

Lunch on the Run

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Introduction

We devised two different models for this pursuit: a purely mathematical model, and a computer model. Both models use the following assumptions:

- All animals are represented as points at their respective centers of mass.
- The simulations and chase both begin when the predator, slowly sneaking up on the prey, is spotted by the prey.
- The chase lasts 15 s or until the prey is killed, whichever occurs first.
- No animal may travel at more than its specified maximum speed.
- Each time that the distance from the prey to the predator is at a local minimum, the prey takes a chance of being killed.

Table 1 summarizes notation used in the paper.

Introduction to the Mathematical Model

The mathematical model also assumes that it takes negligible time to start and stop moving but that the turning radius imposes a maximum angular velocity. This assumption makes the analysis possible without a computer but neglects the finite acceleration capability of real animals. This model can analyze only the one predator/one prey situation; it works quickly and well.

We analyze two predator strategies and one prey strategy. The prey strategy is to run directly away from the predator until the predator gets closer than

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some critical distance, then make a sharp turn to the left or right. The prey can just squeak by the predator, whose larger turning radius makes it lose a few meters. The predator strategies considered were the hungry predator, who always heads straight for the current location of the prey if possible, and the maximal-turning predator, who uses knowledge of the prey's strategy to turn more sharply than the hungry predator in an effort to cut off the prey.

We calculate the probability of the prey's survival, given parameters about the predator and prey paths and the distribution of initial separations.

Introduction to the Computer Model

We use an iterative algorithm to figure out where the predators and prey go and which prey survive. By running several thousand 15-s scenarios, we determined how survival rates change depending on predator strategy, prey strategy, initial separation, the elevation and terrain, animal reaction times, and so on.

The computer model supports n predators chasing m prey across any terrain. It takes into account acceleration/deceleration, reaction times, two predator strategies, and three prey strategies. Written in C++ and running on a PowerPC 604-based 132 mHz workstation, the program can calculate 600 15-s scenarios using a 1-ms timestep in 1 min.

Non-Chasing Phases of the Hunting

Locating Prey

Thescelosaurus is similar in size to *Velociraptor*, so a single kill would provide the predator with sufficient meat for several meals; *Velociraptor* need bring down only one victim every few days. Assuming that each predator-prey interaction is independent, the number of chases required to kill one animal has a geometric distribution with parameter $1 - P$, the probability of a kill on one chase. Thus the expected number of chases per kill is $1/(1 - P)$, with variance $P/(1 - P)^2$. Assuming a typical value for $P = 0.3$, the predator usually succeeds on the first or second attempt. More than four chases will be required only 1% of the time.

Stalking

A predator, having discovered prey as yet unaware of the predator's presence, normally attempts to approach the prey stealthily, in an effort to reduce the length of the inevitable high-speed chase. Likewise, the prey normally attempts to be vigilant, making it difficult for the predator to approach unnoticed.

Table 1.
Notation.

(x_1, y_1)	location of the predator, <i>Velociraptor mongoliensis</i>
(x_2, y_2)	location of the prey, <i>Thescelosaurus neglectus</i>
v_1	speed of the predator; usually 50/3 m/s, or 60 km/h
v_2	speed of the prey; usually 125/9 m/s, or 50 km/h
r_1	full-speed turning radius of the predator; usually 3/2 m
r_2	full-speed turning radius of the prey; usually 1/2 m
$r_v = v_1/(v_1 - v_2)$	ratio of predator speed to closing speed, i.e., how far the predator must run in a straight-line chase to get 1 m closer to the prey; usually 6
θ_1	orientation of the predator, in radians
θ_2	orientation of the prey, in radians
t	time
t_{\max}	maximum chase duration (running time for the predator); usually 15 s
h_I	separation of predator and prey at the beginning of the chase
h_B	separation of predator and prey when the prey attempts to break away by turning
$d_I = r_v(h_I - h_B)$	distance traveled by predator during initial straight-line pursuit
d_B	distance traveled by predator during the prey's breakaway maneuver
d_G	distance traveled by predator to regain ground lost during a successful breakaway maneuver by the prey
$S_i(d)$	closest approach of predator and prey during the first d meters traveled by the predator during the i th phase of the chase ($i = 1$: initial straight pursuit; $i = 2$: breakaway maneuver; $i = 3$: catch-up pursuit following successful breakaway)
$p_S(S)$	probability that the prey survives one close approach to the predator, during which its closest approach to the predator is S
$p_H(h_I)$	probability that the prey survives a complete attack, given initial separation h_I
$f(h_I)$	probability density function for the initial separation of predator and prey
a, b	shape and scale parameters for a gamma distribution
ν, ω	shape parameters for a beta distribution
P	probability of prey surviving a typical attack

Neither of these behaviors appears explicitly in our models. Instead, our models calculate $p_H(h_I)$, the conditional probability of the prey's survival, given the separation at the start of the chase, and combine p_H with $f(h_I)$, the probability density function for the initial separation. We account for the stealth of the predator and the vigilance of the prey by our choice of f . The more attentive the prey, the higher the mean of f ; the more stealthy the predator, the lower the mean. We model f using gamma and beta distributions, whose parameters can be altered easily to reflect conditions.

Analytic Model for Trajectory Selection

Model Development

The problem statement does not specify the acceleration capabilities of predator or prey, but it does specify turning radii (which, considering the speeds involved, are perhaps too small). We choose to permit infinite acceleration, i.e.,

at any given time, each animal may select any speed between zero and its maximum speed. However, to preserve the turning-radius limitations, we also introduce a maximum angular velocity.

The maximum angular velocity is calculated from the maximum speed and minimum turning radius. Given a speed v and radius r , turning $180^\circ = \pi$ radians requires traveling πr m, which can be done in $\pi r/v$ s. Thus, we obtain

$$\left| \frac{d\theta}{dt} \right|_{\max} = \frac{v}{r},$$

which, using the constraints in the problem, results in maximum angular velocities of $100/9$ rad/s for *Velociraptor* and $250/9$ rad/s for *Thescelosaurus*.

Further, we assume that the predator begins running directly toward the prey and the prey begins running directly away from the predator.

The pursuit and evasion strategies consist of recipes for choosing new angular and linear velocities, given current positions and velocities.

Strategy for Predator and Prey Far Apart

If the predator is sufficiently far away, since the predator tires quickly, the prey can escape by simply outrunning the predator. In general, this is possible when $v_1 t < v_2 t_{\max} + h_I$, or, rearranging terms, when $h_I > (v_1 - v_2)t_{\max}$. In the situation of the problem statement, $(v_1 - v_2)t_{\max} = 125/3$ m.

If the predator and prey are closer than $(v_1 - v_2)t_{\max}$ meters, but the separation is still large in comparison to the turning radii, then neither predator nor prey gains any benefit from being the first to deviate from a straight path. If the predator turns, it increases the minimum path length required to catch up to prey moving straight ahead. In addition, when the prey sees the predator turn one way, the prey can respond by turning in the opposite direction, further increasing the separation between them. Similarly, if the prey deviates from its straight course, it is inviting the predator to turn in the same direction; the predator's arc will lie inside the prey's, meaning that the prey has unnecessarily helped the predator to catch up.

Strategy When Predator and Prey Are Near

If the prey is close to the predator, a sharp turn by the prey may enable it to reach a "safe zone" that the predator—faster, but handicapped with a wider turning radius—cannot enter without stopping and turning around.

Since the prey's goal is to reach the "safe zone" while giving the predator a minimum amount of time to respond, the prey should always make a minimum-radius turn. But when is the ideal moment to make the turn? If the prey turns while the separation is still wide, it will run into the waiting jaws of the predator; if it waits too long, it may be within the predator's grasp before

the turnaround maneuver is complete. The answer depends on what strategy the predator uses to respond to the prey's sharp turn, which depends on how much the predator knows about the prey's intentions.

If the predator turns itself around and catches up to the prey again, a second breakaway maneuver may be necessary, then a third, and so on. Even if the idealized "point animals" never touch other, the breakaway maneuver is not risk-free. We assign the prey a probability of surviving each breakaway, which depends on the closest approach distance.

By computing $d[(x_1 - x_2)^2 + (y_1 - y_2)^2]/dt$ and seeing how it depends on dx_1/dt and dy_1/dt , we learn that the predator should continue moving forward only if the prey is in front of, rather than behind or directly alongside, the predator. Computationally, this amounts to finding the angle between the predator's course and the azimuth from predator to prey:

$$\text{Move forward if } \left| \theta_1 - \tan^{-1} \left(\frac{y_2 - y_1}{x_2 - x_1} \right) \right| < \frac{\pi}{2},$$

with the minor caveat that it may be necessary to add 2π to or subtract 2π from θ_1 to ensure that θ_1 and the calculated (normally the principal) inverse tangent differ by π or less. This decision procedure tells the predator only *if* it should move forward, not *how fast*; it is often not always best for the predator to travel at top speed.

For a predator always running at top speed, it is not particularly difficult to compute the locus of all paths that it can follow in a given time. For a predator with speed v and turning radius r at the origin, initially moving along the y -axis, the region is bounded by three curves: the two circles of radius r centered at $(\pm r, 0)$ and the arc described by the parametric equations

$$x = \pm r \left[1 - \cos u + \left(\frac{vt_{\max}}{r} - u \right) \sin u \right], \quad y = \pm r \left[\sin u + \left(\frac{vt_{\max}}{r} - u \right) \cos u \right]$$

for $u \in [0, vt/r]$. The resulting mushroom-shaped region is shown in **Figure 1**. The problem is isomorphic to the familiar geometric problem of a swinging rope hanging between two tangent circles and closely related to the swinging rope hanging from the cusp of a cycloid (i.e., a pendulum of uniform period). These problems are considered in various common references, such as Wells [1991].

For the parameter values of the problem statement, the prey can always get outside of this locus by executing a sharp turn, provided the prey is less than about 1.57 m away. (We conjecture that the condition is $h_B < \pi/2$, but we did not have the time to prove it.)

The Hungry Strategy

"Run directly toward the prey, if possible; if not, turn to face the prey, moving in its general direction if possible." This type of strategy is traditionally called

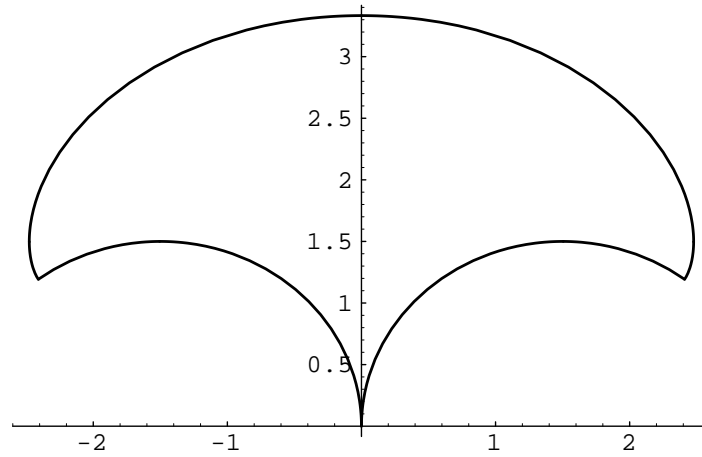


Figure 1. Locus of predator's paths 0.2 s after breakaway.

a “greedy algorithm”; in the context of this problem, “hungry” seems a more evocative name.

For the predator to select an angular velocity, it needs to know how the angle between his course and the prey's position is changing. This amounts to calculating the derivative of $\tan^{-1}[(y_1 - y_2)/(x_1 - x_2)]$, which is

$$\frac{y_2 - y_1}{(x_2 - x_1)^2 + (y_2 - y_1)^2} \left(\frac{\partial x_2}{\partial t} - \frac{\partial x_1}{\partial t} \right) - \frac{x_2 - x_1}{(x_2 - x_1)^2 + (y_2 - y_1)^2} \left(\frac{\partial y_2}{\partial t} - \frac{\partial y_1}{\partial t} \right),$$

where

$$\frac{\partial x_i}{\partial t} = v_i \cos \theta_i, \quad \frac{\partial y_i}{\partial t} = v_i \sin \theta_i.$$

Note that all quantities in this formula— x_1 , x_2 , y_1 , y_2 , v_1 , v_2 , θ_1 , and θ_2 —are assumed known to both animals at all times. In our basic hungry algorithm, the predator charges ahead at full speed all the time (which turns out to be slightly wasteful in certain situations.)

A computer simulation plotted paths resulting from a hungry predator pursuing prey that executed a breakaway maneuver at arbitrary distance h_B from the predator. The ideal moment for the prey to begin turning is when predator and prey are 1.62 m apart; this guarantees that the predator and prey never come nearer to one another than 0.88 m. The predator runs 1.94 m before the hungry algorithm demands that it stop. (Note the inefficiency of the predator's course; it was shown above that for $h_B > 1.57$ m, there is a predator path that prevents the prey's escape.)

Following the breakaway maneuver, the prey is standing very close to, but slightly behind, the predator. At this point, the prey's greater maneuverability is sufficient to prevent the predator from turning around to face the prey. Unable to move toward the prey until facing toward it, the predator will come to a halt and rotate in place. We assumed that time spent rotating but not moving forward does not count in the predator's 15-s allotment.

Given the predator's angular velocity limit of $100/9$ rad/s, the prey can retreat to a distance of 1.25 m from the predator (the greatest radius at which a speed of $125/9$ m/s and an angular velocity of at least $100/9$ rad/s are compatible) and still prevent the predator from turning around.

The prey neither gains nor loses by remaining at the 1.25 m distance; since the prey can't run in a circle forever, eventually it has to make a break for it again. We could not determine analytically the precise distance that the prey could travel before the predator catches up and forces another breakaway attempt.

If the prey begins to run directly away from the predator instead of circling, the predator has to run about 14 m under the strict greedy algorithm to force another breakaway maneuver. By turning in place a while longer, a smarter predator could cut this down to just under 12 m.

Alternatively, the prey could simply begin to run in a straight line. The hungry predator then requires about 15 m to catch up. By turning in place longer, the predator can reduce this to 13 m. Experimentation indicates that an optimal run-at-full-speed strategy is unlikely to change these numbers significantly.

The distances ($h_B = 1.62$ m, $d_B = 1.94$ m, $d_G \approx 14$ m, $S(d_B) = 0.88$ m) are used in a statistical procedure, described later, that uses the probability density of h_I to calculate the prey's chance of surviving for 15 s. The procedure returned survival probabilities of $P = 0.20$ for a reference beta density, $P = 0.28$ for a reference gamma density, $P = 0.44$ for a modified beta density, and $P = 0.43$ for a modified gamma density.

A numerical model discussed later implements a similar greedy algorithm. The results of that algorithm were qualitatively similar, though the exact distances, turning points, and so on were slightly different.

The Maximal Turn Strategy

The hungry strategy is a good all-around strategy for a predator that does not know what its prey is likely to do next. However, an intelligent predator might notice that, once the prey has begun its tight circle, it plans to continue circling tightly. This more intelligent predator, rather than aiming at the prey, might respond by turning in the same direction, as sharply as possible, in an effort to cut off the prey's anticipated escape.

Suppose the predator is at the origin, running along the y -axis, and the prey is at $(0, h_B)$, also running along the y -axis, when the prey initiates a breakaway maneuver. If the predator responds by simultaneously making a minimum-radius turn in the same direction, then the paths of predator and prey are given by the following parametric equations:

$$\begin{aligned} x_1 &= r_1 \left[1 - \cos \left(\frac{v_1 t}{r_1} \right) \right], & y_1 &= r_1 \sin \left(\frac{v_1 t}{r_1} \right) \\ x_2 &= r_2 \left[1 - \cos \left(\frac{v_2 t}{r_2} \right) \right], & y_2 &= h_B + r_2 \sin \left(\frac{v_2 t}{r_2} \right). \end{aligned}$$

With the aid of a Mathematica-type application or a simple program, it is quite simple to calculate $\min\{(x_1 - x_2)^2 + (y_1 - y_2)^2\}$. This figure represents the closest approach of predator to prey during the breakaway. The prey's survival depends on choosing an optimal breakaway time, i.e., the optimal h_B is given by $\arg \max\{\min\{(x_1 - x_2)^2 + (y_1 - y_2)^2\}, h_B\}$, which comes to $h_B = 0.66$ m, $d_B = 1.52$ m, $S(d_B) = 0.25$ m. This indicates that the prey stands a much smaller chance of surviving a single encounter with this more intelligent predator. Should it survive one breakaway maneuver, the earlier remarks about circling at 1.25 m and attempting to flee apply almost unchanged; we have $d_G \approx 14$ m for this case also. The calculated survival probabilities were $P = 0.03$ for the reference beta distribution, $P = 0.15$ for the reference gamma distribution, $P = 0.21$ for the modified beta distribution, and $P = 0.29$ for the modified gamma distribution.

A Refined Trajectory Model

It is sometimes right for the predator not to run at full speed. Neither the hungry nor the maximal-turn strategies are optimal—the predator does better by turning in the same direction as the prey and simultaneously slowing down. This prevents the prey from exploiting the time during which the prey and predator are running in opposite directions on a non-collision course.

Can such a strategy be determined? Doing so requires an algorithm for minimizing travel time given initial position, initial velocity, and final position, subject to the constraints that $v(t) \leq v_1$ and $|d\theta_1/dt| \leq v_1/r_1$. Then we must determine what point along the prey's circular path is the best destination, with the prey trying to maximize, and the predator trying to minimize, the closest-approach distance. We could not solve this problem analytically nor implement a good numeric approximation, so it is probably unrealistic to expect a Cretaceous dinosaur to calculate the solution in its head instantaneously. So this ideal strategy, though of theoretical interest, likely would not be usable.

Flaws of the Analytic Approach

The ability of both dinosaurs to select any speed they wish, that is, to be capable of brief bursts of essentially infinite acceleration, is unrealistic. Neither animal can leap into the chase at full speed or stop on a dime. The predator has to waste some time running in the wrong direction if the prey survives a breakaway. The effect is that d_G , in a practical sense, will always be in the 20–25 m range, not 14 m as proposed above. The prey's survival probability is correspondingly higher. **Table 2** gives P for both the hungry and maximal-turn strategies, recalculated using $d_G = 22$ m. The results agree more closely with the computer simulations than do the earlier numbers for 14 m.

Table 2.
Survival rates with revised d_G .

Distribution	P for hungry strategy	P for maximal-turn strategy
Reference beta	.38	.03
Reference gamma	.35	.15
Modified beta	.51	.21
Modified gamma	.49	.29

Effect of Changing Minimum Turning Radii

Extreme forces are involved in the sharp high-speed turns that we have discussed. Doubling the turning radius of each species would halve the force that each animal would need, increasing the realism of the scenario. The shape of all trajectories would remain unchanged but the scale would be doubled. This increase in realism would greatly improve the prey's chances: The closest approaches would be 1.76 m and 0.50 m, resulting in much lower death rates than the current 0.88 m and 0.25 m. Similarly, d_I would remain unchanged, but d_B and d_G would be doubled, which would substantially reduce the number of breakaway cycles that prey would have to endure to survive a 15-s chase. **Table 3** gives P , recalculated using the doubled values, including $d_G = 44$ m.

Table 3.
Survival rates with doubled turning radii.

Distribution	P for hungry strategy	P for maximal-turn strategy
Reference beta	.84	.08
Reference gamma	.94	.19
Modified beta	.95	.27
Modified gamma	.95	.33

Implications

When the prey is forced to pass very close to the predator to break away, its chance of surviving a single breakaway maneuver is very low, and the chance of surviving two or more such turns is virtually nil. In this case, the probability of survival is essentially equal to the probability of spotting the predator at a distance of 125/3 or more meters. Thus, increased vigilance of the prey would be expected to carry a strong evolutionary reward. On the other hand, if the prey can escape easily during a breakaway cycle (e.g., hungry predator and doubled radii), the predator is exerting minimal selection pressure against inattentive prey.

Comparing our calculated probabilities with a subjective assessment of the survival rates of modern prey, it seems that the hungry strategy with tight turning radii, and the maximal-turn strategy with doubled radii, yield the

most plausible results. This seems reasonable: The strategies involved are simple and “obvious” enough that moderately intelligent animals could probably implement them.

Converting Trajectory Descriptions to Survival Probabilities

Overview of Procedure

The trajectories produced by all of our models have some common structural features. In particular, the trajectories can be divided into three phases:

- The first phase is a straight-run segment, during which the predator gains on, but is virtually never able to kill, the prey.
- The second phase is the breakaway maneuver, during which the prey makes its closest approach to the predator and runs a significant risk of being killed.
- The third phase is a brief period of almost-straight chasing as the predator attempts to reclaim the distance the prey gained via a successful breakaway.

Each trajectory, regardless of the model that produced it, begins in phase one, then alternates between phases two and three for the remainder of its length. Within a given trajectory, all complete phase-two episodes will be the same length, as will all complete phase-three episodes. The final segment, during which the predator’s allotted time expires, will of course be incomplete.

We assume that the prey has a nonzero chance of being killed each time the distance between predator and prey reaches a minimum. We model the chance of survival of each encounter as a function of minimum separation, p_S . The probability of the prey surviving the entire 15-s encounter depends primarily on the number of close encounters, i.e., the number of times the prey must attempt the breakaway maneuver. This number depends on two things. The first is the length of the phase-two and phase-three episodes. This depends only on the model design; we calculated these lengths for each model we subjected to the statistical procedure. The second factor is the length of the initial sprint. This depends on the optimal breakaway separation h_B , which depends on model design, and on the separation at the beginning of the chase, h_I . It is thus possible to plot p_H as a function of h_I .

The initial separation will be different every time the predator goes hunting. Initial separation is influenced by terrain and vegetation, visibility conditions, the alertness of the prey, the stealth of the predator, and countless other factors. Rather than trying to account explicitly for the effect of each factor, we opt instead to treat h_I as a random variable, the shape of the probability density function being chosen based on these factors. Generally speaking, bare ground, good lighting, and attentive prey cause the mean of $f(h_I)$ to be high, while

obstacles, fog, darkness, or particularly stealthy stalking on the predator's part cause the mean of $f(h_I)$ to be low. In addition, the problem statement proposed 15 m and 50 m as minimum and maximum values for h_I .

Once a distribution of h_I has been selected, we can use $p_H(h_I)$ and $f(h_I)$ together to determine P , the probability that prey survive a 15-s attack, given the conditions specified by model design, the choice of p_S , and the choice of f .

Method of Computing P

Three numbers and one function, based on the model design, are required for the computation of P . The three numbers are

- h_B , the optimal separation for attempting the breakaway maneuver;
- d_B , the distance traveled by the predator during a breakaway attempt; and
- d_G , the distance traveled by the predator while regaining ground lost during a successful breakaway.

The function $S(d)$ is the minimum separation during the first d meters traveled by a predator during a phase. During phase one, the function $S_1(d)$ is linear; during phase two, $S_2(d)$ decreases rapidly in a complicated way to a minimum value; that minimum value is characteristic of the model design. The definition of $S_3(d)$ is slightly different, since phase three begins with the prey close to but behind the predator, out of harm's way. The separation rapidly increases to a maximum, then drops approximately linearly as the predator catches back up to the prey, following an ever-straighter path. We define $S_3(d)$ as the minimum separation after maximum separation has already been reached, but infinite before that time. (Some of the path-determining models assume that, immediately after a successful breakaway, the prey can briefly move about in perfect safety.) For the purposes of computing p_H and P , S_2 is the only function of real interest, since the prey has virtually no chance of dying unless S is small.

It is necessary to choose a function p_S that relates the minimum separation to the prey's probability of surviving a close encounter with the predator. The choice of this function is arbitrary, subject to some obvious constraints:

- $p_S(0) = 0$: If the predator and prey actually contact each other, the prey will surely be killed. (Actually, one could realistically let $p_S(0)$ be a small positive number; it is plausible that the prey still has a slight chance of surviving a direct assault by the predator.)
- $p_S(x) \rightarrow 1$ as $x \rightarrow \infty$: If the predator never comes close to the prey, the prey clearly will survive.
- $\frac{dp_S(x)}{dx} \geq 0$: It is always safer to be farther away from the predator.

Velociraptor's most potent weapon was the large claw on each foot, and its legs were approximately 0.5 m long. Its mouth and forearms posed a significant but much smaller danger to the prey [Sattler 1983]. On the basis of these facts, it seems reasonable that the prey is in great danger if it is within one leg length (0.5 m). A distance of two leg lengths (1 m) ought to bring safety from the claws but not from the jaw. At distances significantly greater than 1 m, the danger should be negligible. We decided that $p_S(1) = 0.8$ seemed like a reasonable figure. For general distance x , we use

$$p_S(x) = \left(1 - \frac{1}{1 + 4x^4}\right) = \frac{4x^4}{1 + 4x^4},$$

though any of several other S-shaped functions would serve as well.

Calculating p_H as a function of h_I is the most complex portion of the computation of P . The function is piecewise defined. Letting

$$d_I = \left(\frac{v_1}{v_1 - v_2}\right) h_I,$$

we treat the three phases of the trajectory separately, saving phase two for last because it is computationally most difficult.

Phase One: If $d_I \geq v_1 t_{\max}$, then $p_S(h_I) = p_S(h_I - (v_1 - v_2)t_{\max})$.

If the prey is able to outrun the predator, then the closest approach of predator and prey occurs at time t_{\max} , when the predator is forced to abandon the chase. Unless the prey was about to make its first breakaway attempt, probability of survival is essentially 1. On **Figure 2**, this phase produces a long plateau at the right.

Phase Three: If $d_I + k(d_B + d_G) - d_G \leq v_1 t_{\max} \leq d_I + k(d_B + d_G)$ for some $k \in \{1, 2, 3, \dots\}$, then let

$$d^* = v_1 t_{\max} - d_I - k(d_B + d_G) + d_G, \quad p_H(h_I) = p_S[S_2(d_B)]^k p_S[S_3(d^*)].$$

This looks like an uglier computation than it is. Unless h_B is very small, $S_3(d^*)$, the final term in the product, representing the probability of surviving the beginning of a brief chase, is very close to 1. The first term in the product is simply the probability of surviving a single breakaway maneuver, raised to the k th power; each breakaway attempt is viewed as an independent event for the purposes of this calculation. In **Figure 2**, this phase produces the equally spaced plateaus that occupy most of the left portion of the plot.

Phase Two: If neither of the above is true, then

$$d_I + k(d_B + d_G) < v_1 t_{\max} < d_I + k(d_B + d_G) + d_B,$$

for some $k \in \{0, 1, 2, 3, \dots\}$; and letting $d^* = v_1 d - k(d_b - d_G)$, we have $p_H(h_I) = p_S[S_2(d_B)]^k p_S[S_2(d^*)]$.

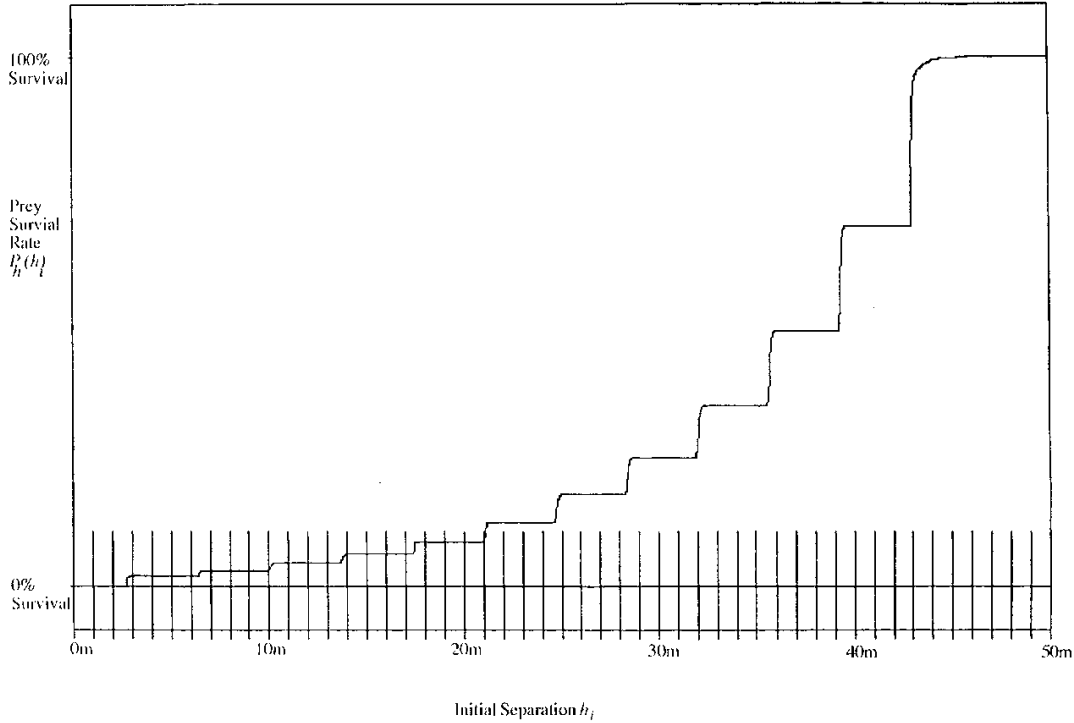


Figure 2. Prey survival rate vs. initial separation (mathematical model).

Phase two comes into play if the 15 s expires while the prey is in the act of attempting to break away. There is no way around computing $S_2(d^*)$ this time; S_2 has to be calculated numerically from a simulation of the phase-two trajectory. It makes a great deal of difference to the prey exactly how close the closest approach is: The prey is almost twice as likely to survive at 36 cm as at 30 cm! The term raised to the k th power represents the previously completed break-aways, while the last term is the probability of surviving the final, incomplete, breakaway. In **Figure 2**, this phase produces the S-shaped pieces connecting the plateaus on the left side of the graph.

Figure 2 is typical of most graphs of p_H . If S is never ignored, then $p_H(h_I)$ is a continuous monotonically increasing function with domain $[0, \infty)$ and range $[0, 1)$. As $p_S(S_2(d_B))$ becomes small, $p_H \rightarrow 0$ for all $h_I < (v_1 - v_2)t$.

The conditional probability of survival given initial separation is given by $p_H(h_I)$. Hence, by the law of total probability [Freund 1992], the unconditional probability of survival is given by $\int_0^\infty p_H(h_I)f(h_I)dh_I$, which, once p_H has been calculated, is extremely easy to calculate numerically.

For our tests, we use the gamma and beta distributions, two flexible and widely known families. We adapt the descriptions by Evans et al. [1993].

Gamma-distributed variates can take on any positive value. The density function has two parameters, with α controlling the shape and β controlling the scale:

$$f_{\text{gamma}}(x) = \left(\frac{1}{\beta^\alpha \Gamma(\alpha)} \right) x^{\alpha-1} e^{-x/\beta}.$$

The gamma distribution has mean $\alpha\beta$, mode $(\alpha - 1)\beta$, and variance $\alpha\beta^2$. To reflect the conditions of the problem, we selected Gamma(6,5) as our reference gamma distribution; this particular density is less than 15 about 8% of the time and greater than 50 about 7% of the time. To determine how much it benefits the prey to be alert, thereby increasing the chance of seeing the predator at considerable distance, we repeated our calculations using the Gamma(6,6) distribution.

Beta variates, in their original form, have a domain of $[0, 1]$. Multiplying by 35 and then adding 15 produces a beta-distribution on $[15, 50]$, reflecting the stipulations of the problem statement. The transformed beta density function has two parameters, ν and ω , which together determine the shape of the density:

$$f_{\text{beta}}(x) = \left(\frac{\Gamma(\nu + \omega)}{35^\nu \Gamma(\nu) \Gamma(\omega)} \right) \left(\frac{x - 15}{35} \right)^{\nu-1} \left(\frac{50 - x}{35} \right)^{\omega-1} \quad \text{for } 15 \leq x \leq 50,$$

with mean $15 + 35\nu/(\nu + \omega)$, mode $15 + 35(\nu - 1)/(\nu + \omega - 2)$, and variance $1225\nu\omega/[(\nu + \omega)^2(\nu + \omega + 1)]$.

The ratio of ν to ω controls the mean of the distribution, while the variance is inversely proportional to $(\nu + \omega)$. We selected the Beta(2,3) distribution as our reference beta distribution. It has a mean, mode, and central “hump” shape very similar to the reference gamma distribution, but no tails sticking out below 15 and above 50. We also examined the Beta(3,2) distribution, with the same shape but a higher mean and mode, to check the effect of increased prey alertness. **Figures 3 and 4** show the four chosen densities. Note, however, that nothing in the calculation procedure limits us to the use of these densities.

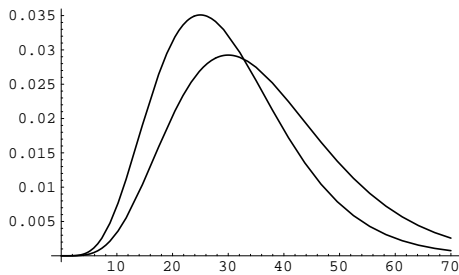


Figure 3. Reference and modified gamma densities.

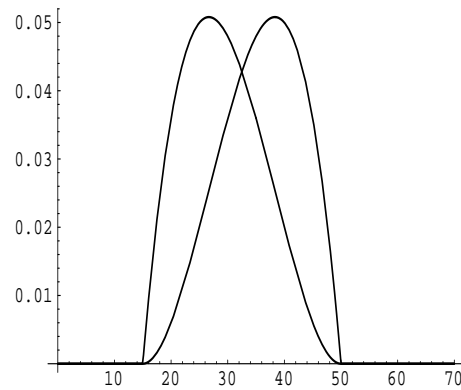


Figure 4. Reference and modified beta densities.

The Computer Simulation Model

Model Overview and Assumptions

The computer model uses physics-based motion, where accelerations are finite, instead of the more-theoretical motion of the mathematical model (in which acceleration is not considered). While there is no explicit limit on the turning radius (it isn't even calculated in the simulation), when we restrict our creatures' acceleration to the assumed value, then at top speed the animals can turn in no less than their minimum turning radius. Hence, although the mathematical and computation models' methods differ, the two models give the same answer.

Computer Model Assumptions

- The predator(s) slowly sneak up on the prey as long as the prey doesn't start to run away. At some distance h_I (where $15 \text{ m} < h_I < 50 \text{ m}$), the prey notices the approach and starts running.
- Each animal has a maximum speed.
- Each animal has a maximum acceleration, derived from $a = \frac{v^2}{r}$, where v is the animal's maximum speed and r is its minimum turn radius at top speed. We further assume that this acceleration can be applied in any direction—centripetal, tangential, or a combination thereof.
- At each instant, each animal figures out in which direction it would like to apply its acceleration, based on its present position and the position of every other animal. However, an animal knows only the position of the other animals 20 ms ago (its reaction time).
- Whenever a predator stops getting closer to the prey (i.e., the predator has made a close pass by the prey), a probability-of-death function, of the smallest distance between the predator and prey, is evaluated. The prey's probability of death depends only on the closest approach distance.
- Simulation continues until the prey dies or 15 s elapses.

Model Design

Our simulation models each animal as a point at its center of mass, which can accelerate in any direction. The simulation outputs smooth curves of the

paths of the centers of motion of the animals, by iteratively solving these vector differential equations using Euler's method (outlined below):

$$\frac{d\vec{P}}{dt} = \vec{V}, \quad \frac{d\vec{V}}{dt} = \vec{A},$$

where \vec{P} , \vec{V} , and \vec{A} are the position, velocity, and acceleration as functions of time.

The simulation cycle begins by determining the optimal direction for the animal to accelerate, based on the animal's strategy. The animal accelerates at its maximum acceleration in that direction. Values for upper bounds on acceleration are parameters to the simulation, derived from the minimum turn radius at top speed via the central acceleration formula, $a = v^2/r$.

The acceleration vector is then added to the local elevation gradient multiplied by the acceleration of gravity, making it easier to go down a hill than up. The elevation gradient is determined from a bilinearly interpolated elevation grid, which is read in from an elevation file.

Once the animal has decided on a direction, the simulation applies one step of Euler's method to update its position and velocity vectors. This method of solving differential equations works by noting that the first two terms of the Taylor series expansion of a function of time depend only on the present condition of the system:

$$f(t + h) = f(t) + h \frac{df}{dt}.$$

Hence, if we know an animal's position, velocity, and acceleration at some time t , we can figure out a first-order approximation for where the animal will be at time $t + \Delta t$ by substituting the vector equations into the Taylor series expansion:

$$\vec{P}(t + \Delta t) = \vec{P}(t) + \Delta t \vec{V}(t), \quad \vec{V}(t + \Delta t) = \vec{V}(t) + \Delta t \vec{A}(t).$$

Taking $\Delta t = 0.001$ s, and given the initial conditions and an acceleration vector, our simulation computes the velocity and position of each animal at each time step.

Life and Death in the Computer

In the computer model, each time the prey passes near the predator, a probability-of-death function is evaluated. The formula that we chose for the probability of death, given minimum separation, is

$$P_{\text{death}}(x) = \frac{1}{1 + 4x^4},$$

whose graph is shown in **Figure 5**. In the notation of the section **Converting Trajectory Descriptions . . .**, this function is $(1 - p_S)$.

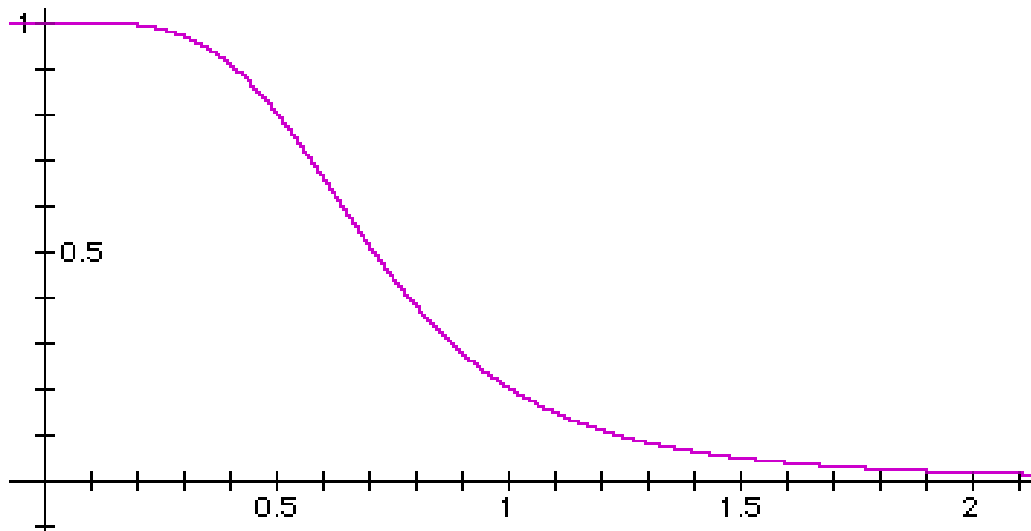


Figure 5. Probability of death vs. closest approach to predator (in meters).

Modeled Hunting Strategies

Every orientation of two animals can be simulated by starting the predator at the origin and the prey a distance h_I along the x -axis, where h_I varies in this simulation from 15 m to 50 m.

The Hungry Hunter

A hungry hunter heads straight for the current position of the closest prey. This is the only strategy that we model both analytically and numerically.

The Smart Hunter

A smart hunter determines the point where it can intercept the closest prey and heads straight for that point. A derivation of the quadratic equation that the smart hunter for the intercept point is given in **Appendix A**. [EDITOR'S NOTE: Omitted for space reasons.]

Modeled Evasion Strategies (One Predator)

The Frightened Prey

Frightened prey flee straight away from the nearest predator. These prey always die if the predator can close the distance between them before its 15 s are up. At a closing rate of 2.78 m/s, the prey will always be overtaken and die if h_I , the initial separation of the predator and prey, is less than 41.7 m.

The Smart Prey

When the nearest predator is far away, smart prey act like frightened prey and flee straight away. But when the predator closes to a critical distance h_B (1.619 m—see **Appendix B** for derivation [EDITOR'S NOTE: Omitted for space reasons]), the prey darts either to the left or to the right. By using its much smaller turn radius, the prey buys some distance, which is again closed by the predator, whereupon the prey can dart again.

For the two-animal case, there are two possibilities for what this looks like: smart prey versus hungry predator, and smart prey versus smart predator. As **Figures 6–7** show, the prey succeeds in outrunning the predator for 15 s.

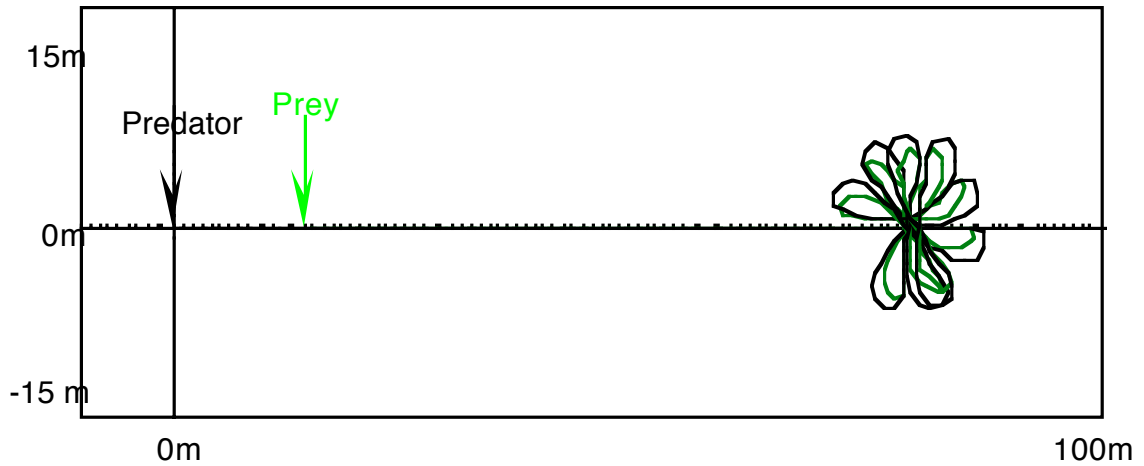


Figure 6. Smart prey vs. hungry predator, $h_I = 15$ m.

The Gradient Prey

Gradient prey are the same as smart prey when the nearest predator is very close (less than h_B) or when there is only one predator. When there are two or more predators, the gradient prey runs in the direction of least danger, i.e., along the gradient of the danger function. If the danger from each predator decreases with the inverse square of its distance, and the danger from each predator is added to produce the danger function, then the danger gradient can be computed by adding the gradient of the danger from each predator:

$$\nabla \left(\sum \frac{1}{d_i^2(x, y)} \right) = \sum \nabla \left(\frac{1}{d_i^2(x, y)} \right).$$

This can be done quickly and easily in the simulation. The gradient prey is different from the smart prey only when there are two predators; their graphs and analysis are presented in the next section.

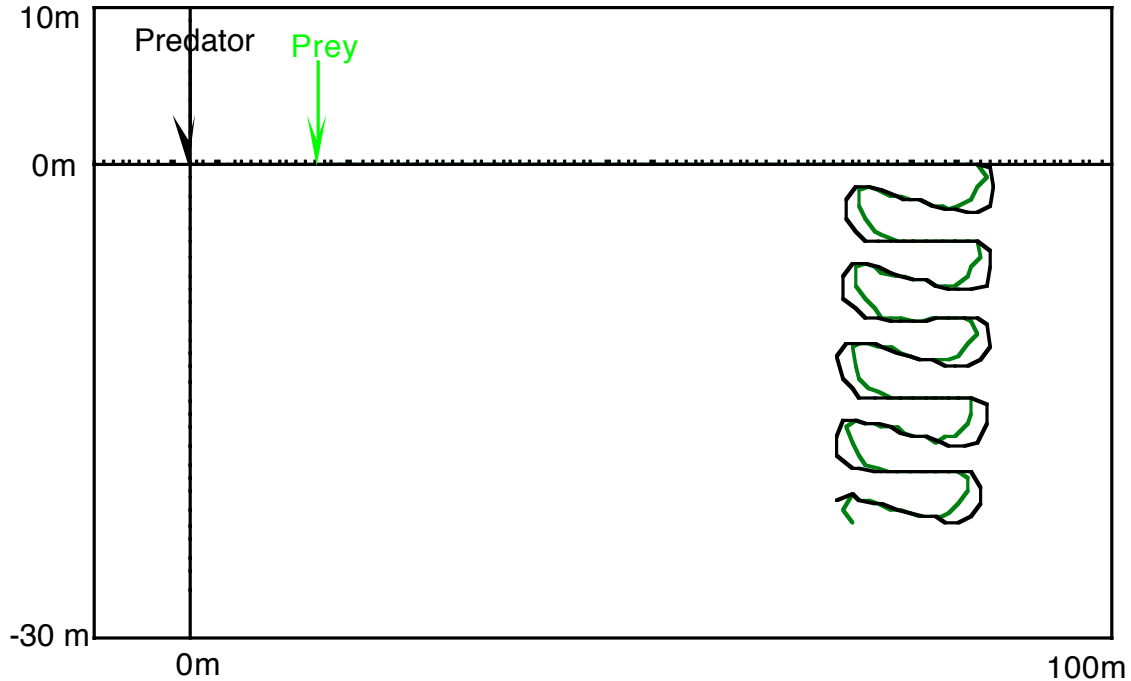


Figure 7. Smart prey vs. smart predator, $h_I = 15$ m.

The Two-Predator Situation

We determined that a good strategy for the predators is for the second predator to follow the first one (by about 8 m), since our prey's strategies hinge around getting behind the first predator.

Frightened Prey

Because frightened prey always die unless they detect the predator(s) more than 41.7 m away, there is no advantage in chasing them with two predators.

Smart Prey and Gradient Prey

Figures 8–11 illustrate typical trajectories taken by smart and by gradient prey when pursued by smart and hungry predators. Each plot shows $x = 60$ to 90 m, $y = -30$ to 5 m. Initial positions are $(-8, 0)$ for predator 1, $(0, 0)$ for predator 2, and $(15, 0)$ for the prey.

Computational Results

If the animals started running with separation determined by the reference beta distribution, the estimates of overall survival rates and their standard errors (2,000 runs) are shown in Table 4. Note that the error bars for some strate-

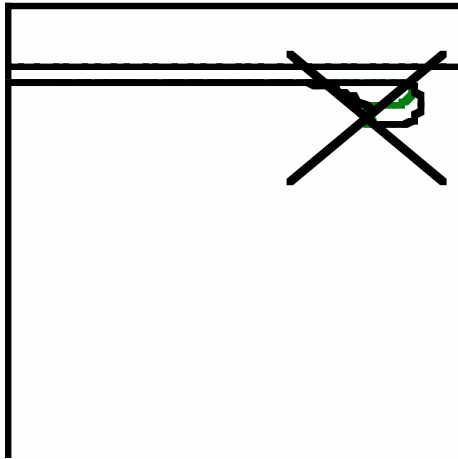


Figure 8. Smart prey, smart predators.

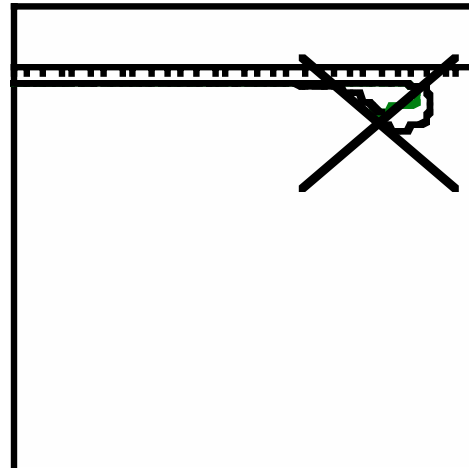


Figure 9. Smart prey, hungry predators.

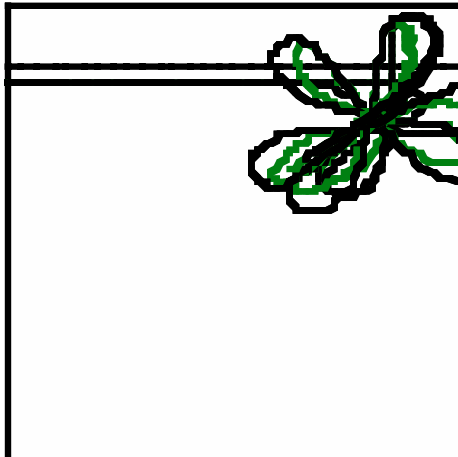


Figure 10. Gradient prey, smart predators.

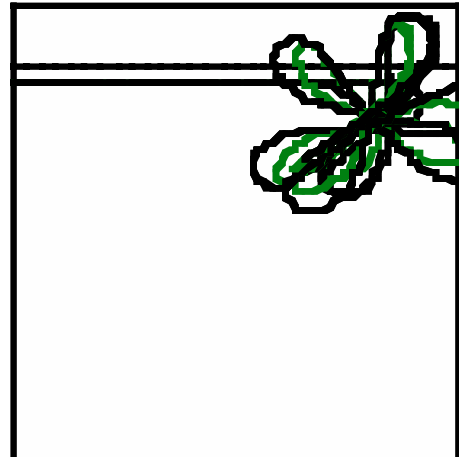


Figure 11. Gradient prey, hungry predators.

gies overlap; for instance, we cannot be certain that smart prey do significantly better than gradient prey against two hungry predators.

Prey Strategies

Frightened Prey: Always fleeing the predator unconditionally leads to the lowest survival rates. This is a bad choice.

Smart Prey: The smart prey, which darts to the side when the predator closes to some critical distance behind it, did quite well in the single-predator runs. This is the best overall evasion strategy for *Thescelosaurus*.

Gradient Prey: On two-predator runs, the gradient prey did quite well against the smart predators but more poorly than the smart prey against the hungry ones!

Table 4.
Estimated survival rates.

Prey strategy	One hungry predator	One smart predator
Frightened prey	$3.2 \pm 0.4\%$	$3.9 \pm 0.4\%$
Smart prey	$35.7 \pm 1.1\%$	$35.5 \pm 1.1\%$
Gradient prey	$35.7 \pm 1.1\%$	$35.5 \pm 1.1\%$
	Two hungry predators	Two smart predators
Frightened prey	$3.2 \pm 0.4\%$	$3.9 \pm 0.4\%$
Smart prey	$3.7 \pm 0.4\%$	$4.0 \pm 0.4\%$
Gradient prey	$3.5 \pm 0.4\%$	$9.4 \pm 0.7\%$

Predator Strategies

Hungry Predator: This predator killed the most prey in both the single-predator and hungry-predator scenarios; it is never misled by the prey's movements. Our data indicate that this is the best overall hunting strategy for *Velociraptor*: Always head straight for the prey.

Smart Predator: This predator is too easily misled by the prey's movements, and, except alone against smart prey, is always worse than the hungry predator. It is especially poor in the two-predator scenario against the gradient prey.

Conclusion

The single most important factor in survival is the distance h_I between the prey and predator at the moment of detection. This is because the most successful prey strategy is to flee the predator directly until the predator closes to another critical distance, h_B (1.6 m), then make a sharp turn. By utilizing its smaller turn radius in this fashion, the prey can get slightly ahead of the predator. The predator rapidly closes this distance, whereupon the prey can pull the same trick again. Each time it does so, however, it takes another chance that the predator will win. Hence the number of breakaway turns is the single most important factor in determining chances of surviving one predator. The chances of survival are very low ($< 4\%$) in the two-predator case when one predator trails the first by 8 m.

Figure 12 reproduces **Figure 2**, a predicted-probability-of-survival graph produced by the mathematical model, for a smart prey pursued by a hungry hunter. **Figure 13** graphs the estimated survival probability from the computer model (50,000 runs, 100 at each h_I). The graphs, aside from the static produced by the random variation of our small sample size, are nearly identical.

Using the mathematical model, we found that changing the turn radii affects the sharpness of curvature of the probability graphs but does not diminish the importance of h_I . With the computational model, and with many different hunting and evasion strategies, h_I was the most important factor in every case.

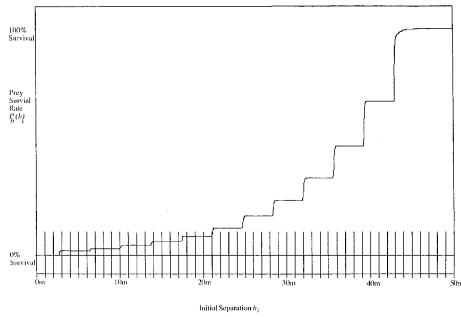


Figure 12. Prey survival rate vs. initial separation (mathematical model).

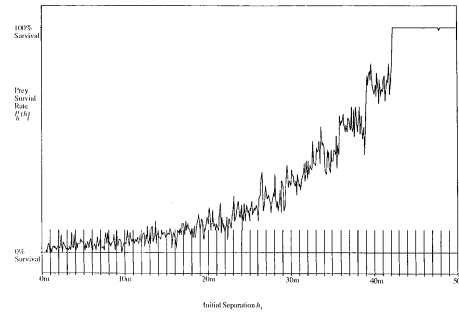


Figure 13. Prey survival rate vs. initial separation (computer model).

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