

Evolutionary Dynamics of Protean Evasion

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ABSTRACT

Pursuit and evasion are among the most widespread interactions in which animals engage. Effective evasion may be promoted by adopting various protean behaviors (erratic, unpredictable, and confusing) that may serve to confuse pursuers and increase their reaction time. In this study, pursuers and evaders were modeled as particles moving at a constant speed, with strategy-dependent feedback control rules for direction. The effectiveness of three evasion strategies (pure evasion, random movement and zigzagging) was examined. Different versions of random movement and zigzagging were assessed, using simulations that determined capture time for each version when confronted by a pure pursuit pursuer. Monte Carlo simulations were used in a discrete-time evolutionary game to examine competition among evasion strategies when pitted against pure pursuit players of varying speed and maneuverability. The evolutionary dynamics converge to a pure strategy of zigzag evasion. Directions for future work on evasion are presented.

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INTRODUCTION

Pursuit and evasion are among the most widespread interactions in which animals engage. The outcome for humans can range from winning a game of tag to determining the outcome of a military campaign (Isaacs 1965, Nahin 2007). In the natural world, pursuit and evasion are linked to such essential endeavors as eating (and not being eaten) as well as competing for access to resources (Caro 2005). For many animals, predator avoidance is central to daily activities; without an effective strategy for avoiding predators, animals will experience a shortened lifespan, while an overly conservative or demanding strategy will divert time and energy away from other important activities. Identifying how animals could best respond to predation threats will help in understanding their decision making.

Much research has been devoted to understanding different pursuit and evasion strategies, often in the context of predation. Studies have examined the mechanical aspects of pursuit and evasion (Howland 1974, Ghose et al. 2006), as well as the physiological aspects that allow for certain strategies (Srinivasan and Zhang 2004). Others have assessed the decisions of individual pursuers and evaders in the context of costs and benefits (Weihs and Webb 1984), or with the strategies of pursuit and evasion as differential games (Isaacs 1965). A more recent approach is to examine different strategies as traits subject to evolution; pursuer-evader interactions are modelled using self-propelled particles as individuals, moving at a constant speed, with feedback control rules for directions (Wei et al. 2009, Pais and Leonard 2010). Given an appropriate characterization of the control rules governing the dynamics of pursuit-evasion interactions, simulations can be used to examine the evolutionary competitiveness of different strategies (Pais and Leonard 2010).

A foundational study examined the predator pursuit strategies of motion camouflage and pure pursuit, while using evaders restricted to nonreactive evasion strategies (linear travel, sinusoidal paths, and random movement; Justh and Krishnaprasad 2006). They formulated a feedback system using particles moving at a constant speed in a planar environment and rules for controlling direction. They explored the dynamics of their system through simulations of pursuit-evasion interactions. Motion camouflage occurs among some predatory insects (Srinivasan and Davey 1995, Mizutani et al. 2003); the pursuer minimizes apparent motion by maintaining the same directional bearing as the evader. The pursuit strategy of motion camouflage is fascinating but has a limited distribution among animals (Mizutani et al. 2003).

In a second study, the effectiveness of three pursuit strategies were compared by first modelling the players as using particles moving at a constant speed, with rules for controlling direction and then allowing the strategies to compete in an evolutionary game (Wei et al. 2009). With a focus on pursuit strategies, nonreactive (linear travel) evasion strategies were used and motion camouflage was identified as a superior pursuit strategy (Wei et al. 2009). However, using different sets of evasion strategies can result in different conclusions on the effectiveness of pursuit strategies (Wei et al. 2009, Pais and Leonard 2010). In their examination of the effectiveness of three evasion strategies against three pursuit strategies, Pais and Leonard (2010) used time to capture as a measure of fitness, reactive evasion strategies and evolutionary dynamics to determine the competitiveness of different strategies. Thus, Pais and Leonard (2010) used more realistic strategies than their predecessors and incorporated evolutionary dynamics as a means of comparing strategies. Next steps in the exploration of pursuit and evasion strategies include examining how control rule parameters influence strategy success and how strategies fare in different competitive environments (Pais and Leonard 2010). For instance, Pais and

Leonard (2010) used a single pair of pursuer/evader speeds and assumed that both pursuer and evader had the same level of maneuverability (= ability to quickly achieve a change in direction; Pais and Leonard 2010). Allowing these parameters to vary may help elucidate some previously unexplored relationships. Predator and prey often differ in maneuverability (Howland 1974); with evaders being smaller than pursuers in predator-prey interactions, evaders should be more maneuverable. Further, the use of pursuers with different speeds may allow for an examination of the anticipated tradeoff between speed and maneuverability (Howland 1974). In addition, other evasion strategies may be more appropriate to certain situations and should be explored (Pais and Leonard 2010). In the natural world, evasion is more directly linked to survival than pursuit, since animals typically only have one chance to fail at evasion (Caro 2005).

Understanding evasion strategies effectiveness have received less attention than pursuit strategy effectiveness. Using the approach of Pais and Leonard (2010), this study examines different evasion strategies' effectiveness.

Evasion

Once an animal chooses to flee, actual evasion behavior may involve multiple tactics, each with potential limitations (Caro 2005, Nahin 2007). Often speed is not sufficient; an evader may not be able to simply outrun its pursuer, making directional evasive maneuvers potentially useful. From the evader's point of view, prolonging the pursuit achieves the goal of increasing the chance of escape (Weihs and Webb 1984). However, if an evasion strategy is too predictable, predators may be able to improve their success by anticipating how prey will react. A thoroughly unpredictable evasion pathway could result in trajectories that bring an evader closer to a pursuer. It has been suggested that effective evasion can be promoted by adopting various protean

behaviors (erratic, unpredictable, and confusing) that may serve to confuse pursuers and increase their reaction time (Chance and Russell 1959, Humphries and Driver 1967, 1970). Protean behaviors include a range of seemingly disparate actions such as the inking discharge of cephalopods and the apparent difficulty associated with trying to pursue individuals in a group (swarm effect; Caro 2005). Likewise, protean strategies include motion that involves fast turns and unpredictable trajectories that might be advantageous for evading pursuers (Cresswell 1993, Edut and Eilam 2004, Caro 2005). Many animals incorporate elements of unpredictability into their evasion strategies. Moths, for example, can engage in various aerial acrobatics (e.g., loops, rolls, and tight turns) as they try to avoid capture by bats (Roeder 1967). Cockroaches generally flee away from a threat but exhibit an element of unpredictability concerning the exact trajectory angle (Domenici et al 2008). Shoals of minnows (*Phoxinus phoxinus*) make use of more dramatic and less predictable evasive tactics as the intensity of predator attacks increases (Magurran and Pitcher 1987). A single maneuver can result in a decreased likelihood of capture (Humphries and Driver 1970, Jones et al. 2011). Among the questions that can be asked: 1) are some unpredictable behaviors more effective than others and 2) can they be evolutionarily successful against more deterministic strategies? The focus on this study is on the protean maneuver of zigzagging, which is exhibited by a diverse group of animals (Vannini 1980, Djawdan and Garland 1988, Caro 2004, Lerner 2011, Eifler and Eifler 2014).

Game Theory and Evolutionary Dynamics

Game theory typically deals with interactions between players and usually assumes rational behavior (Nowak 2006). Evolutionary game theory deals with populations of players who engage in strategies where the players interact randomly and the sum of the payoffs from these

interactions serves as a measure for reproductive success and natural selection (Maynard Smith 1982, Nowak 2006, Broom and Rychtář 2013). The success of a particular biological trait is often framed in terms of *fitness*, which refers to the ability to contribute offspring to the next generation. Natural selection acts according to the relative fitness of traits. For this study, time-to-capture was used as an index of fitness; low values improve a pursuer's fitness, but lower an evader's fitness.

In this study, the work of Pais and Leonard (2010) is extended through a focus on evasion strategies. Using constant speed particles moving in a planar environment, they identified control rules for direction, simulated discrete-time interactions between pursuers and evaders, and used Monte Carlo simulations to explore the evolutionary dynamics of competition among different strategies. Their most effective strategies were pure pursuit and pure evasion (defined below). In the current study, variations of pure pursuit are used, where different combinations of relative pursuer speed and maneuverability are employed, with the condition that speed and maneuverability trade-off. For evasion, the current study uses pure evasion, a random movement strategy and a protean strategy of zigzagging.

METHODS

The general approach of this study was to 1) model pursuit and evasion strategies, 2) use simulations of pursuer-evader interactions to assess the impact of different control rule parameters on fitness and 3) use Monte Carlo simulations of pursuer and evader evolutionary dynamics to examine strategy competitiveness. Time until capture was used as a measure of

fitness, with *capture* meaning the Euclidean distance between pursuer and evader has reached a specified minimum.

Pursuit-evasion model

Pursuit-evader system:

Pursuer (P) and evader (E) were modelled as particles moving on a two dimensional surface, where each player moved with constant speed and direction was determined by control laws and interactions between the participants. The state space for the pursuer-evader system was $G \times G$, where $G = SE(2)$ is the special Euclidean group. The pursuit-evader system is based on the work of Justh and Krishnaprasad (2006) and Pais and Leonard (2010).

Pursuers and evaders were viewed as moving on a complex plane with positions $r_p = x_p + iy_p$ and $r_E = x_E + iy_E$ and bearings are θ_p and θ_E on a unit circle. Changes in player location are represented by:

$$\dot{r}_p = e^{i\theta_p}, \dot{\theta}_p = u_p \quad (1)$$

$$\dot{r}_E = v e^{i\theta_E}, \dot{\theta}_E = u_E.$$

Pursuer speed was 1 and evader speed was $v < 1$; pursuers were assumed to be faster than evaders. The baseline vector r is the relative position of the pursuer with respect to the evader.

$$r = r_p - r_E \quad (2)$$

$$\dot{r} = e^{i\theta_p} - v e^{i\theta_E}$$

Capture during a pursuer-evader interaction occurs when the distance between pursuer and evader ($|r|$) reaches some capture radius threshold ε .

Notation: For complex numbers $c_1, c_2 \in \mathbf{C}$, $\langle c_1, c_2 \rangle := \text{Re}(c_1 c_2^*)$, the real part of $c_1 c_2^*$ where c_2^* is the complex conjugate of c_2 . $|c_1|$ is the complex modulus of c_1 .

Pursuit control rules:

- 1) *Pure pursuit* refers to instances where the pursuer aligns itself with the baseline vector (Pais and Leonard 2010); the pursuer travels directly toward the instantaneous location of the evader (Nahin 2007). Figure 1 shows the path of a pure pursuer approaching an evader travelling in a line. The basic control rule for steering pure pursuit is adapted from the “classic pursuit” law of Pais and Leonard (2010)

$$u_P = -\eta_P \left\langle \frac{r}{|r|}, i e^{i\theta_P} \right\rangle - \frac{1}{|r|} \left\langle \frac{r}{|r|}, i \dot{r} \right\rangle, \quad (3)$$

where η_P is a constant gain that reflects the maneuverability of the pursuer. For this study, it was assumed that evaders were more maneuverable than pursuers ($\eta_P \leq \eta_E$). Three distinct pure pursuer types were employed: *dodger* with relatively high η_P and relatively low speed (high v), *joe* with intermediate η_P and intermediate speed, *speedy* with low η_P and relatively high speed (low v). To identify the parameter values for these types, the speed ($v = 0.6$) used for both pursuers and evaders by Pais and Leonard (2010) was designated the fastest pursuer speed; the other two speeds were 10 and 20% slower. These represent relative speeds that fall within the range for real pairs of predators and prey (Furuichi 2002). The middle speed ($v = 0.66$) was then used to identify three η_P

levels. A single-turn pure pursuit of a linear moving object was simulated for different η_P values (Figure 2), and values were selected that produced capture times differing by approximately 10%. The range of predator speeds (presented as v) and accompanying η_P values for Monte Carlo simulations were: $v = (0.6, 0.67, 0.75)$ and $\eta_E = (0.4, 0.55, 0.9)$.

Evasion control rules:

- 1) *Pure evasion* refers to instances where the evader aligns itself with the baseline vector (Pais and Leonard 2010) and moves directly away from the evader. The basic control rule for steering pure evasion is adapted from the “classic evasion” law of Pais and Leonard (2010)

$$u_E = -\eta_E \left\langle \frac{r}{|r|}, i e^{i\theta_E} \right\rangle, \quad (4)$$

where η_E is a constant gain that reflects maneuverability. Evaders are always at least as maneuverable as pursuers ($\eta_P \leq \eta_E$).

- 2) *Random evasion* was defined as:

$$\begin{aligned} & \text{piecewise linear paths with a probability } P_t \text{ of a turn} \\ & \text{every } \alpha \text{ time units and } u_E \text{ selected uniformly randomly} \\ & \text{from } [-k, k] \text{ at every turn.} \end{aligned} \quad (5)$$

This nonreactive strategy is adapted from the “random motion evasion” law of Pais and Leonard (2010). To evaluate potential values for P_t and k , pure pursuit ($v = 0.6, \eta_P = \eta_E$) of random evaders was simulated 1000 times each for a range of values ($P_t = (0.3, 0.5)$ and $k = (\frac{\pi}{4}, \frac{\pi}{2}, 2, \pi)$). The combination of P_t and k that resulted in the longest mean capture time was used in the simulations of evolutionary dynamics.

3) *Protean zigzag evasion* was defined as:

$$u_E = -\eta_E \left\langle \frac{r}{|r|}, i e^{i\theta_E} \right\rangle, \text{ while } |r| \geq \tau, \quad (6)$$

Otherwise, u_E is selected uniformly randomly from $\pm \left[\frac{\pi}{6}, \frac{\pi}{3} \right]$,

followed by linear travel with duration selected uniformly randomly

from $[1,2]$ time units and the next u_E selected uniformly randomly

from $\left[\frac{\pi}{6}, \frac{\pi}{3} \right]$, with opposite sign,

where τ is a threshold for $|r|$, the distance between pursuer and evader. This is a reactive strategy where the evader engages in pure evasion for distant pursuers and employs a sequence of unpredictable turns at close quarters. To evaluate values for τ , pure pursuit ($v = 0.6, \eta_P = \eta_E$) of zigzagging evaders was simulated 1000 times each for a range of threshold values ($\tau = (1.5, 2, \dots, 6.5)$).

Simulation of pursuer-evader interactions:

The control rules were used to simulate pursuer-evader interactions in a series of discrete moves. The following approach was employed:

- 1) *Determine pursuer and evader initial positions:* The evader started at the origin with bearing (θ_E) zero and the pursuer was located uniformly randomly on the square $[-10,10] \times [-10,10]$ and had an initial bearing (θ_P) selected uniformly randomly on a unit circle.
- 2) *Calculate pursuers and evader's next positions:* Pursuers and evaders were advanced in the direction of their bearings, respectively at the speeds of 1 and v . New positions were calculated at 0.2 time unit increments.

- 3) *Reorient the pursuers and evaders*: After a movement, the changes in bearings ($\dot{\theta}_P$ and $\dot{\theta}_E$) and the new bearing (θ_P and θ_E) were determined.
- 4) *Continue interaction*: Steps 2 and 3 were repeated until the distance between pursuer and evader reached the capture radius. Capture time was recorded.
- 5) *Determine capture time variation*: Simulations were run 1000 times with new initial pursuer locations and bearings generated for each simulation. To examine the influence of different parameter values on pursuit and evasion success, simulations were run 1000 times for each parameter value of interest.

Evolutionary Dynamics

Population structure and change:

To examine the evolutionary potential of different pursuit and evasion strategies, their ability to persist over time in populations that were composed of different founding proportions of strategy users was examined. As in Pais and Leonard (2010), the population structure of pursuers (\mathbf{p}) and evaders (\mathbf{q}) can be represented as vectors where p_i (or q_j) represents the proportion of the population that employs strategy i (or j),

$$\mathbf{p} = [p_1 \quad p_2 \quad p_3]^T, \quad (7)$$

$$\mathbf{q} = [q_1 \quad q_2 \quad q_3]^T.$$

The values in vectors \mathbf{p} and \mathbf{q} sum to one and cannot be negative. Population structure for a given generation depends on the population structure of the proceeding generation and the relative fitness of each strategy; capture time was used as a measure of fitness. Following Pais and

Leonard (2010), fitness values were calculated using a capture time matrix $\mathbf{C} \in \mathbf{R}^{3 \times 3}$ developed by pitting each pursuit strategy against each evasion strategy. The element C_{ij} is the capture time for p_i versus q_j . If $\mathbf{C}(g)$ represents the capture matrix used for generation g , then $\mathbf{M}(g) = \mathbf{C}^R(g)$ where m_{ij} is the reciprocal of c_{ij} . The fitness vectors are represented by $\mathbf{f}_P \in \mathbf{R}_+^3$ and $\mathbf{f}_E \in \mathbf{R}_+^3$, where f_{p_i} is the fitness of the pursuit strategy (p_i) and f_{E_j} is the fitness of the evasive strategy (q_j). The fitness vectors used for determining the next generation were defined:

$$\mathbf{f}_P(g) = \mathbf{M}(g)\mathbf{q}(g) \quad (8)$$

$$\mathbf{f}_E(g) = \mathbf{C}^T(g)\mathbf{p}(g).$$

The fitness of pursuer strategies depends on the population structure of evaders and the fitness of evader strategies depends on the population structure pursuers. Evolutionary fitness focuses on the relative contribution to the next generation, so fitness vectors are divided by mean fitness, before determining the structure of the next generation. Population mean fitnesses were defined as $\hat{f}_P = \mathbf{p}^T \mathbf{f}_P$ and $\hat{f}_E = \mathbf{q}^T \mathbf{f}_E$. Population structure from one generation (g) to the next ($g+1$) can be determined using the discrete update equations of Pais and Leonard (2010):

$$\mathbf{p}(g+1) = \mathbf{p}(g)\mathbf{f}_P^T \left(\frac{1}{\hat{f}_P} \right), \quad (9)$$

$$\mathbf{q}(g+1) = \mathbf{q}(g)\mathbf{f}_E^T \left(\frac{1}{\hat{f}_E} \right).$$

Example of population change:

For illustration, initial populations of pursuers and evaders are provided by the vectors:

$$\mathbf{p}^T(0) = \begin{array}{ccc} \textit{Speedy} & \textit{Joe} & \textit{Dodger} \\ [0.1606 & 0.1991 & 0.6403] \end{array}'$$
$$\mathbf{q}^T(0) = \begin{array}{ccc} \textit{Pure} & \textit{Random} & \textit{Zigzag} \\ [0.6117 & 0.1684 & 0.2199] \end{array}'$$

These initial populations, for instance, are composed of pursuers who will primarily be using the dodger version of pursuit (64% of individuals) and evaders who will be relying primarily on pure evasion (61% of individuals).

For illustration, the capture matrix (\mathbf{C}) for the populations is provided by the matrix:

$$\mathbf{C}(0) = \begin{array}{ccc} & \textit{Pure} & \textit{Random} & \textit{Zigzag} \\ \textit{Speedy} & [16.80 & 7.92 & 18.30] \\ \textit{Joe} & [21.40 & 10.32 & 22.62] \\ \textit{Dodger} & [27.00 & 9.70 & 28.12] \end{array}'$$

Values in the capture matrix (\mathbf{C}) represent capture times for different pairings of pursuit and evasion strategies. For instance, a speedy pursuer is able to capture a random evader more quickly than a zigzagging evader (7.92 vs 18.30 time units) and a zigzagging evader can delay capture longer against a dodger than a speedy pursuer (28.12 vs 18.30 time units). The reciprocal matrix (\mathbf{M}) that corresponds to the capture matrix (\mathbf{C}) is shown below:

$$\mathbf{M}(0) = \begin{array}{c} \text{Speedy} \\ \text{Joe} \\ \text{Dodger} \end{array} \begin{array}{ccc} \text{Pure} & \text{Random} & \text{Zigzag} \\ \begin{bmatrix} 0.0595 & 0.1263 & 0.0546 \\ 0.0467 & 0.0969 & 0.0442 \\ 0.0370 & 0.1031 & 0.0356 \end{bmatrix} \end{array}$$

Whereas larger values in capture matrix (\mathbf{C}) imply greater success when comparing evasion strategies, larger values in reciprocal matrix (\mathbf{M}) imply greater success when comparing pursuit strategies.

Fitness vectors are calculated for both pursuers and evaders:

$$\mathbf{f}_P = \mathbf{M}(0)\mathbf{q}(0) = \begin{bmatrix} 0.0595 & 0.1263 & 0.0546 \\ 0.0467 & 0.0969 & 0.0442 \\ 0.0370 & 0.1031 & 0.0356 \end{bmatrix} \begin{bmatrix} 0.6117 \\ 0.1684 \\ 0.2199 \end{bmatrix} = \begin{array}{c} \text{Speedy} \\ \text{Joe} \\ \text{Dodger} \end{array} \begin{bmatrix} 0.0697 \\ 0.0546 \\ 0.0476 \end{bmatrix},$$

$$\mathbf{f}_E = \mathbf{C}^T(0)\mathbf{p}(0) = \begin{bmatrix} 16.80 & 21.40 & 27.00 \\ 7.92 & 10.32 & 9.70 \\ 18.30 & 22.62 & 28.12 \end{bmatrix} \begin{bmatrix} 0.1696 \\ 0.1991 \\ 0.6403 \end{bmatrix} = \begin{array}{c} \text{Pure} \\ \text{Random} \\ \text{Zigzag} \end{array} \begin{bmatrix} 24.2467 \\ 9.5376 \\ 25.4776 \end{bmatrix}.$$

The values of these vectors indicate which strategies are more successful in the current generation. In this example, speedy and zigzag appear to be the fitter strategies. Since evolutionary fitness focuses on the relative contribution to the next generation, fitness vectors are divided by mean fitness, before determining the structure of the next generation. Population mean fitness for pursuers and evaders is calculated as:

$$\hat{f}_P = \mathbf{p}^T \mathbf{f}_P = [0.1606 \quad 0.1991 \quad 0.6403] \begin{bmatrix} 0.0697 \\ 0.0546 \\ 0.0476 \end{bmatrix} = 0.0527,$$

$$\hat{f}_E = \mathbf{q}^T \mathbf{f}_E = [0.6117 \quad 0.1684 \quad 0.2199] \begin{bmatrix} 24.2467 \\ 9.5376 \\ 25.4776 \end{bmatrix} = 22.0338.$$

In the next generation, strategies are represented in the population in relation to their proportions in the current generation and the relative fitness of the strategy.

$$\begin{aligned} \mathbf{p}(1) &= \mathbf{p}(0) \mathbf{f}_P^T \left(\frac{1}{\hat{f}_P} \right) = \begin{bmatrix} 0.1696 \\ 0.1991 \\ 0.6403 \end{bmatrix} [0.0697 \quad 0.0546 \quad 0.0476] \left(\frac{1}{0.0527} \right) \\ &= \begin{matrix} \textit{Speedy} & \textit{Joe} & \textit{Dodger} \\ [0.2124 & 0.2064 & 0.5812] \end{matrix} \end{aligned}$$

$$\begin{aligned} \mathbf{q}(1) &= \mathbf{q}(0) \mathbf{f}_E^T \left(\frac{1}{\hat{f}_E} \right) = \begin{bmatrix} 0.6117 \\ 0.1684 \\ 0.2199 \end{bmatrix} [24.2467 \quad 9.5376 \quad 25.4776] \left(\frac{1}{22.0338} \right) \\ &= \begin{matrix} \textit{Pure} & \textit{Random} & \textit{Zigzag} \\ [0.6732 & 0.0729 & 0.2539] \end{matrix} \end{aligned}$$

Over one generation, speedy pursuit has become a bit more prevalent and dodger pursuit a bit less, while both pure and zigzag have become a bit more prevalent at the expense of random evasion. The values in vectors $\mathbf{p}(1)$ and $\mathbf{q}(1)$ sum to one.

Simulation of evolutionary dynamics:

Using the relationships outlined above, Monte Carlo simulations were used to examine long-term (evolutionary) population dynamics. The following approach was employed:

- 1) *Generate initial populations:* Pursuer and evader populations ($\mathbf{p}(0)$ and $\mathbf{q}(0)$) were generated randomly from uniform distributions. For example, p_1 was generated from a distribution on $[0,1]$, then p_2 was generated on $[0,1-p_1]$ and $p_3 = 1-p_1-p_2$.
- 2) *Determine capture matrix:* Calculation of the capture matrix followed Pais and Leonard (2010). The evader started at the origin with bearing (θ_E) zero and the pursuer was

located uniformly randomly on the square $[-10,10] \times [-10,10]$ and had an initial bearing (θ_p) selected uniformly randomly on a unit circle. Each pursuit strategy was pitted against each evasion strategy and the capture times used to generate a capture matrix. For each generation, ten such matrices were calculated $\mathbf{C}_k, k \in \{1, \dots, 10\}$ and the average matrix $\bar{\mathbf{C}}$, where $\bar{c}_{i,j} = \frac{1}{10} \sum_{k=1}^{10} c_{kij}$ was used in simulations. If $\bar{\mathbf{C}}(g)$ represents the capture matrix used for generation g , then $\bar{\mathbf{M}}(g) = \bar{\mathbf{C}}^R(g)$ where \bar{m}_{ij} is the reciprocal of \bar{c}_{ij} and $\bar{\mathbf{C}}^T(g)$ is the transpose of $\bar{\mathbf{C}}(g)$.

- 3) *Determine fitness and population structure*: Population vectors and capture matrices were used to calculate fitness values and population structure for the next generation.
- 4) *Repeat*: Using the new population structure, steps 2 and 3 were repeated to advance the population another generation.
- 5) *Repeat more*: Each simulation was extended to 100 generations
- 6) *Determine variation*: Fifty 100-generation simulations were conducted, each with new initial pursuer and evader populations.

RESULTS

Pursuit-Evasion Model

Evasion:

- 1) *Random evasion* is influenced by both the probability P_t of turning and the range of possible turn angles, as illustrated in Figure 3. For the range of angles examined $(k = \pm (\frac{\pi}{4}, \frac{\pi}{2}, 2, \pi))$, a tighter range of angles was associated with longer capture times (Figure 3). Also, longer capture times were associated with the lower frequency

of turning (P_t : 0.3 vs 0.5; Figure 3). For Monte Carlo simulations $k = \pm \left\lceil \frac{\pi}{4} \right\rceil$ and $P_t = 0.3$ were used.

2) *Protean zigzagging* capture time can be strongly influenced by the distance threshold for initiation (Figure 4). When evaders use the zigzag strategy with a threshold equal to the capture radius, capture times were no different from those for pure evasion (Figure 4). Protean evasion was most effective (and better than pure evasion) at distances very close to capture; protean evasion became less effective (and worse than pure evasion) at larger threshold distances. Figure 4 illustrates the capture times for evaders using zigzag evasion, with different initiation thresholds. A threshold of $\tau = 2$ was used for Monte Carlo simulations.

Evolutionary Dynamics

The results of Monte Carlo simulations suggest that employing a protean zigzag evasive strategy can be superior to pure evasion. At the end of 100 generations, the zigzag strategy typically comprised more than 99% of the evader population (Table 1). Thus, over time the zigzag strategy tended to out-compete the pure evasion and random evasion strategies. Similarly, the speedy pursuer strategy tended to dominate over other pure pursuit abilities.

DISCUSSION

Several characteristics of effective evasion are suggested by this study, as well as a need to reassess the notion of protean behavior. Against pure pursuit, a strategy already known to be effective, random evasive movement can be of varying effectiveness. Clearly, being unpredictable is not sufficient for effective evasion; as with Pais and Leonard (2010), random evasion was not as effective as pure evasion, in this study. In an examination of different degrees of random evasion, random movement was more effective when the range of turn angles and frequency of turning were reduced. In essence the more “predictable” the random evader, the more effective its flight, which is contrary to the notion that simply adopting an unpredictable evasion strategy will improve fitness. If evasion strategies have random characteristics, future research should focus on identifying which aspects of a strategy are affected. For example, cockroaches and shrimp use initial escape trajectories (θ_E) that are both restricted to a range of angles, but variable within that range (Arnott et al. 1999, Domenici et al. 2008).

The effectiveness of the zigzag evasion strategy suggests at least one way in which unpredictability can improve evasion efforts. The general observation that zigzagging is effective at close range has been suggested by previous authors on theoretical grounds (Furuichi 2002) and empirical studies have also suggested that certain evasive maneuvers may have optimal distances for effectiveness (Arnott et al. 1999, FitzGibbon 1990). Many empirical studies have examined the relationship between pursuer-evader distance and the initiation of evasive behavior (Cooper and Frederick 2007). The results of this study suggest that future work examining the relationship between pursuer-evader distance and the type of evasive behavior employed would be fruitful.

The results of the simulation of evolutionary dynamics suggest that zigzag-like behavior could successfully compete in populations dominated by pure pursuit and pure evasion. The current zigzag control rule is based on personal observations of lizards fleeing across the sand dunes of Namibia; it is not the product of an exhaustive attempt to find evolutionary stable strategies for evasion and suggests that there is plenty of opportunity for identifying evasion strategies in the natural world.

A final thought at the end of this study is: what exactly does *protean* imply? The random movement evasion was the least predictable evasion strategies as well as the least successful. The zigzag strategy was employed under a fairly narrow range of conditions and against pursuers that were not controlled by anticipatory rules or who could be confused. Confusion in the sense of “where did the octopus go?” or “I cannot keep track of my target in this fish school” seems qualitatively different from the mechanism underlying the zigzagging evader’s success, which hinges on differences in momentum and turning ability. Forcing decisions, limiting the ability to anticipate and relying on differences in maneuverability maybe should be seen as different phenomenon. Protean as a catchall phrase may have limited value.

DIRECTIONS FOR FUTURE WORK

This study points to several directions where both additional modelling and empirical efforts may be fruitful. The simulations employed in this study used capture time as a measure of fitness. This approach has been successfully used by several studies of pursuit and evasion and assumes that capture will occur in a finite time (Justh and Krishnaprasad 2006, Wei et al. 2009, Pais and Leonard 2010). Many animals operate close to refuges and adjust their flight behavior based on

proximity to retreats (Cooper and Frederick 1997). The approach used in this study could be adjusted to incorporate the possibility of escape. Comparing capture time and probability of escape as measures of fitness could provide insight concerning how different evasions strategies persist in nature. Random movement was the least effective evasion strategy, but its effectiveness could be influenced by the range of turn angles and probability of turning. Additional modelling efforts could focus on the extent to which these parameters influence success; empirical work could focus on characterizing the evasive movements of animals deemed to be evading randomly. The zigzag strategy worked best when initiated at close quarters. Future work will explore the influence of pursuer-evader distance on simulated and real evasion behavior.

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Table 1. Mean population structure for pursuers and evaders before and after evolutionary simulations. Values represent the proportion of a population employing a particular pursuit or evasion strategy. The simulation was run 50 times, with each simulation lasting 100 generations.

	SPEEDY	JOE	DODGER
PURSUER START	0.5037	0.2017	0.2946
PURSUER FINISH	1.00	0.00	0.00
	PURE EVASION	RANDOM	ZIGZAG
EVADER START	0.5005	0.2729	0.2266
EVADER FINISH	0.0018	0.00	0.9982

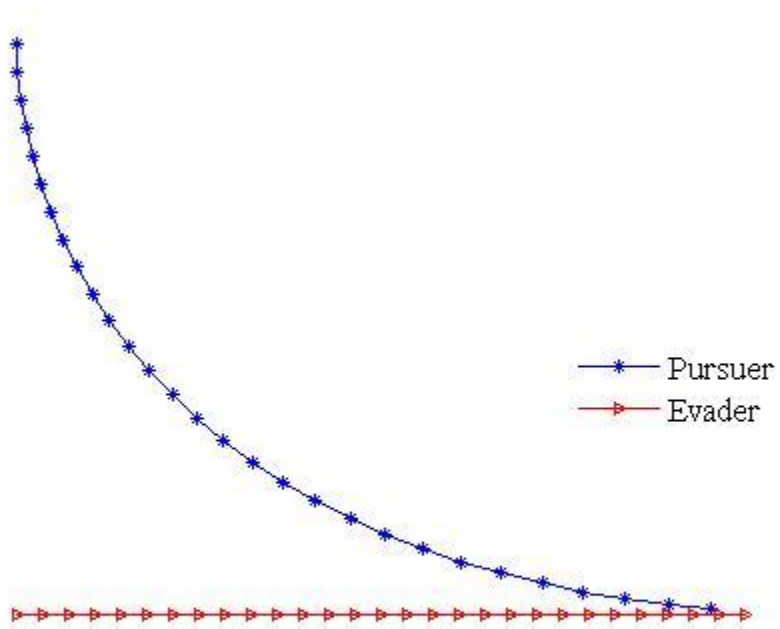


Figure 1: Path of pursuer employing pure pursuit against an evader employing non-reactive linear travel.

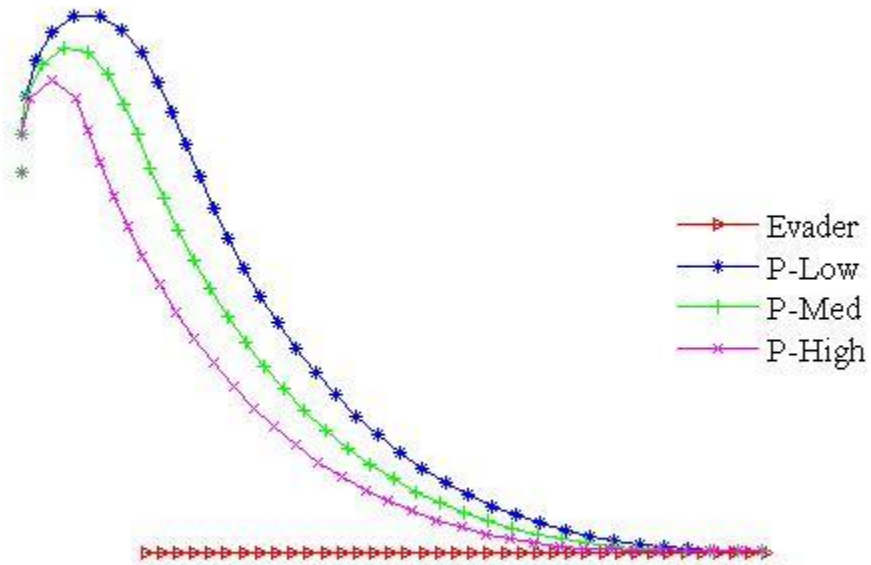


Figure 2: Paths of three pursuers employing pure pursuit against an evader employing non-reactive linear travel. Pursuers vary in maneuverability and are all initially oriented away from the evader. Adjacent pursuer curves vary by approximately 10% in capture times.

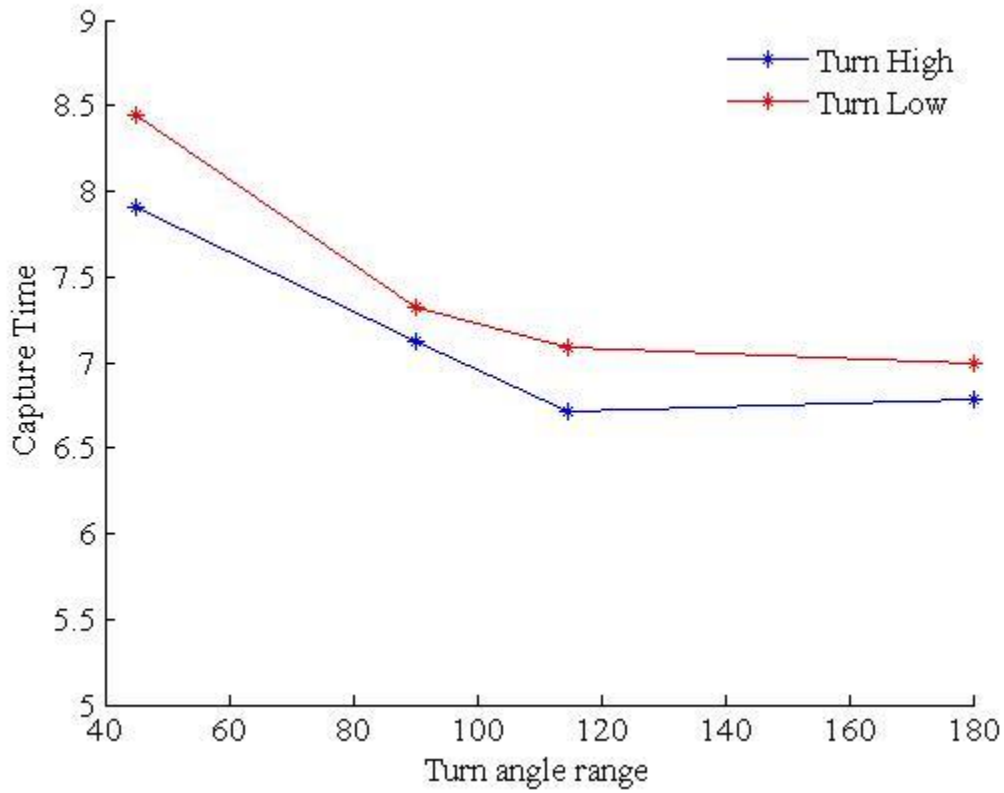


Figure 3: The relationship between range of turn angles, probability of turning and capture time.

Values represent the mean for 1000 pure pursuit simulations.

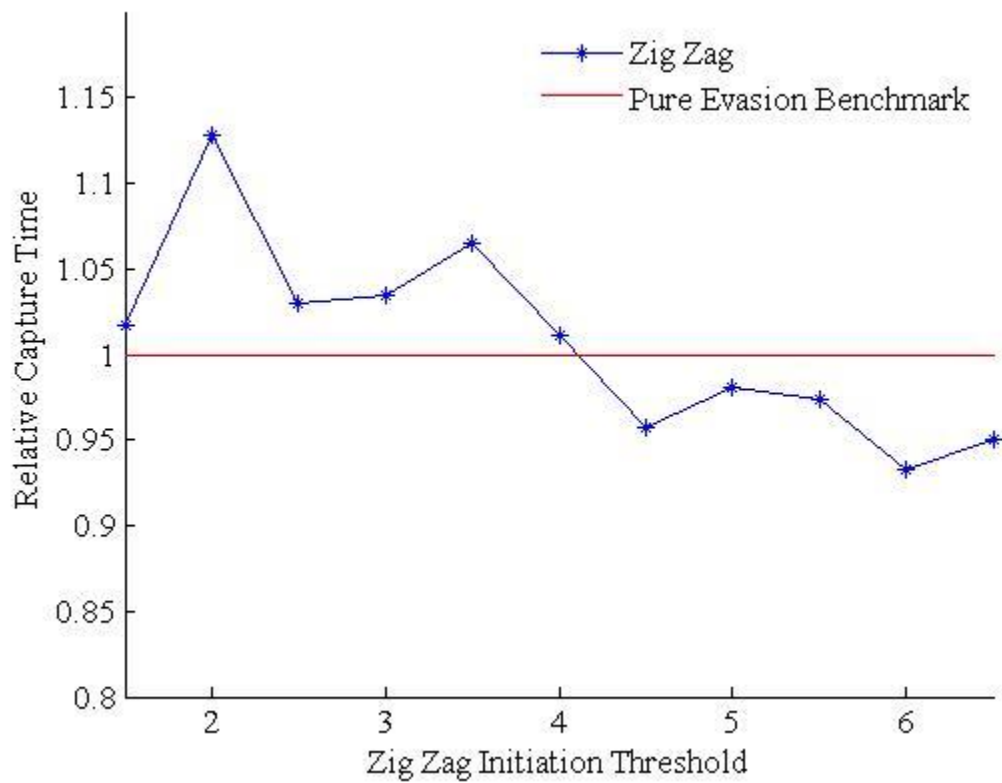


Figure 4: The relationship between zigzag initiation threshold and capture time. Capture times are relative to the mean for pure pursuit. Values represent the mean for 1000 simulations.