A Three-Phase Model for Predator–Prey Analysis

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Abstract

We model the hunt as a game of three explicit stages: the stalk, the attack, and the subdual. We implemented this model in Matlab to simulate a velociraptor hunting a thescelosaurus and an African lion hunting a gazelle.

During the attack phase, also known as the *macroscopic game*, the speed constraints are binding but the curvature and acceleration constraints are not. The predator's goal for this game is to minimize the time that it takes to intercept the prey. We introduce a two-predator strategy that is space-optimal for both the predator and prey and conjecture that it is also time-optimal.

In the subdual phase, also known as the *microscopic game*, the time constraints are insignificant. In this game, the predator's goal is to minimize its closest approach to the prey. The prey's strategy is to use its smaller turning radius to outmaneuver the predator until time runs out.

Based on our model and simulations, we conclude that the hunting strategies of an African lion and of a velociraptor differ. The lion has a slower maximum speed but has greater acceleration and is more maneuverable than a gazelle. Conversely, the velociraptor has greater speed but less maneuverability than a thescelosaurus. An ambush is the most effective strategy for a pair of lions, and chasing from behind is the most effective strategy for a pair of velociraptors.

The three-phase model may apply to other situations, such as a guided missile chasing an aircraft.

Introduction

We have structured our model in accordance with a modified version of Elliott et al.'s framework that divides the hunt into three distinct sections: stalk, attack, subdue [1977].

Stalking refers to the predator's attempt to reduce the predator-prey distance while the prey is unaware of the predator's actions. The predator has the choice of whether to use a sneaking approach or a running approach. In the *sneaking* approach, the chance of detection by the prey is given by a probability distribution based on the predator-prey distance. In the *running* approach, the predator rushes the prey, attempting to benefit from the element of surprise while sacrificing the chance that the prey remains unaware of its position.

The attack phase refers to an active approach taken by the predator seeking to maximize the chance of predator-prey contact. The attack phase effectively begins when the prey detects the predator and ends when the predator-prey separation is reduced to a specified level, beginning the subdue stage.

The subdue stage can be viewed as microscopic, as opposed to the macroscopic attack stage. Curvature constraints become increasingly important when the predator-prey distance is reduced to this level, and the chance of physical contact approaches certainty. When the predator achieves a specified level of separation (the *capture radius*), the prey is deemed captured.

In the stalking phase, the predator seeks to minimize the effective separation. As the predator sneaks toward the prey, there is a point at which the risk of a detection balances the benefit of a closer approach. We find (depending on the choice of reflex times and a probability distribution for the detection range) that the optimal target distance for a stalk is 24.7 m.

The two-player phase begins when either the prey or predator starts running and the other reacts. We model the positions $x_P(t)$ ("P" for pursuer) of the predator and $x_E(t)$ ("E" for evader, as in Hajek [1975]) of the prey as moving subject to maximum speed, minimum curvature radius, and eventually acceleration constraints. Let $R_{\min}$ be the closest approach of the predator to the prey within 15 s; it is the predator's goal to minimize $R_{\min}$ and the prey's goal to maximize it. We show that for the given parameters of the velociraptor and thescelosaurus, the two-player game may be decomposed into phases: the macroscopic and microscopic games.

In the macroscopic game, distances are large enough that the curvature constraints are nonbinding. Since velociraptors have a turning radius of 1.5 m, the macroscopic game begins at about 3 to 5 m of separation. The predator's goal is to minimize the time needed to approach the prey and enter the microscopic game; it is the prey's goal to maximize this time. We show analytically that the prey's best macroscopic strategy when facing a single predator is to run directly away, and (ignoring the 15-s time limit) we explain the optimal macroscopic strategy for two predators and one prey.

The microscopic game is more difficult to analyze directly; we instead simulated it by computer. Compared with the macroscopic game, the microscopic

game takes an insignificant amount of time. Since the microscopic games starts after an extended macroscopic game, we assume that predator and prey enter the microscopic game at maximum velocity. Thus, the only consideration of the microscopic game is the closest approach R. We summarize the decomposition in **Table 1**.

Table 1.
Summary of model stages.

	Lion hunt	Our model	Predator's goal	Prey's goal
Phase 1	Stalk	One-player game	Minimize effective distance	
Phase 2	Attack	Macroscopic game	Minimize pursuit time	Maximize pursuit time
Phase 3	Subdue	Microscopic game	Minimize closest approach	Maximize closest approach

We prove upper bounds for the closest approach of the predator to the prey given that a microscopic game commences. Based on the bounds, smaller bounds found through simulation, and the sizes of a velociraptor and a thescelo-saurus, we conclude that in a microscopic game, a lone velociraptor can achieve physical contact. Since lions are successful in killing 71% of the large prey that they touch [Elliott et al. 1977] and only 17% of all prey hunted (which includes what they do not touch) [Stander 1992], we argue by analogy that the velociraptors always win the microscopic game.

In our model, the only random factor is the distance the predator can approach undetected. Similarly, the stalking phase of a lion hunt is the most important factor in determining success [Elliott et al. 1977].

In our model, the prey live if and only if the effective distance at the end of the stalking phase is greater than $(S_P - S_E)t_{\max}$. If the value of $t_{\max}$ is exactly 15 s, then during the stalking phase the velociraptor has a trivial strategy: Approach until some critical point is reached, then jump.

Basic Model: The Two-Car Problem

The logic behind the two-car problem proposed by R. Isaacs [Hajek 1975; Isaacs 1965] is the basis of our model. Car P (the pursuer) chases car E (the evader). If car P ever gets closer to car E than a specified distance δ (the capture radius), then car P wins the contest. Both cars have minimum turning radii ρ_P and ρ_E and move at constant speeds S_P and S_E. In the special case of a perfect capture, $\delta = 0$ signifies that P captures E only if their positions coincide exactly. The two-car problem with perfect capture was solved exactly by E. Cockayne [Cockayne 1967; Cockayne and Hall 1975].

Theorem 1 (Cockayne). *P can capture E from any initial state if and only if* $S_P > S_E$ *and* $S_P^2/\rho_P \geq S_E^2/\rho_E$.

Much research in differential games was conducted during the Cold War for military purposes. For example, the two-car problem might model a dogfight between two airplanes or one boat chasing another. Tellingly, roughly half the articles with direct military application or support were written in Russian, half in English.

Additions to the Model

We modify the basic model to incorporate the hunting strategies of the African lion. We assume that the probability of capture depends on the closest approach to the prey:

$$A = \min_t |x_P(t) - x_E(t)|.$$

The paths $x_P(t)$ and $x_E(t)$ of the centers of gravity of the pursuer and evader satisfy the maximum speed and minimum curvature radius constraints. The predator tries to minimize, and the prey tries to maximize, A. We introduce delay times γ_P and γ_E, typically 0.05 s, which may be thought of as either reflex times or imperfect information [Schreuer 1976]. For instance, P can only react to the actions that E took γ_E ago.

The performance data for lions and their prey [Elliott et al. 1977, Stander 1991] do not include the turning radius; those for velociraptors and thescelosauri do not include forward acceleration. Hence, we assume for all species a constant ratio f of maximum forward acceleration a to maximum lateral acceleration S^2/ρ. A value of $f = 0.5$ gives reasonable values for the inferred constants.

Table 2.

Model parameters for different species.

Values for S, ρ, and K are from the problem statement or from Hajek [1975]; the others are inferred.

	S	ρ	K	S^2/ρ	$S^2 f/\rho = Ks$	force in turn	baton distances
	(m/s)	(m)	(1/s)	(m/s^2)	(m/s^2)	(g's)	(m)
Velociraptor	16.6	1.5	5.6	18.5	93	1.89	3.0
Thescelosaurus	13.9	0.5	13.9	386	193	39.4	1.0
African lion	14.3	10.5	0.68	19.4	9.7	1.98	21
Thomson's gazelle	27.1	80	0.17	9.2	4.6	0.94	159
Zebra	16.4	26.4	0.31	10.2	5.1	1.04	53
Wildebeest	14.7	18.9	0.39	11.4	5.7	1.16	38

The Stalk: A One-Person Game

The stalking phase is the most important factor affecting the success of a lion's hunt [Elliott et al. 1977]. During the stalk, the predator tries to minimize its effective separation from the prey. The effective separation accounts for the actual separation, the acceleration capabilities of the two species, and which player jumps first.

For the predator, the advantage of sneaking closer is a decrease in the actual separation. The disadvantage is the risk of being noticed and losing the element of surprise.

We define the effective separation to have the following property. If the prey runs directly away from the predator, then starting from a standstill and assuming that one species surprises the other is "equivalent" to starting from the effective separation with both species running at full speed. By "equivalent," we mean that the time that it takes the predator to catch the prey is the same. Explicitly,

$$R_{\text{effective}} \approx R_{\text{actual}} - b_E + b_P - \begin{cases} -\gamma_E S_E, & \text{if predator jumps first;} \\ +\gamma_P S_P, & \text{if prey jumps first.} \end{cases}$$

The prey and predator approach their maximum speed asymptotically but never reach it. However, our model parameters imply that with a 10-m head start, the thescelosaurus will be traveling at nearly full speed. Since the velociraptor is only slightly faster, it too must be running at near full speed when it captures the thescelosaurus. The approximation above would be equality if full speed was attained by both species before contact.

The constants b are "baton distances." For example, the baton distance b_P is the initial separation that a stationary velociraptor on a relay team needs from its teammate in order to accelerate to full speed and receive the baton as the teammate catches up. By the acceleration assumptions of our model, $b = S/K = \rho/f$.

The reflex term can be either positive or negative depending on which species reacts first. If P jumps first, we assume that E immediately notices, takes γ_E s to react, and loses an effective distance of $\gamma_E S_E$ m. If E notices the predator and jumps first, the predator needs γ_P s to react and loses an effective distance of $\gamma_P S_P$. Since the prey is not anticipating flight, but the predator is anticipating a detection, we assume that $0.05 = \gamma_P < \gamma_E = 0.20$.

We now devise a cumulative probability distribution function $P(x)$ for the distance at which the prey first notices the stalking predator. We wish to fit a twice-differentiable and easily analyzable function P to the constraints $P(15) = 0$ and $P(50) = 1$. We choose

$$P(x) = \frac{x - 15}{35} - \frac{\sin\left(\dfrac{2\pi(x - 15)}{35}\right)}{2\pi}.$$

The predator will try to stalk until reaching its target separation $x = R$ and then jump; of course, the predator may have to jump sooner if detected. The expected effective distance is 24.7 m, as discussed below.

Figure 1 shows the expected effective distance as a function of the target distance. For our choice of parameters and probability distribution, there is a unique minimum, the optimum target separation for the stalking predator. We locate the minimum at 24.7 m by taking the derivative of the expected effective distance with respect to target distance. The derivative shown in **Figure 2** does not adequately represent the predator's disadvantage in advancing from 20 m to 15 m, because the strategies with targets 20 m and 15 m vary only in the rare case that the predator reaches 20 m undetected. We account for this effect by considering the expected benefit for a predator at x m to advance infinitesimally and obtain the conditional derivative by dividing by $P(D)$. The conditional derivative is shown in **Figure 3**.
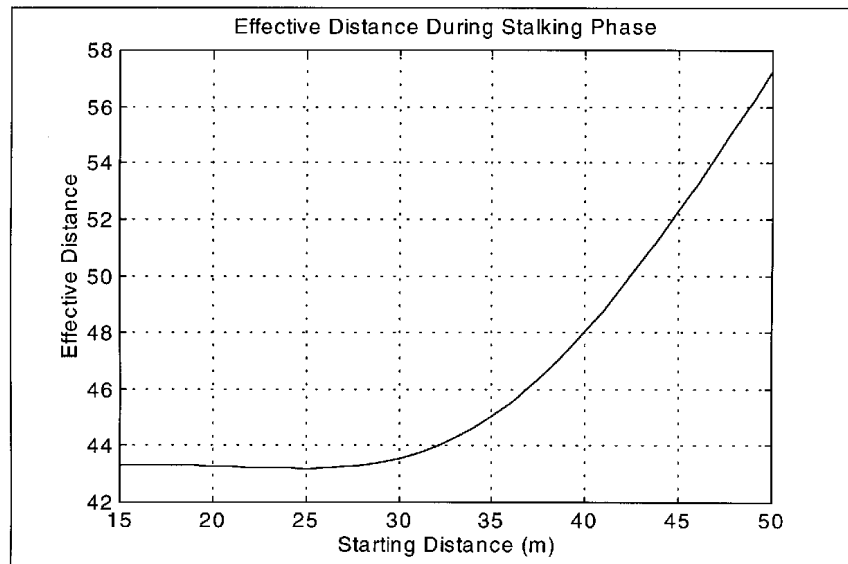
Figure 1. Effective distance.

The Macroscopic Game

This phase of the game is the simplest strategically for both the predator and the prey. The predator's goal is to use the least amount of time to reach the prey. The prey's goal is to use as much time as possible before being reached by the predator. Using simple trigonometry, it is easily shown that the prey will then run directly away from the predator to extend the time spent in the chase. Obviously, the best strategy for the predator is to run directly toward the prey. Because of differences in top velocity, the predator will reach the prey and the microscopic game will begin in $R_{\text{effective}}/(S_P - S_E)$ s, where $R_{\text{effective}}$ is the initial effective distance between the prey and the predator.
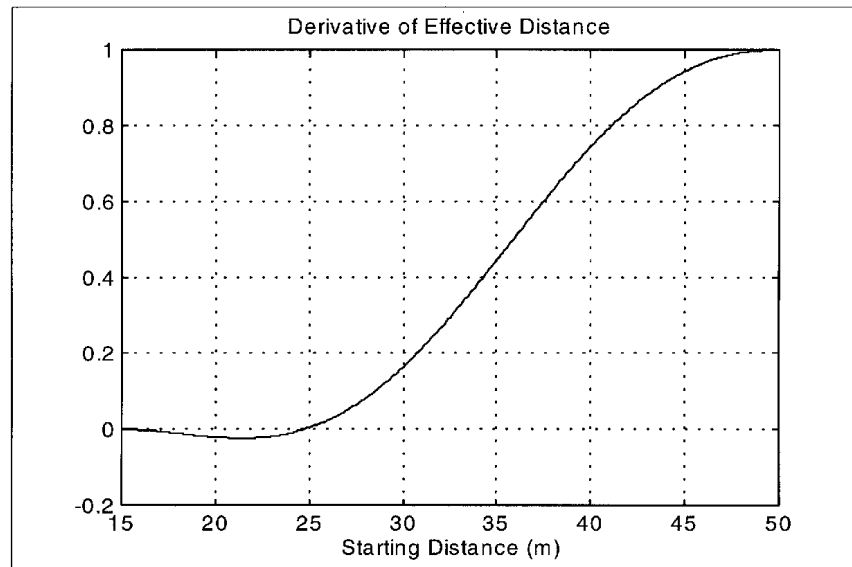
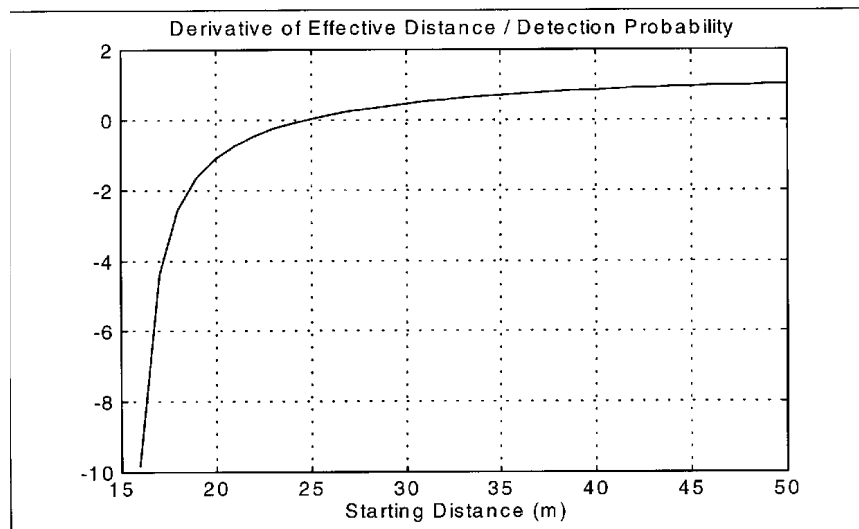**Figure 2.** Derivative of effective distance.

Figure 3. Conditional derivative of effective distance.

The Microscopic Game

We prove in **Theorem 2** that the predator, simply by running directly toward the prey, can approach very close to the prey no matter what the prey does. The following lemma is instrumental in this proof. When the predator is as close as **Theorem 2** allows, then the microscopic game has begun.

Lemma. *Suppose that the predator always tries to run directly at the prey. Then the predator can run directly at the prey until the separation distance is $\rho_E(S_E/S_P)$ meters.*

Proof: We may assume that for large distances the predator can line up with the prey. The predator can maintain this orientation as long as the predator's ability to change direction is greater than the prey's ability to change the direction of of the vector from predator to prey:

$$\frac{|x'_E|}{d} \leq \frac{S_P}{\rho_P}.$$

Since $|x'_E| < S_E$, the condition $d \geq \rho_P S_E / S_P$ suffices. □

A similar result holds for the prey: If the prey's strategy is to run directly away from the predator, then the prey can keep the predator directly behind it at least until the separation distance is $\rho_E(S_P/S_E)$ m.

Theorem 2. *A predator with maximum speed S_P, turning radius ρ_P, and reflex time γ_P is guaranteed to approach within $\rho_P(S_E^2/S_P^2) + \gamma_P S_E$ of a prey with maximum speed S_E.*

Proof: First, we consider the zero-reflex case when $\gamma_P = 0$. The predator can run directly at the prey until the separation is $\rho_P(S_E/S_P)$. Then the predator continues in a straight line to the point where the prey is at this instant. In the time that it takes to reach this point, the prey travels at most $\rho_P(S_E^2/SD_P^2)$ m.

For nonzero reflex time, the predator should always choose the point where the prey was γ_P s ago. When the predator comes within $\rho_P(S_E^2/S_P^2)$ of the pursued point, it is within $\rho_P(S_E^2/S_P^2) + \gamma_P S_E$ of the prey. □

The only physical advantage of the prey over the predator is the prey's much smaller turning radius. However, to use this advantage, the prey must allow the predator to approach close by. Assuming perfect capture and instantaneous reaction, and more than 1.4 m separation, if the prey turns as hard as it can, then the predator can capture it. In our model, with nonzero reaction time, the predator instead aims directly for the prey. **Figure 4** shows a typical result of such a turn: The prey can maneuver more quickly and the predator must make a larger turn, using more time. **Figure 5** shows the minimum distance between the centers of gravity for the predator and the prey at different turning distances, assuming instantaneous reactions but using the parameters for velociraptor and
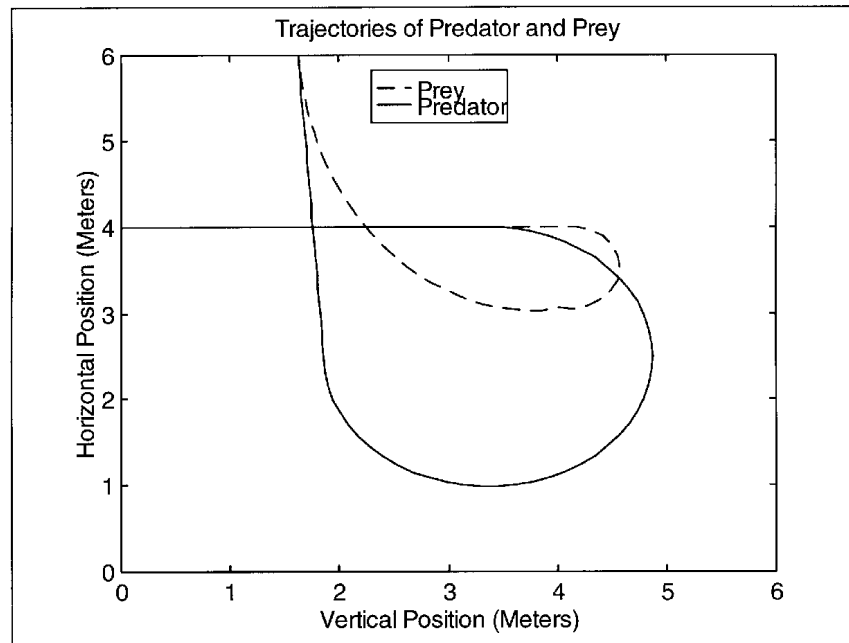
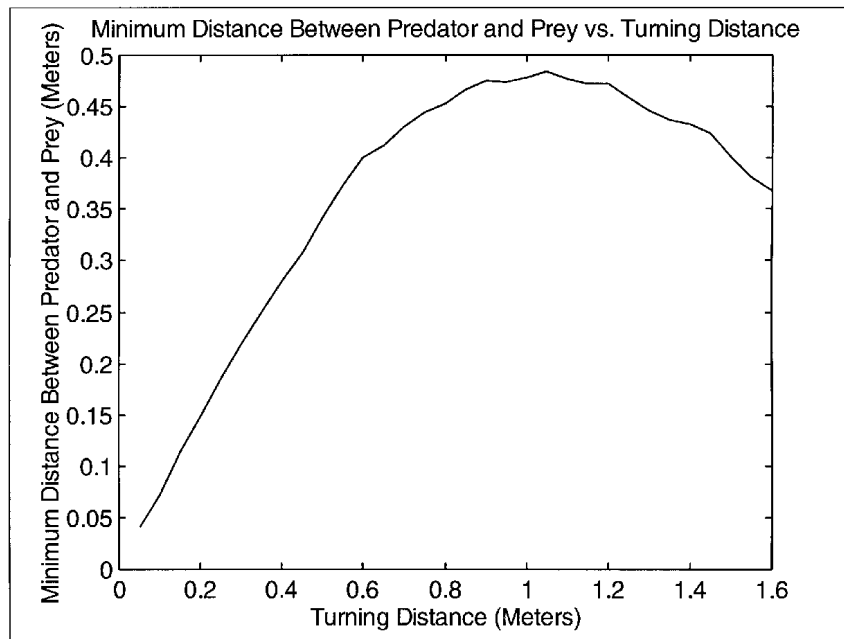**Figure 4.** Trajectories of hard turn maneuver.

Figure 5. Minimum approach vs. turning distance.

thescelosaurus. The predator is kept the farthest from the prey if the prey turns when the predator is about 1 m behind. **Figures 6–7** show the effect of reaction time on the optimal time to turn (optimality is keeping the predator as far away as possible). **Figure 6** shows what the minimum approaches are with various reaction times; and **Figure 7** shows at what separation the prey should turn to obtain that minimum approach, given the reaction times.
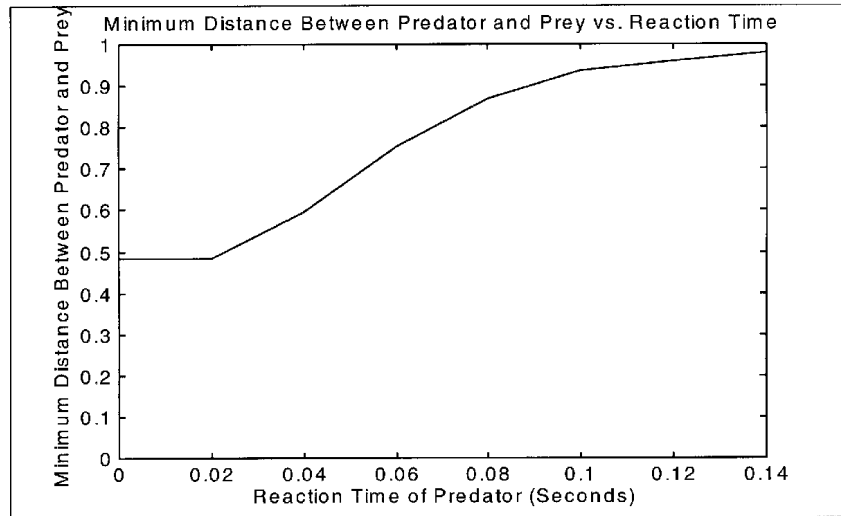
Figure 6. Minimum approach vs. predator reaction time.
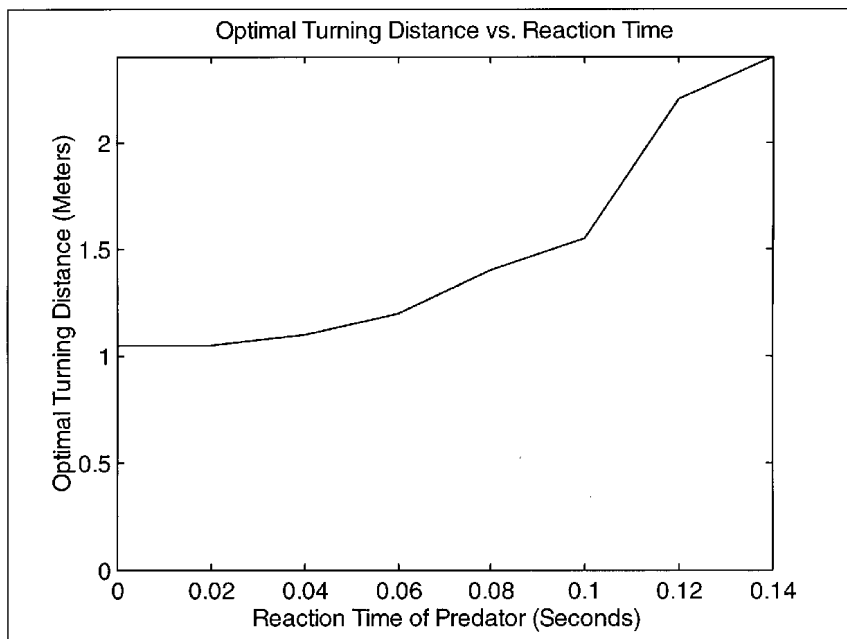
Figure 7. Optimal turning distance vs. predator's reaction time.

Hunting Strategy of Multiple Lions

For a multiple lion hunt, Stander [1992] proposes a three-part framework to model the predators' strategies. The most effective strategy for the lion is a coordinated ambush, with a probability of success of 26% for large prey. A single lion initiates the attack, driving the prey towards the other lions lying in wait. Multiple lions have been observed to use this strategy in 52% of their large-prey hunts.

Another strategy is convergence, in which two lions jointly initiate the attack phase, pursuing the prey from the same direction. For large-prey hunts with multiple lions, this strategy is pursued 14% of the time with a probability of success of 14%.

The least effective strategy for group hunting is an uncoordinated ambush, which usually occurs when one lion startles the herd before the others are in position to receive the prey. While Stander observed a 34% occurrence rate for large prey hunts, not a single animal was killed under this approach out of 68 attempts [1992].

The Two-on-One Macroscopic Game

The two-predator game is similar to the one-predator game in several respects. In both, the goal of the predator is to reach the prey as soon as possible. With two predators, one goal for the prey would be to avoid being contacted by any predator as long as possible; another goal would be to avoid being contacted by both predators as long as possible. The second goal implies that a situation in which one predator is quickly encountered might be preferable if that meant that the time until the second predator joins the fight is delayed.

For the sake of simplicity, assume that the pursuers are faster than the evader and have no constraints on turning, acceleration, or time. The optimal strategies for each goal are provided by circles of Apollonius.

For two points P and E in the plane and a constant k, the locus of all points Q that satisfy $PQ = k \cdot QE$ is a circle (for $k \neq 1$), known as a *circle of Apollonius*. The points P and E are the positions of the predator and prey, and k is the ratio S_P/S_E of their speeds. For $k > 1$, the circle contains E. As the pursuer and evader proceed, their positions and the circle change; the area of the circle decreases continuously as the pursuer and evader approach each other.

We omit proofs of the following results.

Theorem. *Regardless of the pursuer's strategy, the evader can reach any point in or on the boundary of the original circle of Apollonius. If the pursuer follows an optimal strategy, the evader can reach the boundary only by traveling in a straight line.*

Theorem. *If the evader runs in a straight line, the fastest way for the pursuer to capture the evader is by following a straight line.*
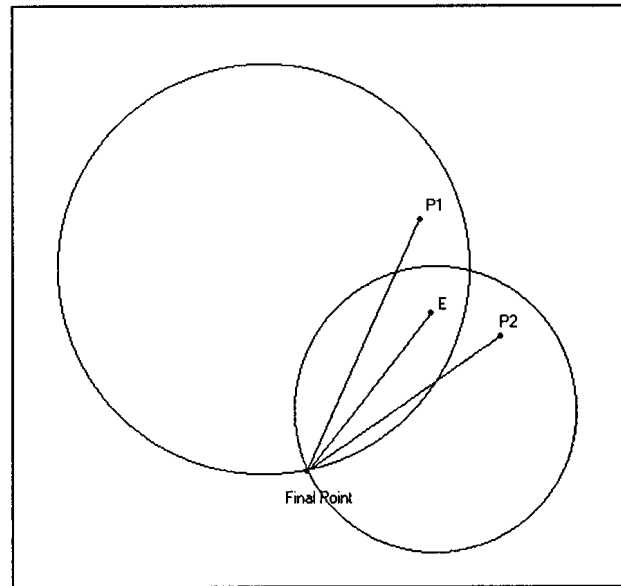
Figure 8. Example of circles of Apollonius.

Assuming that the prey can survive a microscopic game with one predator but not with two, the prey's goal in the microscopic game is to delay the entrance of the second predator into the microscopic game. Assuming further that the microscopic game takes up very little space compared to the macroscopic game, the prey's optimal macroscopic strategy is to engage the first predator as far from the second as possible. Thus, the prey aims for the point on the Apollonius circle with P_1 (the closer predator) that is farthest from P_2.

Based upon the different assumption that the prey's macroscopic goal is to delay the first contact with either predator, we conjecture that the optimal strategy for the prey is to run towards an intersection of the circles of Apollonius with the two predators, if such a point exists. If none exists, the prey's optimal strategy is to run away from the closest predator.

The Ambush

The ambush is an effective strategy for lions because they have greater maneuverability and acceleration than their prey. Indeed, Stander empirically confirms that the most effective hunting strategy for multiple lions is a coordinated ambush. He witnessed a 27% success rate for the coordinated ambush strategy vs. an average success rate of 15%. In addition, Stander notes that while the lions pursued a coordinated ambushed strategy in 68% of the total hunts, the figure increases to 87% if only large prey are considered [1992].

Figure 9 shows the results of our model simulating an ambush of a gazelle by a lion. We assume, based on Stander's observations, that the lion's ambush is 15 m from the gazelle. At this distance, the probability of a single lion capturing a gazelle from behind is essentially zero. The gazelle, after being scared by a

second lion, runs in a direction that, if unaltered, would pass within 10 m of the hidden lion. Just after the gazelle starts running, the hidden lion leaps out. The gazelle accelerates through a turn in order to escape the lion but is unsuccessful. We experimented with different angles for the lion and different degrees of aiming for a point in front of the gazelle. In this simulation, we assumed zero reaction time for the gazelle.

We also considered a velociraptor attempting to ambush a thescelosaurus. We assume, since the agile thescelosaurus has 15 m to accelerate, that it is traveling at full speed when near the ambush. The constant speed assumption makes an analytic solution possible. Let D be distance at which the thescelosaurus would pass from the ambush if it continues in a straight path. We assume a reaction time of $\gamma = 0.2$ for the thescelosaurus, whose strategy is to try and cut away from the ambush as soon as the predator reveals itself. We assume also that the predator's strategy is to run in a straight line to intercept the thescelosaurus after the thescelosaurus has turned by an angle of θ. Based on these assumptions, the velociraptor's leap must be perpendicular to the thescelosaurus's original path. For a zero capture radius, the maximum distance D from which the ambush will be successful is

$$D(\theta) = S_P \left(\frac{\rho_E \theta}{S_E} + \gamma_E \right) - \frac{S_P}{K_P} \left\{ 1 - \exp \left[-K_P \left(\frac{\rho_E \theta}{S_E} + \gamma_E \right) \right] \right\} - \rho_E (1 - \cos \theta).$$

The optimum value of θ is 1.0681 radians, which allows a range of 1.51 m for the ambush, as seen in **Figure 10**. Note that in our simulation of the velociraptor's ambush, all of the assumptions except zero capture radius favor the velociraptor, so we are confident that 1.5 m is an upper bound for the maximum distance of effective ambush.
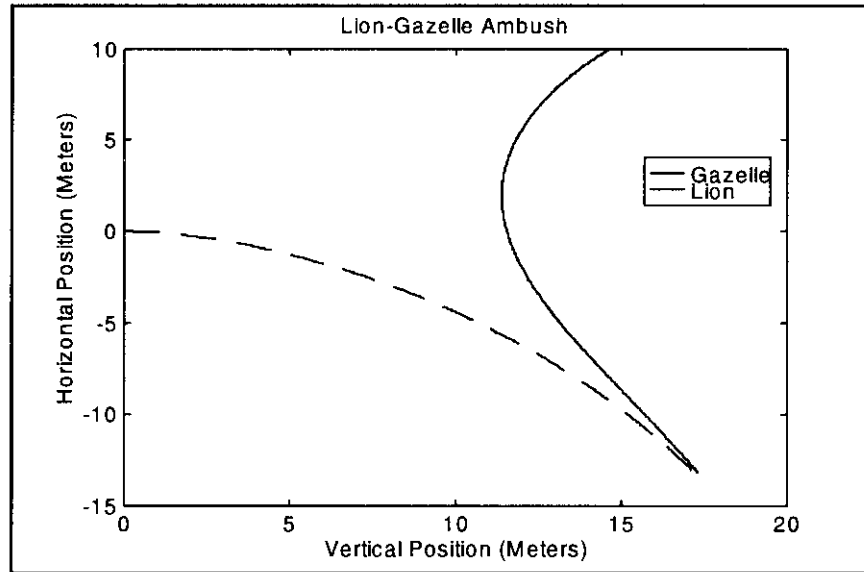
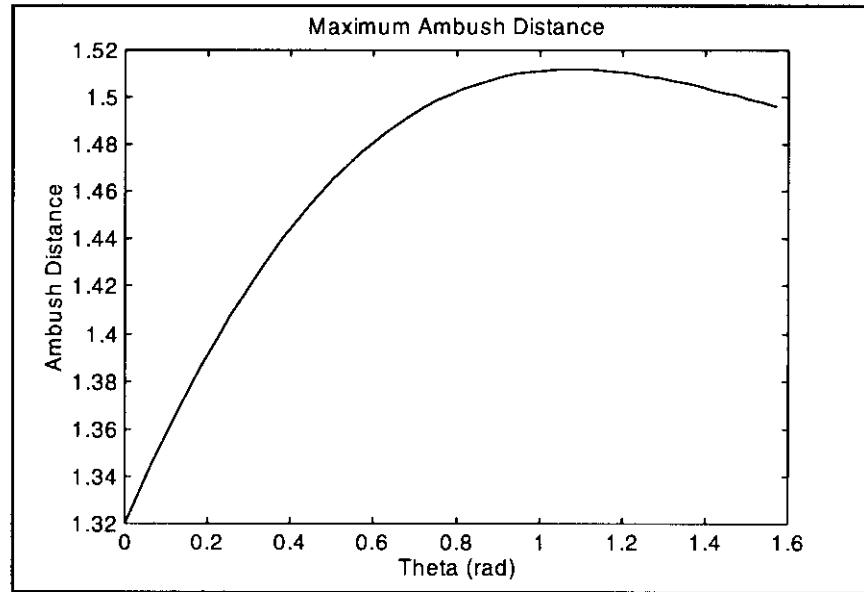**Figure 9.** Ambush of a gazelle by a lion.

Figure 10. Maximum ambush distance by a velociraptor.

Our model accurately predicts that the lion should be able to capture a gazelle from 10 m and that a velociraptor should be able to capture a thescelosaurus from 1.51 m. This difference explains why the ambush is a useful strategy for the lion but not for the velociraptor. The lion has a slower maximum speed but has greater acceleration and is more maneuverable than a gazelle, while the velociraptor has greater speed but less maneuverability than a thescelosaurus. An ambush is the most effective strategy for a pair of lions, and chasing from behind is the most effective strategy for a pair of velociraptors.

Testing the Model

We determined reasonable parameter values for the velociraptor hunt by comparing the predictions of our model with the success rates of different strategies for the African lion. Our model could be validated by testing it on another known species, such as the cheetah, for which there are data. One particularly significant assumption that should be tested is the ratio f of maximum forward acceleration to maximum lateral acceleration (f), whose value of 0.5 was chosen because it produced realistic results in the lion–gazelle hunt.

Extensions

We could make the capture a stochastic process. One alternative scoring function [Friedman 1970, Marec and Van Nhan 1977] is to integrate some func-

tion of time and the positions with respect to time:

$$B = \int \mu(t, x_P(t), x_E(t)) \, dt.$$

The probability of a capture is e^{-B}. We briefly considered both

$$\mu = \frac{1}{|x_P - x_E|} - \frac{1}{3}$$

and

$$\mu = 1 + \cos\left(\frac{\pi|x_P - x_E|}{3}\right)$$

for $0 \leq |x_P - x_E| \leq 3$ but disagreed with their predictions. The "chicken maneuver" from Cockayne's proof of **Theorem 1**, in which the prey charges at the predator but swerves at the last moment, gives the prey a good score. Although the predator and prey come close together, they are close for only a short time, hence the integral with respect to time is small.

For the velociraptor–thescelosaurus hunt, the closest approach in the chicken maneuver is less than the size of the prey and would probably result in a kill. We conclude that the probabilistic approach is not appropriate for the given model parameter values.

Since the closest approach scales linearly with turning radius, the probabilistic approach may be appropriate for situations in which the turning radius is much larger than the predator and prey, such as a missile chasing an airplane.

Strengths and Weaknesses

We took advantage of the fact the turning radii and the distances needed to accelerate to full speed are negligible compared with the overall distances. This fact allowed us to decompose the chase into a macroscopic phase and a microscopic phase. The players have different restrictions and goals in each phase. We feel that the decomposition of a difficult problem into more manageable problems is the major strength of our approach.

The assumptions that $t_{\max} = 15$, $\rho_P = 1.5$, $\rho_E = 0.5$, $S_P = 16.67$, and $S_E = 13.89$ are unrealistic for a biomechanical analysis of dinosaurs. In particular, a thescelosaurus turning at full speed in a radius of 0.5 m has a centrifugal acceleration of 39 times the force of gravity. We might fix the g-force by linearly scaling the given constants ρ and $t_{\max}$ and scaling the assumed reflex time. Since our model is invariant under this change of scale, the strategic analysis will be unchanged, with the possible exception that the capture radius stays constant and thus the microscopic game does not always favor the velociraptor.

A disadvantage of our model is that the transition between the macroscopic and microscopic games is not well defined. The exact transition would be unimportant if the initial distances are much larger than the curving radii, but we were not able to quantify their importance.

A second disadvantage is that the decomposition does not apply in all situations, since the macroscopic phase explicitly assumes that the predator's maximum speed is greater than the prey's. For instance, the macroscopic phase does not apply to the lion–gazelle hunt, because the lion is slower than its prey.

We could not find general strategies for the microscopic game by mathematical analysis. Instead, we used simulations to conjecture and test strategies.

An unforeseen advantage of our model is its potential application to other situations in which the initial distances are large compared to the turning radii, such as air combat or naval warfare.

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