

You can run—or you can hide: optimal strategies for cryptic prey against pursuit predators

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We consider the optimal behavior of a cryptic prey individual as it is approached by a predator searching for prey. Although the predator has not yet discovered the prey, it has an increasing likelihood of doing so as it gets closer to the prey. Further, the closer the predator is to the prey when it discovers it, the more likely the predator will be to capture the prey. These arguments suggest that the prey should flee before the predator discovers it. However, the act of fleeing will alert the predator to the presence of the prey and trigger an attack that might not have occurred otherwise. We capture these conflicting outcomes in a mathematical model, which we then use to predict the optimal behavior of the prey and predator. We argue that the optimal strategy for the prey is either to run as soon as they detect a predator approaching or to only flee in response to having been detected by the predator. Running as soon as the predator is detected is associated with low predator search speeds, a low nonpredation cost to running, a large advantage to the prey in initiating chases rather than reacting, limited ability to spot the predator at distance, a high ability to spot prey by the predator, and a high probability that chases will be successful. The optimal strategy for the predator depends on whether its current trajectory is taking it closer to or further from the prey. In the latter case, the predator should attack immediately on discovering the prey; in the former case, it should delay its attack until it reaches the point on its current trajectory where distance to the prey is minimized. *Key words:* antipredator strategies, coursing predators, crypsis, fleeing, flight, predation, predator-prey interactions, prey detection. [*Behav Ecol* 16:534–540 (2005)]

Predation is an important selection pressure on many species. Encounters between predators and prey are ubiquitous in the natural world and can take a variety of forms. Here, we are interested in interactions where prey can escape the predator by fleeing. Further, we assume that provided it has a sufficient head start, the prey can evade predation, either by being able to outrun the predator or by safely reaching a refuge. The only previous theoretical work on this subject is the graphical model of Ydenberg and Dill (1986). The key prediction of their model was that prey may not immediately flee from an approaching predator, even if the probability of escaping from the predator is reduced by this delay. The mechanism behind delaying is that the prey must often trade off the cost of being predated against other potential benefits, such as food gathering. If delaying flight allows animals to feed for a little longer, then under some conditions it may be optimal for the prey to pay an increased risk of predation for this extra food. As they acknowledge, with this model Ydenberg and Dill (1986) were making explicit an assumption which several previous authors had considered implicitly: for example, Dill, 1974; Greig-Smith, 1981; Lazarus, 1979; Margurran et al., 1985; Passano, 1957; Seghers, 1981. Here, we introduce a mathematical model that allows us to explore issues surrounding fleeing from predators that simpler graphical arguments cannot adequately describe.

We have in mind prey that are initially stationary and to some extent cryptic in their environment such that predators

cannot detect them at a distance. Examples include ungulate calves hiding in long grass, many cryptically colored ground-nesting birds, and flatfish lying on the sea bottom. We consider a predator-prey encounter to begin when the prey detects an approaching predator. Implicit in this is that prey can detect a predator at a greater distance than the predator can detect the prey. This will be reasonable for many systems where predators are bigger than their prey. Also, the fact that we consider cases where the predator is moving and the prey is still argues that the prey is likely to detect the predator first. Since the predator has yet to detect the prey when the interaction begins, there is no reason to expect that its trajectory will be taking it directly toward the prey. However, even if not heading directly for the prey, the distance between the two individuals can close if the predator is moving broadly in the direction of the prey. The closer the predator gets to the prey, the more likely it is to detect it. Worse still for the prey, the closer the predator is when it detects it, the more likely it is that the ensuing attack by the predator will be successful. Hence, fleeing immediately on detecting the predator appears an attractive strategy to the prey. However, there is a potential cost to fleeing over and above the lost opportunity for other activities considered by Ydenberg and Dill (1986). Fleeing from the predator will in most cases alert the predator to the presence of the prey individual. The predator may respond to this discovery with an attack, which might be successful. Hence, there may be a countervailing pressure for the prey to sit tight, rely on its crypsis, and only flee if it perceives that the predator has detected it and is attacking. This strategy may allow the prey to survive simply because the predator passes by without detecting the prey's presence. In the next section, we will introduce a model that explores how animals might trade off these selection pressures. In this paper, we model fitness in a very simple

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Table 1
Definitions of variables used in the models

r	the maximum distance at which prey can detect predators
v	this identifies a point on the trajectory of the predator scaled such that $v \in [-1,1]$
θ	angle between the predator's trajectory and a radial line from the prey to the point where the predator enters the circle of radius, r
s	speed of movement of the predator while searching for prey
$d(v)$	distance from predator to prey when predator is at point v on its trajectory
$f[d(v)]$	the probability of the predator successfully catching the prey if it initiates an attack at point v on its trajectory
Δ	the advantage (measured as distance covered) the prey gets from initiating a chase itself
$g[d(v)]$	the probability (per unit time) that the predator (when at point v) detects the prey
$A(v)$	the probability that the prey has been detected by point v (starting at $v = -1$)
t	time taken by the predator to reach point v
c	the cost of surviving through outrunning a predator, compared to surviving by avoiding running
α	increasing α increases the capture success of the predator (at all distances) for the example functional form for the function f
β	increasing β increases the effect of distance in reducing capture success for the example function form for the function f
a	increasing a increases probability of detection in the example functional form for the function g

way; the payoff to the prey is solely about its probability of surviving a given encounter with a predator. The key difference between our model and that of Ydenberg and Dill (1986) is in the cost to the prey associated with fleeing early. In the model of Ydenberg and Dill (1986) this cost is the opportunity costs associated with reduced time spent feeding, for example; in our model, the cost to the prey is in alerting the predator to its presence and position. These costs are not mutually exclusive, so our model can be seen as complementary to the previous theory of Ydenberg and Dill (1986).

It is likely that prey can perceive the difference between a predator that has not detected it and is searching its environment and a predator that has detected the prey and is launching an attack directly toward it. This will often be revealed in a change in direction of motion of the predator accompanied by an increase in speed of movement (e.g., Woodbury, 1986). However, if during its search, a predator detects a cryptic prey item and its current trajectory takes it nearer the prey (albeit not directly toward it), then the predator may benefit from delaying its attack, carrying on its current trajectory, and only launching an attack when it has reduced the distance between itself and the prey. The predator gains if the prey requires the actual launch of an attack to reveal to it that the predator has discovered its presence and position. Hence, another aim of our paper will be to simultaneously explore optimal strategies of the predator as well as the prey. In contrast, Ydenberg and Dill (1986) focussed purely on prey behavior and did not consider any flexibility in predator strategy.

GENERAL MODEL DESCRIPTION

We assume that the predator moves in an undeviating straight line, unless it detects the prey individual. The interaction

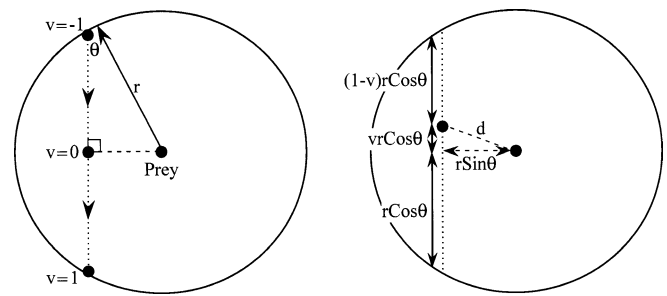


Figure 1
 The trajectory taken by the predator can be represented as a chord of a circle of radius r centered on the prey (see vertical line on left panel with arrows giving direction of travel). We denote the point when the prey enters this circle as $v = -1$, the point when predator and prey are closest as point $v = 0$, and the point when the predator leaves the circle as point $v = 1$. Hence, any point on the trajectory can be described by a unique v value in the range $[-1,1]$. The position of the trajectory is described by the angle between the trajectory and a radial line from the prey to point $v = -1$, denoted θ in the left panel. The length of the trajectory is given by $2r \cos \theta$ and the minimum distance between predator and prey (occurring when $v = 0$) is $r \sin \theta$. At any point v on the trajectory, the distance between predator and prey can be found by simple triangular geometry (see right panel).

between prey and predator starts when the predator is a distance r from the prey (see Table 1 for definitions of all variables used in the model). This can be thought of as the maximum distance at which the prey can perceive the predator. The consequence of this assumption is that we begin our consideration when the predator is at a distance r from the prey, at which point it is assumed to not have detected the prey yet.

We consider the path of the predator until such time as it is beyond the visual range of the prey again, that is, more than a distance r away from the prey. This path is shown as the line from $v = -1$ to $v = 1$ within the circle of radius r in Figure 1. All points on this line can be uniquely defined by a value $v \in [-1,1]$. The trajectory of the predator makes an angle θ with a radial line from the point when the predator first enters the circle (defined by $v = -1$). By simple triangular geometry, the predator travels a distance $2r \cos \theta$ before leaving the circle again. Its point of nearest approach to the prey occurs halfway along this line (i.e., when $v = 0$). At this point, the geometry of right-angled triangles means it is at a distance $r \sin \theta$ from the prey. We assume that the predator moves at a constant searching speed s . At a given point v (see Figure 1), the distance from predator to prey is $d(v)$ given (using Pythagoras' theorem; see Figure 1) by

$$[d(v)]^2 = (r \sin \theta)^2 + (vr \cos \theta)^2, \tag{1}$$

which (using the identity $\sin^2 \theta + \cos^2 \theta = 1$) simplifies to

$$d(v) = r\sqrt{[1 - (1 - v^2) \cos^2 \theta]}. \tag{2}$$

If at this point the predator starts to chase down the prey (hereafter "attacks"), then the prey will flee in response and the predator will be successful in catching the prey with probability $f[d(v)]$. We assume that attacks are less likely to be successful if launched from a greater distance and that the probability of success falls to zero if predator and prey are sufficiently far from each other.

If alternatively the prey runs without being triggered by the predator (hereafter "flees"), then the predator will respond by chasing it. This chase will have a probability of capture $f[d(v) + \Delta]$ for some positive constant Δ . This constant can be interpreted as the advantage that the prey gets from

initiating a chase itself (fleeing) rather than responding to a predator’s attack. It can be seen as the distance covered by the prey in the time it takes the predator to detect and respond to the fleeing prey.

While on its initial trajectory, the probability per unit time that the predator will detect the prey is $g[d(v)]$, where $d(v)$ is the distance from predator to prey at that time. We assume that the prey is less likely to be discovered from a greater distance away and that the probability of discovery falls to zero if predator and prey are sufficiently far apart. If we define $A(v)$ as the probability that the prey has been detected by point v (starting at $v = -1$), then the probability of the prey not being detected by point v , $[1 - A(v)]$, is the accumulation of it not being detected at any point on the predator’s trajectory; mathematically this is given by the integral

$$1 - A(v) = \exp \left\{ - \int_0^t g[d(v)] dt \right\}, \tag{3}$$

where t is the time taken by the predator to reach point v . Taking the logs of both sides gives this equation in a more convenient form:

$$- \ln[1 - A(v)] = \int_0^t g[d(v)] dt. \tag{4}$$

It would be easier to evaluate this as an integral over scaled distance v than over time t , so we need a relation between these two variables. Since we know that the predator travels at speed s and it travels a distance $2r \cos \theta$ as v changes from -1 to 1 , it is easy to derive the relation

$$t = \frac{(v + 1) r \cos \theta}{s}. \tag{5}$$

Differentiating this with respect to v and using this to change the variable of the integral in Equation 4 gives

$$- \ln[1 - A(v)] = \left(\frac{r \cos \theta}{s} \right) \int_{-1}^v g[d(v)] dv. \tag{6}$$

Let us assume that surviving by not running is preferable to the prey to surviving by successfully evading the predator in a chase. Hence, if a chase occurs and the prey survives, we will decrement the prey’s payoff by a small fixed factor c . This could be seen as the time, energy, or injury costs associated with running. There are three possibilities for an interaction between a predator and a prey: no chase can occur, a chase can be initiated by the predator attacking, or a chase can be initiated by the prey fleeing; the payoffs to the predator and prey from these three situations are given in Table 2. We now explore the model’s predictions in a number of different cases.

Case 1

The predator must attack as soon as it detects the prey, and it can see behind it (and so may still attack after it has passed the point of closest approach [$v = 0$]).

We are interested in the optimal fleeing strategy for the prey. One strategy (which we call strategy N) would be to only run if attacked (i.e., the prey never initiates a chase by fleeing). The payoff for never fleeing is given by

$$R(N) = \int_{-1}^1 \{1 - f[d(v)]\} (1 - c) \left[\frac{dA(v)}{dv} \right] dv + [1 - A(1)]. \tag{7}$$

The first term in the above equation is the payoff for escaping an attack initiated by the predator at each point v

Table 2

Payoffs to both predator and prey from the three different outcomes of an interaction; see Table 1 for definitions of all variables

Situation	Prey’s payoff	Predator’s payoff
No chase	1	0
Attack-initiated chase	$(1 - c) \{1 - f[d(v)]\}$	$f[d(v)]$
Fleeing-initiated chase	$(1 - c) \{1 - f[d(v) + \Delta]\}$	$f[d(v) + \Delta]$

multiplied by the probability density that the attack is initiated at that point and integrated over the whole trajectory from $v = -1$ to 1 . The second term is the payoff for never having to run multiplied by the probability of no attack being launched by the predator over the whole trajectory.

An alternative strategy (strategy V) could be to flee if the predator attacks or if the predator reaches point $v = V$ without attacking, for some point $V \in [-1, 1]$. The payoff from this strategy is

$$R(V) = \int_{-1}^V \{1 - f[d(v)]\} \left[\frac{dA(v)}{dv} \right] dv + [1 - A(V)] (1 - c) \times \{1 - f[d(V) + \Delta]\}. \tag{8}$$

Now the first term is the payoff from the predator initiating an attack at some point $v \in [-1, V]$ multiplied by the probability density that an attack is launched at this point and integrated over all possible v values. The second term is the payoff from fleeing at point V multiplied by the probability that the predator has not attacked by this point.

The case of fleeing as soon as the predator is detected (strategy -1) is obtained by simply substituting $V = -1$ in Equation 8

$$R(-1) = [1 - f(r + \Delta)] (1 - c). \tag{9}$$

From the form of Equation 8, we can see that for any $V \neq -1$, $R(V)$ is a weighted average of terms of the form $(1 - c) [1 - f(v)]$ that are never bigger than $R(-1)$ and so $R(-1) > R(V)$ for any $V \neq -1$. This means that the optimal strategy is either to run immediately on seeing the predator [with payoff $R(-1)$] or never to initiate a chase but only to run when the predator initiates an attack [with payoff $R(N)$]. Which of these two is the optimal strategy depends simply on which of these payoffs is greater, which in turn depends on the exact functional forms assumed for f and g and specific values assigned to parameters.

Case 2

We assume that the predator can still see behind it, but it now need not attack as soon as it has seen the prey. Rather, it may choose to close the distance between it and the prey before launching an attack.

We will assume that the prey can play the same two strategies as considered above: strategy N (never fleeing unless attacked) or strategy V (flee if attacked or when predator reaches point V).

The predator plays a strategy U , which involves delaying an attack until point U if the prey is detected before this point or attacking immediately on detecting the prey if detection occurs after this point ($U \in [-1, 1]$).

If $V < U$, then the prey will always flee before a predator attacks and (from Table 2) will receive payoff

$$R(V, U) = (1 - c) \{1 - f[d(V) + \Delta]\}. \tag{10}$$

Again, from Table 2, the predator receives payoff

$$P(V, U) = f[d(V) + \Delta]. \tag{11}$$

If $V > U$, then there are three possible outcomes of an interaction: the predator may initiate an attack at point U , it may initiate an attack at some point $U < v < V$, or the prey may flee at point V . These three alternatives (respectively) lead to three terms in the payoffs for prey and predator.

$$R(V, U) = A(U)(1 - c)\{1 - f[d(U)]\} + \int_U^V (1 - c)\{1 - f[d(v)]\} \left[\frac{dA(v)}{dv} \right] dv + [1 - A(V)](1 - c)\{1 - f[d(V) + \Delta]\}, \tag{12}$$

$$P(V, U) = A(U)f[d(U)] + \int_U^V f[d(v)] \left[\frac{dA(v)}{dv} \right] dv + \{1 - A(V)\}f[d(V) + \Delta]. \tag{13}$$

If the prey plays strategy N , then the predator will initiate an attack at point U , it will initiate an attack at some point between U and -1 , or no attack will occur. These three possibilities (respectively) lead to three terms in the payoffs to prey and predator:

$$R(N, U) = A(U)(1 - c)\{1 - f[d(U)]\} + \int_U^1 (1 - c) \times \{1 - f[d(v)]\} \left[\frac{dA(v)}{dv} \right] dv + [1 - A(1)], \tag{14}$$

$$P(N, U) = A(U)f[d(U)] + \int_U^1 f[d(v)] \times \left[\frac{dA(v)}{dv} \right] dv. \tag{15}$$

The payoff to the prey for running immediately on detecting the predator is obtained by simply substituting $V = -1$ in Equation 12

$$R(-1, U) = (1 - c)[1 - f(r + \Delta)]. \tag{16}$$

By a similar argument to that used before for Equation 8, $R(-1, U)$ is greater than the weighted average of similar terms that constitutes $R(V, U)$ for all $V \neq -1$. This is true for any U , so whatever the predator’s strategy, the prey’s best strategy will be to either never flee unless attacked (strategy N) or flee immediately on detecting the predator (strategy -1). If strategy -1 is adopted, then the payoffs to both parties are independent of the predator’s strategy. Let us then consider the case where the prey picks strategy N and consider what value of U maximizes the predator’s payoff $P(N, U)$ given by Equation 15.

We would expect that if the predator is more successful the nearer it is to the prey when it attacks, then $f[d(v)]$ reaches its maximum when $v = 0$ and $f[d(v)] > f[d(y)]$ for all $v \in [0, y)$. That is, $P(0, N) > P(y, N)$ for any $y > 0$. Hence, the predator’s best value of U lies in $[-1, 0]$ and not in $(0, 1]$. This makes intuitive sense, as it never pays the predator to delay attacking until a point when it is further away from the prey than when it originally spotted it. It is also clear that $f[d(0)] > f[d(x)]$ for all $x \in [U, 0)$, and since the prey will not flee unless the predator attacks, $P(U, N)$ is less than $P(0, N)$ for any $U < 0$. Thus, the predator maximizes its payoff by playing strategy $U = 0$. Since the predator’s strategy does not matter when the prey plays strategy -1 , then under all circumstances the predator should play strategy 0. That is, the predator should delay attacking until the point of closest approach if it detects

the prey while the distance between prey and predator is still declining. However, if the prey is detected after the point of minimum separation, then an attack should be launched as soon as the prey is detected. The payoff to the prey when the predator plays this strategy is simply obtained by substituting the appropriate strategy into the general expression of Equation 14, giving either

$$R(N, 0) = A(0)(1 - c)\{1 - f[d(0)]\} + \int_0^1 (1 - c) \times \{1 - f[d(v)]\} \left[\frac{dA(v)}{dv} \right] dv + [1 - A(1)] \tag{17}$$

if it plays strategy N or

$$R(-1, 0) = (1 - c)[1 - f(r + \Delta)] \tag{18}$$

if it plays strategy -1 . Hence, the prey should flee immediately on detecting the predator if $R(-1, 0) > R(N, 0)$ or only flee if attacked otherwise. Which of these situations occurs depends on the specific functional forms and parameter values chosen.

Case 3

Similar to Case 2, but the predator cannot detect prey after it passes the point of closest approach (i.e., it cannot see behind it).

From consideration of the way we developed our arguments in Case 2, it is clear that these arguments apply in almost unchanged form to Case 3. Specifically, the argument for why the predator should adopt strategy 0 remains unchanged, as does the argument for why the prey should adopt either strategy N or -1 . As before, in order to evaluate which of these is optimal, the payoffs must be compared.

$R(-1, 0)$ is unchanged from Case 2, but consideration of the structure of Equation 17 shows that $R(N, 0)$ simplifies to

$$R(N, 0) = A(0)(1 - c)\{1 - f[d(0)]\} + [1 - A(0)]. \tag{19}$$

The prey should adopt strategy -1 when $R(-1, 0) > R(N, 0)$. Using Expressions 18 and 19 and rearranging the resultant inequality gives this condition as

$$1 - A(0) < \frac{f[d(0)] - f(r + \Delta)}{f[d(0)] + \frac{c}{1-c}}. \tag{20}$$

An example situation with specific functional forms for f and g

We will now introduce specific functional forms into the general Case 3. Specifically, we will assume that the probability of an attack being successful declines exponentially with distance between predator and prey at the point when the predator begins its attack: that is,

$$f(d) = \alpha \exp(-\beta d), \tag{21}$$

for positive constants α and β . We also need to specify the probability per unit time of detecting the prey a distance d away. This too should decline with distance, and we adopt the form

$$g(d) = \frac{a}{d^2}, \tag{22}$$

for positive constant a . With these two functional forms, the encounter is exactly specified by the values given to $r, \theta, \Delta, c, s, \alpha, \beta$.

Using Equations 2 and 6 together with the standard integral

$$\int \frac{dx}{x^2 + a^2} = \frac{1}{a} \tan^{-1}\left(\frac{x}{a}\right) \tag{23}$$

and the identity

$$\tan^{-1}\left(\frac{-1}{\tan \theta}\right) = \theta - \frac{\pi}{2}, \quad (24)$$

we can obtain a simple expression for the left-hand side (LHS) of Equation 20

$$1 - A(0) = \exp\left[-\left(\frac{a}{sr \sin \theta}\right)\left(\frac{\pi}{2} - \theta\right)\right]. \quad (25)$$

The right-hand side (RHS) can also be simplified. First, we note that $d(0) = r \sin \theta$, then using Equation 21 we obtain

$$\frac{f[d(0)] - f(r + \Delta)}{f[d(0)] + \frac{c}{1-c}} = \frac{1 - \exp[-\beta(r + \Delta - r \sin \theta)]}{1 + \left[\frac{c}{\alpha(1-c)}\right] \exp(\beta r \sin \theta)}, \quad (26)$$

so the condition for prey to adopt strategy -1 is

$$\exp\left[-\left(\frac{a}{sr \sin \theta}\right)\left(\frac{\pi}{2} - \theta\right)\right] < \frac{1 - \exp[-\beta(r + \Delta - r \sin \theta)]}{1 + \left[\frac{c}{\alpha(1-c)}\right] \exp(\beta r \sin \theta)}. \quad (27)$$

If Equation 27 is not satisfied, then strategy N should be adopted. If $\theta = 0$, then the predator is heading directly for the prey, and in this case, the best strategy is to flee immediately (strategy -1) since the predator will ultimately discover the prey. In the opposite extreme case where $\theta = \pi/2$ N is the best strategy as the predator immediately leaves the interaction circle of radius r and disappears out of the prey's visual range. Notice also that the LHS of Equation 27 increases with increasing θ , and the RHS decreases with increasing θ . Hence, for all combinations of parameter values there exists a range of initial angles $[0, \phi]$ for which -1 is the best prey strategy and a range of angles $[\phi, \pi/2]$ for which N is the best strategy. This critical angle ϕ is given by

$$\exp\left[-\left(\frac{a}{sr \sin \phi}\right)\left(\frac{\pi}{2} - \phi\right)\right] = \frac{1 - \exp[-\beta(r + \Delta - r \sin \phi)]}{1 + \left[\frac{c}{\alpha(1-c)}\right] \exp(\beta r \sin \phi)}. \quad (28)$$

Consider the effect of increasing the value of ϕ in Equation 28. On the LHS, increasing ϕ decreases the magnitude of the argument of the negative exponential and so increases the magnitude of the term on the LHS of the equality. In contrast, increasing ϕ can be seen to decrease the magnitude of the RHS of the equality. Thus, if we increased ϕ alone, then the equality would break down unless we alter the value of another parameter to increase the magnitude of the RHS, decrease the magnitude of the LHS, or both. Decreasing s can be seen to act to increase the magnitude of the LHS, and so we can deduce that (quite generally, regardless of the values attached to other parameters) decreasing the predator's speed of movement while searching (s) acts to increase the attractiveness of running as soon as the predator becomes visible (increasing ϕ). By similar reasoning, increasing ϕ and so increasing attractiveness of the strategy of running as soon as the predator becomes visible is associated with a low nonpredation cost to running (small c), a large advantage to the prey in initiating chases rather than reacting (large Δ), limited ability to spot the predator at distance (low r), a high ability to spot prey by the predator (high a), and a high probability that chases will be successful (large α). All these relationships make intuitive sense except perhaps the nature of the association between ϕ and α . It might initially appear that if chases are very likely to end in success for the predator, then the prey might be better to sit tight and hope that it is not detected. However, this does not occur because α is a multiplicative constant and increasing α increases the

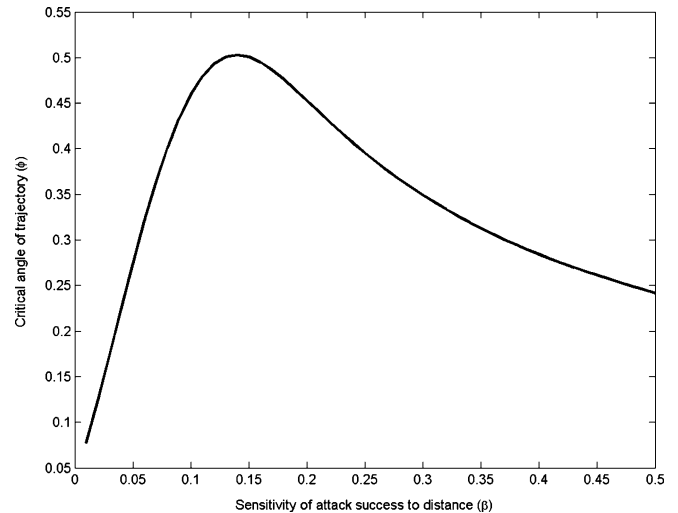


Figure 2

The critical value of trajectory angle (ϕ)—calculated from Equation 28—as a function of the sensitivity of attack success to distance between predator and prey (β). For angles below this critical angle, the prey should play strategy -1 and run immediately on detecting the predator; for angles above this, it should play strategy N and only flee if attacked. (Other parameters, as defined in Table 1, are given the following values $a = 2$, $s = 1$, $r = 30$, $\Delta = 5$, $c = 0.01$, and $\alpha = 0.8$.)

probability of being caught at all distances by an equal multiple. In fact, the strategy would be independent of α were it not for the small cost of running (c). When α is low, the strategy of not running unless attacked becomes more attractive because this gives the prey the chance to save the cost c (if it is not detected) for very little increase in its risk of being captured. In fact, it is β which governs the relative risk in running early or late. The relationship between ϕ and β is nonmonotonic (see Figure 2). When β is very low, running as soon as the predator is sighted becomes less attractive because there is little advantage to be gained from initiating a chase compared to responding only to an attack (i.e., the effect of Δ is small) and the risk of an attack is relatively insensitive to changing d if the predator is allowed to approach. At very high β values, the predator must get very close to the prey before initiating an attack to have a substantial change of success and so fleeing when the predator is first spotted becomes less attractive unless the trajectory of the predator will bring it very close. Hence, there is an intermediate value of β that maximizes ϕ (see Figure 2).

DISCUSSION

Model predictions

We have demonstrated that the optimal strategy for the prey is either to run immediately on seeing the predator or never to initiate a chase but only to run when the predator initiates an attack. This occurs because, unlike the case in the model of Ydenberg and Dill (1986), there is no advantage to delaying fleeing so as to gain a little more time for some activity such as feeding; hence, if the prey is going to flee of its own volition, it should do so as soon as possible. We further demonstrate that this holds true whether the predator attacks immediately on discovering the prey or whether the predator hides the fact that it has discovered the prey and delays its attack until it has closed the distance to the prey. The optimal strategy for the predator depends on whether its current trajectory is taking it closer to or further from the prey. In the latter case, the

predator should attack immediately on discovering the prey; in the former case, it should delay its attack until it reaches the point on its current trajectory where distance to the prey is minimized. Interestingly, this is the best strategy even though delay appears to give the prey the opportunity of gaining advantage by fleeing of its own volition before the attack occurs. In fact, it is never optimal for the prey to do this; as discussed above, it is never optimal for the prey to flee of its own volition except when it initially detects the predator (which is always before the predator has detected the prey in our model). Running as soon as the predator becomes visible is associated with low predator search speeds, a low non-predation cost to running, a large advantage to the prey in initiating chases rather than reacting, limited ability by the prey to spot the predator at distance, a high ability to spot prey by the predator, and a high probability that chases will be successful.

Testing theoretical predictions

Detection of fleeing and of change in the behavior of the predator (specifically, initiating an attack) should be relatively easy from a videotape of predator-prey interactions, but we note that obtaining such data on naturally occurring predation events is logistically challenging, although not impossible (e.g., Caro, 1995; Fitzgibbon and Fanshawe, 1988). Much more challenging methodologically will be to detect when a prey individual has become aware of the presence of a nearby predator, but this may be revealed by an alert posture, changes to vigilance patterns, measurable neurophysiological responses such as heart rate, or even by calls to conspecifics (e.g., Brown et al., 1999; Caro et al., 1995; Gabrielsen et al., 1977; Holley, 1993; Leal and Rodriguez-Robles, 1997).

Our model makes testable predictions about predator behavior. When a predator can disguise from a prey individual that it has detected the position of that prey individual, then we predict that predators moving on a trajectory that will bring them closer to the prey should delay attacking until they reach the point of closest approach to the prey. If anything, it will be more methodologically challenging for a scientist to detect when a predator has detected a prey item than vice versa if the predator seeks to avoid altering its behavior in a way that would reveal its state of awareness to the prey. However, our prediction can be explored indirectly, as we predict that attacks are more likely to occur when the predator is moving away from the prey (v values near 1 in the model) than when the predator is the same distance away but moving toward the prey (v values around -1).

The model makes a further set of predictions about prey behavior. Specifically, it predicts that two strategies may be observed: either fleeing immediately when the predator is detected (and before the predator has detected the prey) or only fleeing in response to a direct attack by the predator (i.e., on receiving confirmation that the predator has detected it). The frequency with which one strategy or the other should be used depends on a range of different environmental circumstances. The strategy of fleeing as soon as the predator becomes visible is associated with slow predator search speed, a low nonpredation cost to running, a large advantage to the prey in initiating chases rather than reacting, limited ability to spot the predator at distance, a high ability to spot prey by the predator, and a high probability that chases will be successful. These predictions should be amenable to empirical testing either by comparative analysis or by manipulation of the environment.

Because of the general unpredictability of naturally occurring predation events, both in space and in time, there is an obvious attraction to staging predation events in the

laboratory. There are clearly ethical issues with such experiments, but our predictions about optimal prey behavior may be effectively studied using a model predator. Small riverine fish, such as sticklebacks and minnows, that commonly use both hiding in available cover and fleeing as ways of evading predation may be a good system for empirical testing of the predictions of our model. Perhaps, a model predatory fish moving along a wire could be used as the "predatory" stimulus. Our model predicts that fish that are to some extent cryptic should flee only when they first detect the predator; otherwise they should maximize their crypsis. The prey fish could be provided with a clump of weed in the experimental arena to provide opportunity for crypsis. The point when the predator can first be detected can be modified by use of opaque barriers in the arena. We would expect that non-fleeing fish that have detected the model predator will still change their behavior, perhaps by moving further into the weed cover or by freezing. We can also manipulate factors predicted to influence the attractiveness of fleeing. Particularly easy to manipulate in this putative experimental system would be the speed of the searching predator (s in the model) and the maximum distance at which prey can detect the predator (r in the model).

Other issues

Although the cost of fleeing considered here and that considered by Ydenberg and Dill (1986) are not mutually exclusive, we can make the following general predictions about the relative importance of the two costs in different ecological circumstances. If the prey is particularly obvious such that predators can see them from a considerable distance (e.g., an adult zebra grazing on the Savannah during the day), then the Ydenberg and Dill (1986) model will be more appropriate. Whereas, if the prey is cryptic such that predators can pass reasonably close to it without detecting it (e.g., a juvenile gazelle lying motionless in long grass), then our model should be more appropriate. Further, if attempted predation is a frequent event, such that costs of flight are significant to the daily energy or time budget of the prey, then the Ydenberg and Dill (1986) model will be more appropriate; whereas, if predation attempts happen relatively infrequently to a prey individual (such that avoiding predation makes up a small part of an animal's time or energy budget), then our model should be more relevant. If fleeing causes the predator to lose a food item that it has invested time in acquiring (e.g., a cheetah being driven from a kill by approaching lions), then Ydenberg and Dill's model is more relevant. Whereas, if the animal can quickly return to its previous feeding behavior as soon as the predator has passed (e.g., many grazers), then our model may be more relevant. These yardsticks should be open to empirical testing, since the two models make clearly different predictions. Specifically, our model predicts that (when searching predators never spontaneously change direction or do so sufficiently rarely that this situation can be ignored) prey will only flee from a predator (initiating a chase) at the point when they first detect a predator; if they do not flee at that point, then they will only break cover and run at some later point in response to an attack by the predator. Conversely, the Ydenberg and Dill model suggests that fleeing may not necessarily occur when the predator is first detected (in agreement with our model) but may occur at some subsequent point even if the predator does not initiate an attack (unlike our model). Hence, predicting which model appears to fit a particular ecological situation amounts to determining whether prey delay fleeing after detection of a predator and then subsequently flee at some later point not triggered by a change in the behavior of the predator. If such

a delay is commonplace, then this fits with the predictions of Ydenberg and Dill; if such delays are not observed, this is more in accord with our model.

The general model presented here should also provide the theoretical framework for interpreting the evolution of fleeing behavior in the wide range of ecological situations where a searching predator approaches hiding prey. Further, much of the methodology should be easily applicable to the reverse situation: where a prey individual unwittingly approaches a hidden predator waiting in ambush. Exploration of this situation should yield predictions about when the predator should break cover and attack the prey.

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