

# Gone Huntin': Modeling Optimal Predator and Prey Strategies

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## Summary

We develop a model for the hunting strategy of *Velociraptor mongoliensis* pursuing *Thescelosaurus neglectus*. Regarding their characteristics, there are discrepancies between the problem statement and the literature; so we parameterize our model in terms of both physical and mechanical characteristics.

The primary locomotive differences between the animals are their relative speeds and turning radii. We show that the optimal strategies are simple, and we present equations and illustrations for the key components of the model. Since the optimal strategy for the predator includes a stochastic component, we present an equation for the probability of a successful encounter.

We also model the interaction of multiple predators and multiple prey. With a reasonable assumption regarding cooperative hunting, two or more velociraptors should have an insurmountable advantage, barring earlier detection.

Finally, we discuss an alternative approach, outlining a genetic programming solution that would evolve optimal strategies for both animals. We begin with the primitives required to evolve such a solution, and we discuss the nature of the evolution required to produce optimal solutions. We show that the evolutionary traits identified by this supposition mirror the known traits.

## Background

*Velociraptor*, member of genus *Theropod*, lived in Central and East Asia during the Late Cretaceous period (97.5 to 66.4 million years ago). It was a fairly

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small animal, reaching a length of roughly 1.8 m and a mass of no more than 45 kg [Encyclopædia Britannica 1997]. *Velociraptor* is thought to have hunted small herbivorous dinosaurs. Current speculation is that velociraptors hunted in pairs or packs. It is estimated that a velociraptor was capable of brief bursts of speed, roughly 15–20 s in duration, of up to 60 km/hr. They possessed a sickle claw on each foot and an ossified tendon in the tail, which together enabled them to strike and slash while maintaining balance. The velociraptor is closely related to the slightly larger *Deinonychus*, indigenous to North America during the Early Cretaceous period (144 to 97.5 million years ago).

*Thescelosaurus neglectus*, a member of genus *Ornithomimid*, lived in North America during the Late Cretaceous period. Thescelosauri were herbivores roughly 3.4 m in length. They were fast runners, capable of sustained speeds of up to 40–50 km/hr. While they were of the general type of prey that velociraptors would probably hunt, it is not apparent that the two species inhabited the same continent at the same time. It is more likely that *Deinonychus* or its descendants were predators of *Thescelosaurus*. In any event,

Mongolia during the Cretaceous period was generally arid, and vegetation was probably quite sparse. Thus, the habitat and hunting grounds of *Velociraptor* were probably large open areas with few obstacles and fewer hiding places [American Museum of Natural History 1997].

North America during the Cretaceous was quite wet and heavily vegetated, an environment probably less conducive to high-speed pursuit and better fit for stealthy hunters. Forests and swamps may have provided hiding places for the prey but also served as boundaries or obstacles to escape routes.

## Assumptions and Limitations

We assume that both predator and prey adopt optimal strategies. This assumption is probably not realistic, since it requires the prey to have relatively perfect information about an approaching predator. Since turning and looking would undoubtedly decrease speed, it is not clear that the prey can both maintain optimal speed and possess optimal information. However, sufficient information might be gathered from other senses to approximate an approaching predator's velocity vector and form a reasonable distance estimate.

The problem statement advises that *Velociraptor* can turn with a 1.5 m radius, and that *Thescelosaurus* can turn with a 0.5 m radius, while running at full speed. It is highly unlikely that these radii were achievable by either animal. At 60 km/hr, *Velociraptor* would experience a centripetal acceleration of  $185 \text{ m/s}^2$ , or roughly 20 g's. *Thescelosaurus* at 50 km/hr would experience 40 g's. We doubt that the animals could make these turns. A more reasonable acceleration would be 2 g's, corresponding to radii of 14.2 m and 9.8 m respectively. We are also somewhat suspicious of the assertion that *Thescelosaurus* has a shorter turning radius than *Velociraptor*. *Velociraptor*'s higher muscle-to-mass ratio, smaller size, and longer claws suggest that it should be capable of tighter turns at equivalent

speeds; being more compact, it should be able tolerate higher g-forces as well.

Our model ignores the direct impact of terrain, for several reasons:

- We parameterize velocity, acceleration, and maximum duration of maximum speed for both predators and prey, so it would be easy to accommodate in our model the adverse impact of terrain on either animal.
- We are not confident that we can estimate the impact of terrain on the relative velocity of the two animals. We have not found sufficient information on their foot structures to judge their abilities to pass through non-ideal terrain.
- We are not sure what terrain is appropriate for an encounter. Mongolian terrain of the Cretaceous period is close to ideal for optimal speed, whereas North American terrain could vary significantly.

We have assumed that random movements (left or right) are captured in a probability function. This seems a reasonable guess, though the literature indicates that mammals favor a particular direction. This is a rather important issue, since the predator would presumably learn the prey's pattern, anticipate any favored turn, and improve its success rate significantly.

We parameterize acceleration as the maximum acceleration that the animal would tolerate in any direction, though we could assign different values for linear acceleration and centripetal acceleration, or separately limit positive and negative acceleration (starting up and stopping, respectively). We also assume that acceleration is constant at this maximum rate, and that changes in speed would be done prior to initiating a turn. Since optimal turning radius is achieved by decreasing speed prior to turning, this assumption is beneficial to both predator and prey. However, it is somewhat unlikely that an animal would slow down, turn tightly, then accelerate to full speed, rather than begin the turn at full speed and decrease linear velocity while turning.

We make no attempt to quantify the relative costs to each animal relative to the pursuit game. For example, since the prey dies if it loses, it would be reasonable to assume that the prey would adopt a risk-adverse strategy until capture is imminent, followed by a "try anything" strategy, including attacking the predator at the last minute. The predator, on the other hand, can make multiple attempts at the game, so it would be reasonable for it to attempt a high-risk maneuver with a reasonable probabilistic success rate, since failure implies only a delay in lunch rather than death.

For flexibility, we parameterize several variables, such as reaction time, attack success probability, and attack radius.

In the multiple predator model, we focus on the two-predator game. Two predators are virtually certain to win; adding more just doesn't seem fair.

We do not consider multiple prey models, since a single predator is not going to attempt to capture multiple prey, and multiple predators vs. multiple prey ultimately resolve down to multiple instances of "two or greater vs. one" or "one versus one."

We ignore the search costs, encounter rates, and stealth strategies, except to note that the predator benefits from minimizing the distance prior to beginning the chase and the prey benefits from maximizing the detection distance. We include a parameter for the detection distance in our model, and we compute the maximum distance at which the predator can expect success.

Finally, we make no attempt to deal with visibility, weather, presence of alternate animals, presence of other prey, obstacles, obstructions, boundaries, bodies of water, or other possibilities. Mathematically speaking, these are relatively minor omissions. Boundary conditions limit the regions of safety and danger and as such introduce variations to the probability of capture, but these calculations are fairly simple. Obstacles tend to favor the predator, since its reaction time will be longer and it will have seen the prey's response to the obstacles. This is somewhat equivalent to a shortening of the relative distance between the two animals, which can be easily accommodated in our model. Water, weather, and similar environmental considerations favor the animal with superior physical adaptations, and we are not clear as to which animal that is under each of the possible conditions. Again, the impact is most likely to be a change in relative velocities, a condition our model can accommodate.

## Model 1: Single Prey, Single Predator

We consider the optimal strategy for a single predator and a single prey. We initially ignore stalking activity by the predator. At some time  $t_i$  and location  $d_i$ , the prey becomes aware of the presence of the predator and flees. The speeds of the predator and prey are  $v_v$  and  $v_t$ , the maximum duration over which the predator and prey can maintain their maximum speeds are  $M_v$  and  $M_t$ , and their minimum turning radii are  $r_v$  and  $r_t$ .

At any time during the chase, the prey has the option of changing direction, subject to the minimum turning radius. If the distance between the predator and the prey is sufficiently large—specifically, if the predator is capable of adjusting its approach trajectory to intercept all points on any circular path taken by the prey—it is never prudent for the prey to make such a direction change, since the result of such a path would decrease the net distance between the two animals without increasing the chance of escape.

If, as shown in **Figure 1**, the predator can reach the point where its minimum turning radius touches the circle representing the prey's minimum turning radius prior to the prey arriving at that point, then the prey has committed a highly unfavorable action. As long as this condition persists, the prey can maintain the maximum distance between itself and the predator by fleeing along a linear path directly away from the predator. Provided that the minimum turning radius of the prey is smaller than the minimum turning radius of the predator and the prey can execute a turn whose path crosses the intersection before the predator's does, then the prey can exploit this advantage by executing a minimum-radius turn to escape from the danger area [Howland

1974, 334–335]. Such escape is a temporary solution, since the predator will eventually adjust its approach vector and resume the chase. However, if the prey is capable of executing these maneuvers for a sufficiently long period of time, then the predator may have to abandon the chase. Therefore, the optimal strategy for the prey is to run directly away from the predator until the distance decreases to the point where the turning gambit is effective.

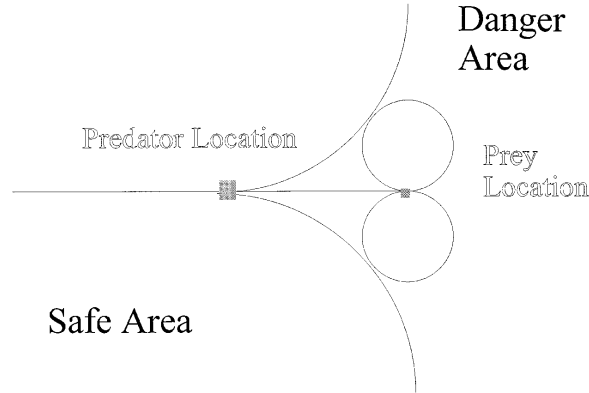


Figure 1. Ineffective turning region.

Both the predator and prey are assumed to be traveling at extremely high speeds. In the problem statement, the maximum speeds of predator and prey are 60 km/hr and 50 km/hr, with minimum turning radii 1.5 m and 0.5 m. The equation for centripetal acceleration is

$$a = \frac{v^2}{r}.$$

Therefore, the centripetal acceleration of the predator and prey, given their maximum speeds and turning radii, are

$$a_v = \frac{\left( \frac{60 \text{ km}}{\text{hr}} \cdot \frac{1000 \text{ m}}{1 \text{ km}} \cdot \frac{1 \text{ hr}}{3600 \text{ s}} \right)^2}{1.5 \text{ m}} = 185.2 \text{ m/sec}^2 = 18.9 \text{ g's},$$

$$a_t = \frac{\left( \frac{50 \text{ km}}{\text{hr}} \cdot \frac{1000 \text{ m}}{1 \text{ km}} \cdot \frac{1 \text{ hr}}{3600 \text{ s}} \right)^2}{0.5 \text{ m}} = 385.8 \text{ m/sec}^2 = 39.4 \text{ g's}.$$

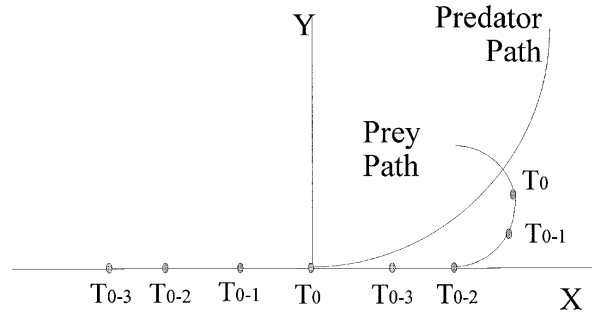
These are not reasonable acceleration rates. Either the turning radii must be significantly larger, or else the animals must decelerate prior to entering the turns. We define  $G_v$  and  $G_t$  as the maximum number of g's that the animals can tolerate, either as linear or centripetal acceleration. We estimate 2.0 to be a reasonable value for both of these constants, which result in turning radii of 14.2 m for the predator and 9.8 m for the prey, or else speeds of 5.4 m/sec for the predator and 3.1 m/sec for the prey.

We include a reaction time and a deceleration period during which the animal adjusts its velocity to achieve its minimum turning radius. The ratio

of the turning radii is more relevant than their actual values, since this ratio determines whether the prey will successfully reach the safe area. We therefore normalize the radii relative to the radius of the predator's minimum turn. Following the example of Howland [1974], we normalize the speeds in a similar manner. Therefore the predator's speed is arbitrarily set to 1, as is the predator's radius. The prey's speed is set to  $v_t/v_v$ , and the prey's radius is set to  $r_t/r_v$ . To create a parametric equation in dimensionless units, we normalize time,  $x$ , and  $y$  as follows:

$$t = \frac{Tv_v}{r_v}, \quad x_v = X_v/r_v, \quad y_v = Y_v/r_v.$$

We define the starting point of the turning gambit to be  $T_0 = 0$ , which implies that  $t = 0$  at the beginning of the maneuver. The total time of the chase is the sum of the time spent in the linear chase, plus the time spent in the maneuver, plus the time spent following the maneuver, assuming that it is successful. In **Figure 2**, we label the four critical time events.



**Figure 2.** Turning gambit.

At  $T_{0-3}$ , the prey begins to decelerate. At  $T_{0-2}$ , the prey enters the turn. At this point the predator recognizes the turn and experiences a reaction period. At  $T_{0-1}$ , the predator begins to decelerate while the prey continues on the turn. At  $T_0$ , the predator begins his turn. The gambit is successful if the prey is able to reach the intersection prior to the predator reaching that point. Since the interval between  $T_{0-3}$  and  $T_0$  is easily calculable, and the distance traveled by the predator is along a straight path, we calculate this time and distance separately:

$$[T_0 - T_{0-3}] \text{ s}, \quad [(T_{0-1} - T_{0-3})V_v + (T_0 - T_{0-1})V_v + \frac{1}{2}G_v g(T_0 - T_{0-1})^2] \text{ m},$$

and begin our calculations for the turning gambit at point  $T_0$ . The equations for the two arcs are as follows:

$$\begin{aligned} x_v &= \sin t, & y_v &= 1 - \cos t; \\ x_t &= x_0 + r \sin \left( \frac{v[t + (t_0 - t_{0-3})]}{r} \right), & y_t &= r - r \cos \left( \frac{v[t + (t_0 - t_{0-3})]}{r} \right). \end{aligned}$$

The prey reaches the safe area if it arrives at the intersection of the two arcs prior to the arrival of the predator. The intersection occurs at  $x_v = x_t$ ,  $y_v = y_t$ . These values can be computed using the bisection method, or alternatively by Newton's method, since the predator's path is limited to the first quadrant. Using a relative speed of 0.33, a combined normalized reaction and deceleration time of 0.2 (which corresponds to a real time significantly less than 0.2 s, so in essence this is reaction time only, with no deceleration), and a normalized  $x_0$  value of 1.06, intersection occurs at (0.9, 0.66), and both animals arrived simultaneously. Thus, this starting point was a poor choice for the prey.

Once we have solved the intersection problem, it is easy to find the minimum distance required for the gambit to be successful. If detection has not occurred outside of this range, then the prey's gambit will fail and the predator will win. An effective stealth strategy is therefore beneficial to the predator.

The intersection calculated above, which reflects the assumptions in the problem statement, represents the critical point: Any  $x_0$  less than 1.06 that does not permit the predator to catch the prey on the predator's linear path will result in escape. Assuming a 1.5 m radius for the predator, this represents a negligible elapsed time; but if we assume a more reasonable radius of 14.2 m, this corresponds to 23.9 m, or roughly 1.5 s. During this time, the predator has completed roughly one-fourth of a circle, so an additional 3.0 s will expire prior to its re-establishing a linear vector with respect to the prey. So if the prey bolted when the predator was 30 m or farther away, and  $M_v$  is 15 s or less, then the predator will have failed to capture the prey and the game is over.

In fact, with a relative radius of 0.33, the prey can repeat the winning strategy indefinitely, regardless of the actions of the predator, assuming that the predator reacts to the prey's maneuvers. Therefore, we would recommend that a single predator attempt to anticipate the optimal distance for a turning maneuver, guess the direction, and turn preemptively. If the predator notices that the prey has not turned after the beginning of the predator's preemptive move, then the predator should change to the opposite direction. This will force the prey to turn in the revised direction, decreasing the length of the arc prior to intersection with the predator's path. This results in a probability function for the predator of

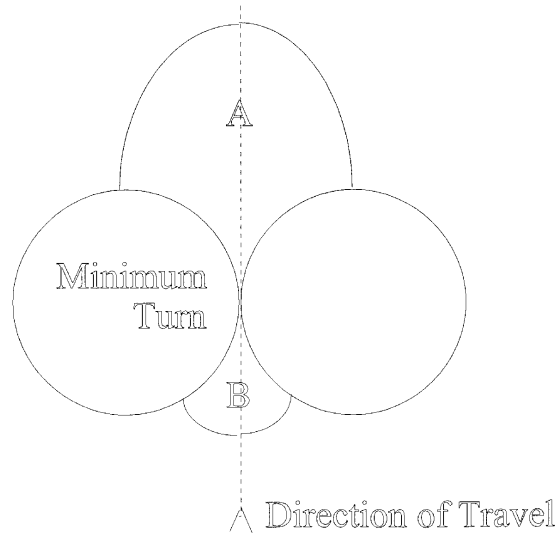
$$\frac{(t_0 - t_{0-1}) + (t_{0-2} - t_{0-3})}{(t_0 - t_{0-3})} \cdot P[\text{successful attack when within range}].$$

## Model 2: Multiple Predators, Single Prey

Our first objective is to define a distance function representing the prey's possible destinations, given a finite escape window. We assume that the prey can either continue in the forward direction at its maximum speed, or make a turn with a radius less than or equal to its minimum turning radius, or it can come to a full stop and resume in any direction. Although we account for acceleration and deceleration time when the animals change direction, we

assume that their deceleration time going into a curve and their acceleration times coming out of curves are instantaneous. This somewhat overstates the available forward region; but it overstates it for both predator and prey, and it doesn't change the characteristics of the safety and danger regions (as we will show). So we believe that it will result in a slight understatement of the "double danger" region, and an even smaller impact upon the overall probability function.

As we discussed in the one-one model, a tighter turning radius implies a smaller speed, given a limiting acceleration rate. In **Figure 3**, the region that can be reached in a finite time period, in the forward direction, is the area in the figure marked "A".



**Figure 3.** Accessible area.

The area marked "B" represents the reachable area if the animal comes to a complete stop, turns  $180^\circ$ , then resumes travel in the reverse direction and remains subject to the minimum turning radius. In fact, the animal could resume travel in any direction; however, given the reality of high-speed pursuit, it likely will resume maximum speed as quickly as possible, so the area inscribed by the figure is accurate, although the direction may not be. The area in region B and the area in region A are described by the same equation, although the time value in the B area is smaller since the deceleration time must be deducted. The equations for determining these areas are

$$r = \frac{V^2}{a}, \quad \theta = \frac{tv}{r} = t\sqrt{\frac{a}{r}},$$

$$x = r(1 - \cos \theta), \quad y = r \sin \theta,$$

$$\text{Area}(A) = 2 \int_{V^2/M}^{\infty} r \sin \left( t\sqrt{\frac{a}{r}} \right) dr - 2 \int_0^D \sqrt{\left( \frac{V^2}{M} \right)^2 - x^2} dx,$$



where

$$D = \left[ 1 - \cos \left( t \sqrt{\frac{a}{V^2/M}} \right) \right] \frac{V^2}{M}.$$

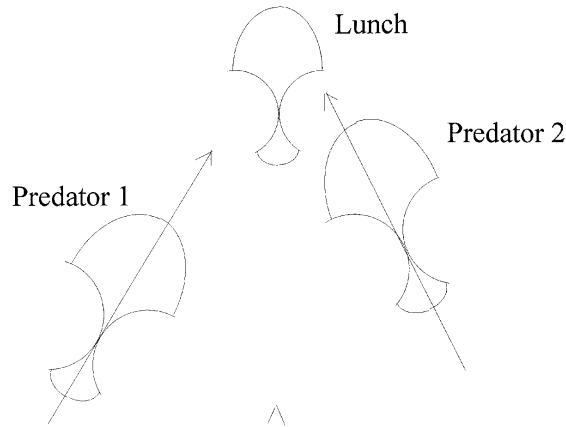
The calculation for  $\text{Area}(B)$  uses the same equation, except that the time value  $t$  is replaced by  $(t - t_b)$ , where  $t_b$  is the total time required to decelerate, stop, and accelerate to full speed in the new direction.

Given our area equation, we now have the necessary tools to develop an optimal chase strategy. The probability of a successful hunt is

$$\begin{aligned} P[\text{successful hunt}] = & \{ \text{Overlap}(\text{Prey}, \text{Predator1}) + \text{Overlap}(\text{Prey}, \text{Predator2}) \\ & - 2 \times \text{Overlap}(\text{Predator1}, \text{Predator2}) \} \\ & \times P[\text{successful hunt with single predator}] \\ & + \text{Overlap}(\text{Predator1}, \text{Predator2}) \times P[\text{success of two predators}], \end{aligned}$$

where  $\text{Overlap}(A, B)$  is a function computing the area of the overlapping region between areas  $A$  and  $B$ . This function can be constructed as a combination of two iterations of the same area integral used previously, with adjustment for the relative positions and orientations of the two areas. We have not constructed this function during this project.

Given our probability function, and the existence of an Overlap function, we can numerically solve for the optimal displacement and orientation vectors that maximize the value of  $P[\text{successful hunt}]$ . With reasonable values of the two success functions, we would expect a strategy of converging attack, with one predator remaining sufficiently behind, such that the probability of capturing the prey throughout its entire region is at least  $P[\text{successful hunt with a single predator}]$ , as shown in **Figure 4**.



**Figure 4.** Optimal attack vectors.

Note that we have drawn the accessible regions quite smaller than their actual size, to illustrate the relationships without the clutter of overlapping lines and curves. Any strategy where the predators are parallel to the  $x$ -axis

is inferior, since at some point in the chase the  $B$  region of the prey will be uncovered by either probability function. This in turn gives rise to an effective prey strategy. It is in the prey's interest to have such an uncovered region exist. Therefore, the prey's best strategy is to alter course in the direction of the trailing predator, in an attempt to achieve a normal escape vector with respect to the lines between the two predators. If the prey is able to get directly between the two predators, with a direction vector directly towards one of the two, it can employ the strategy outlined in the first model, effectively reducing the problem to a single-predator problem. These simple assertions address all of the possible cases of the two-one problem.

Adding additional predators increases the successful hunt probability and effectively eliminates the prey's linearization strategy, since getting three or more predators collinear is more difficult than two. Whether this total probability is superior to the case where two or more separate games (of one-one or two-one) are conducted concurrently depends on the probability values assigned to each function. With the exception of assuring that all predators avoid collinearity, the strategy employed by each predator in a group, except for the lead predator, is identical. This results in the prey being coerced into a spiral path with decreasing predator-to-prey distances. In any case of two or more predators, the prey is in a very poor situation.

## Limitations of the Model

As with most mathematical models, our model has a number of limitations.

- Our model deals with a one-time chase and gives no indication of the result of a second encounter between the same prey and the same predator. We have not explored the learning that each animal undergoes between chases.
- Our model deals solely with the optimum distance at which the prey should initiate a turning strategy and does not take into account the scenario of detection of the predator by the prey. If the distance at which the prey first detects the predator is smaller than the optimal distance at which the prey should employ its turning maneuver, then the prey will not escape successfully.
- Although the probability functions that assign probabilities of a successful hunt to various areas of overlap exist, these functions may be difficult to derive explicitly.
- Our models do not rely extensively on the actual biological or mechanical aspects of the dinosaurs themselves, and this limitation is probably the most difficult one to overcome, since the only data regarding these dinosaurs are found in fossils.

- We have limited knowledge of the *Velociraptor's* hunting habits. We are uncertain whether they are search-oriented creatures (as we have assumed from the outset) or whether they wait and hide for their prey.
- We have treated the dinosaurs as point masses. In reality, even if their trajectories do not cross at exactly the same time, it is still possible that the two dinosaurs come sufficiently close that the predator can reach the prey, or the predator may otherwise jump out to capture the prey.

## Discussion of Alternatives

Our model addresses the most obvious variable characteristics of a predator-prey relationship but it does so in an idealized manner. We assume that the prey and the predator are making relatively informed decisions and that they are making rational choices based on perceived information. While we are confident that we in fact do model the behavior of the animals, we are uncomfortable with the premise that the animals are solving optimization problems while running for their lives. In this section, we discuss a method by which the predator and prey can essentially choose the expected actions but that does not require the assumption of advanced cognition. Specifically, we are searching for general strategies that optimize success in all of the various  $n \times m$  models while minimizing both the information-gathering and cognitive-processing requirements.

Our method uses genetic programming to develop both the prey and predator models. The essence of this method is the generation of “chromosomes” that contain “genes” in a manner that selects for fitness. In this context, the chromosomes represent entire programs and the genes represent individual program steps. Given their differing objectives, the predators and prey have different genes and chromosomes. The process of genetic programming is to generate randomly several hundred “individuals,” to test each individual’s fitness, then to select the most fit individuals for reproduction.

Reproduction involves copying the individuals in the culled pool and randomly applying certain mutations. At the end of the reproduction stage, the new pool of individuals is again tested; and the process is repeated until the pool is comprised exclusively of fit individuals.

It is fairly easy to develop a predator model that can always converge on a stationary prey or set of prey. Koza [1992] describes two genetic programs relating to ant behavior. The first involves a trail of food with an objective of passing over each item in a limited amount of time [1992, 251–257]. Using an extremely limited function set consisting of

- terminal actions Move, Right, and Left;
- decision functions If-food-present-do-next-else-do-subsequent, Do-two-actions-sequentially, and Do-three-actions-sequentially;

- 20 genes,

it took only 21 generations to evolve a program that successfully located 89 of 89 food objects. Expanding the function set to a total of nine operations, including Drop-pheromone and Move-to-adjacent-pheromone, with 47 genes, resulted in a single program produced by generation 38 that could be executed by each member of an ant colony, with the result that the colony was able to locate and transport 144 food objects from two locations within a limited time period [1992, 310–317].

We developed a set of primitives for both the prey and predator programs that could be used to evolve effective strategies genetically. The requirement of adapting to the presence of one or more additional predators makes both the prey and predator programs significantly more complex than Koza's ant functions, but they are entirely reasonable as possibilities for higher animals. Thus, we would expect to need a chromosome with roughly 1,000 genes, and we would expect a minimum of several hundred generations before an adequate program evolved. If dinosaur cognition is primarily instinctive, as is the case for ants, one might argue that the predators are unlikely to survive a learning process of such a duration. On the other hand, if the dinosaurs learn their hunting strategies, then an individual need only participate in a few hundred hunts to master or develop a successful technique. The prey do not get the opportunity to learn from their mistakes. Thus, we would suspect that their responses need to be more instinctual. We would therefore argue that necessary conditions for this mechanism to be adopted by both prey and predator would be *r*-favored reproduction by the prey and relatively high intelligence in the case of the predators. These traits are consistent with current theory regarding both animals.

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