Behav.* **48**, 226–227.

Elcavage, P. & Caraco, T. 1983 Vigilance behavior in house sparrow flocks. *Anim. Behav.* **31**, 303–304.

Elgar, M. 1989 Predator vigilance and group size in birds and mammals: a critical review of the evidence. *Biol. Rev.* **64**, 13–33.

Ferriere, R., Cazelles, B., Cézilly, F. & Desportes, J.-P. 1996 Predictability and chaos in bird vigilant behaviour. *Anim. Behav.* **52**, 457–472.

FitzGibbon, C. D. 1989 A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. *Anim. Behav.* **37**, 508–510.

Hart, A. & Lendrem, D. W. 1984 Vigilance and scanning patterns in birds. *Anim. Behav.* **32**, 1216–1224.

Lazarus, J. 1979 The early warning function of flocking in birds: an experimental study with captive quelea. *Anim. Behav.* **27**, 855–865.

Lendrem, D. W. 1983 Predation risk and vigilance in the blue tit (*Parus caeruleus*). *Behav. Ecol. Sociobiol.* **14**, 9–13.

Lendrem, D., Stretch, D., Metcalfe, N. & Jones, P. 1986 Scanning for predators in the purple sandpiper: a time-dependent or time-independent process? *Anim. Behav.* **34**, 1577–1578.

Lima, S. L. & Bednekoff, P. A. 1999 Back to the basics of anti-predatory vigilance: can nonvigilant animals detect attack? *Anim. Behav.* **58**, 537–543.

Pulliam, H. R. 1973 On the advantages of flocking. *J. Theor. Biol.* **38**, 419–422.

Roberts, G. 1994 When to scan: an analysis of predictability in vigilance sequences using autoregression models. *Anim. Behav.* **48**, 579–585.

Roberts, G. 1996*a* Why individual vigilance declines as group size increases. *Anim. Behav.* **51**, 1077–1086.

Roberts, G. 1996*b* Testing for patterns in sequences of vigilance behaviour. *Anim. Behav.* **51**, 1179–1182.

Ruxton, G. & Roberts, G. 1999 Are vigilance sequences a consequence of intrinsic chaos or external changes? *Anim. Behav.* **57**, 493–495.

Stewart-Oaten, A. 1982 Minimax strategies for a predator–prey game. *Theor. Popul. Biol.* **22**, 410–424.

Studd, M., Montgomerie, R. D. & Robertson, R. J. 1983 Group size and predator surveillance in foraging house sparrows (*Passer domesticus*). *Can. J. Zool.* **61**, 226–231.

Sullivan, K. A. 1985 Vigilance patterns in downy woodpeckers. *Anim. Behav.* **33**, 328–329.

Suter, R. B. & Forrest, T. G. 1994 Vigilance in the interpretation of spectral analyses. *Anim. Behav.* **48**, 223–225.

Ward, P. I. 1985 Why birds in flocks do not coordinate their vigilance periods. *J. Theor. Biol.* **114**, 383–385.

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