

# Co-Evolution of Pursuit and Evasion I: Biological and Game-Theoretic Foundations\*

Geoffrey F. Miller<sup>†</sup> and Dave Cliff

Technical Report CSRP 11, August 1994.

School of Cognitive and Computing Sciences  
University of Sussex, BRIGHTON BN1 9QH, U.K.  
Email: geoffm@cogs.susx.ac.uk, davec@cogs.susx.ac.uk  
Phone: +44 27 606755 ext. 102  
Fax: +44 27 671 20

## Abstract

Animals often chase each other about. These pursuit-evasion contests require the continuous dynamical control of complex sensory-motor behavior, and give rise to some of the most common and challenging co-evolutionary arms races in nature. This paper argues for the importance and fruitfulness of studying pursuit-evasion scenarios using evolutionary simulation methods, and reviews the relevant literatures; in a companion paper, our simulation methods and results will be presented. We first review the biological ubiquity of pursuit-evasion contests, the *protean* (adaptively unpredictable) behavior that often evolves in evasion strategies (e.g. when prey zig-zag to evade predators), and the relevant neuroethology of capture by predators and escape by prey. The *differential game theory* relevant to analyzing pursuit-evasion games is then reviewed, including the proven optimality of *mixed strategies* (corresponding to protean behavior) in many such games, and the difficulty of deriving analytical solutions in realistically complex games. Previous work on evolving pursuit-evasion tactics in simulation and in real robots is then reviewed, and directions for further research are identified. We conclude with some possible engineering applications and scientific implications of pursuit, evasion, and their co-evolution.

**Keywords:** pursuit-evasion contests; co-evolution; protean behavior;

# 1 Introduction

control systems that are slow, brittle, easily confused, or error-prone do not survive long in pursuit-evasion scenarios. For these reasons, traditional artificial intelligence methods may prove particularly poor as models of pursuit-evasion behaviors (imagine the famously slow robot “Shakey” trying to evade a fast predator), and newer reactive, behavior-based, bottom-up approaches (e.g. Braitenberg, 1984; Brooks, 1989; Beer, 1990; Maes, 1990; Wilson, 1991) may prove particularly apt.

Third, pursuit and evasion are scientifically interesting, because they evolve against one another in an ongoing, open-ended, frequency-dependent way, so pursuit-evasion contests often give rise to co-evolution within or between species. Because pursuit-evasion scenarios may be the simplest and most common cases of behavioral co-evolution, their investigation may illuminate behavioral arms races in general (see Futuyama & Slatkin, 1983). Such sustained co-evolution reinforces all of the challenges discussed in the previous paragraph: temporary adaptive advantage is continually eroded under co-evolution as new tactics arise. Co-evolution probably drives the evolution of both special perceptual capacities to entrain, track, and predict animate motion, and special motor capacities to generate complex, robust, unpredictable behavior (Miller & Freyd, 1993). Understanding both perception and motor control may thus depend on appreciating the role of pursuit-evasion contests in behavioral evolution. Moreover, pursuit-evasion co-evolution is the simplest situation that can favor “protean” (adaptively unpredictable) behavior, as when prey animals zig-zag unpredictably to escape predators (see e.g. Chance, 1957; Chance & Russell, 1959; Driver & Humphries, 1988). Further, because effective pursuit may often require prediction and ‘mind-reading’, while effective evasion may require the use of unpredictable or deceptive tactics (Driver & Humphries, 1988), such contests raise issues of signaling, communication, and tactical deception (Dawkins & Krebs, 1978; Harper, 1993; Krebs & Dawkins, 1984), and may provide a natural bridge from the evolution of basic sensory-motor control to the evolution of social psychology and ‘Machiavellian intelligence’ (Byrne & Whiten, 1988; Miller, 1993). Some complex social, sexual, communicative, and political behavior could be viewed as pursuit-evasion contests carried out on more abstract levels, with respect to state spaces involving social information, status, resources, kinship, and sexual relationships.

Fourth, pursuit-evasion contests have received serious attention from at least three scientific disciplines: behavioral biology, neuroethology, and game theory. Animal behavior studies have revealed the ubiquity and importance of pursuit-evasion tactics, anti-predator behaviors, and fighting skills (Driver & Humphries, 1988; Endler, 1991). The centrality of such behaviors is revealed by the fact that pursuit-evasion games are the most common form of animal play behavior (Fagen, 1981; Symons, 1978); such play facilitates learning sensory-motor coordination through “developmental arms races” between play-mates. Neuroethology (e.g. Camhi, 1984; Hoyle, 1984) has spent much effort understanding neural systems for pursuit (“approach”) and evasion (“avoidance”), including: explorations of specific circuits for rapid startle and escape behaviors (e.g. Camhi, 1988; Krasne & Wine, 1987; Eaton, 1984); the role of the (very fast) tecto-spinal pathway in mediating the pursuit behavior of vertebrate predators such as salamanders, frogs, cats, and owls (e.g. Alstermark, Gorska, & *et al*, 1987; Meredith, Wallace, & Stein, 1992; Westby, Keay, Redgrave, Dean, & Bannister, 1990); and the specific attunement of sen-

sory cells to patterns of animate motion relevant to pursuit and evasion (e.g. Arbib & Cobas, 1991; Ewert, 1987; Nakayama, 1985; Perrett, Harries, Mistlin, & Chitty, 1990). The possibilities for computational neuroethology (Beer, 1990; Cliff, 1991) and behavioral modelling in this area are obvious. Game theorists have also studied pursuit-evasion contests intensely for several decades, because of their importance in tactical air combat (e.g. telling pilots how to evade guided missiles) and other military applications (see Yavin & Pachter, 1987). “Differential game theory” (Isaacs, 1965) has developed a vocabulary for analyzing the structure and complexity of pursuit-evasion games, and a number of formal results concerning optimal strategies for particular pursuit-evasion games. We will review the relevant animal behavior studies, neuroethology, and game theory at length in the following sections.

Fifth, the study of pursuit-evasion behaviors has many scientific implications and practical applications.

of the environment insofar as their potential fitness effects exist regardless of whether the organism facing them knows or cares of their existence, but FAs are relational insofar as their biological significance exists only in relation to organisms with particular modes of survival and reproduction (e.g. what is food to one species is poison to another in a perfectly objective and yet perfectly relational way). Most FAs are spatially localized (at some scale), and only impose their fitness effects on organisms immediately adjacent to them.

animal escape behavior in asymmetric pursuit-evasion contests generally breaks down into three phases: (1) directional fleeing if a predator (or other negative, mobile FA) is threatening but still distant; (2) erratic zig-zagging if the predator begins catching up; and (3) convulsive ‘death-throes’ if caught. Directional fleeing is about as simple as directional chasing, but the last two tactics, zig-zagging and convulsing, are examples of a more interesting type: protean behavior.

Animals generally evolve perceptual and cognitive capacities to entrain, track, and predict the movements of other biologically-relevant animals such as prey, predators, and potential mates (Camhi, 1984; Miller & Freyd, 1993). Such predictive abilities mean that unpredictable behavior will inevitably be favored in many natural pursuit-evasion situations. For example, if a rabbit fleeing from a fox always chose the single apparently shortest escape route, the very consistency of its behavior would make its escape route more predictable to the fox, its body more likely to be eaten, its genes less likely to replicate, and its fitness lower. Predictability is punished by hostile animals capable of prediction. This is the basic logic behind the theory of protean behavior: the effectiveness of almost any behavioral tactic can be enhanced by endowing it with characteristics that cannot be predicted by an evolutionary opponent (Driver & Humphries, 1988). An arms race between perceptual capacities for predicting animate motion, and motor capacities for generating protean behavior, will generally result from evolutionarily recurring pursuit-evasion contests (Miller & Freyd, 1993).

Along with directional fleeing, protean escape behaviors are probably the most widespread and successful of all behavioral anti-predator tactics, being used by virtually all mobile animals on land, under water, and in the air. Driver and Humphries (Driver & Humphries, 1988) review examples from hundreds of species, including insects, fish, birds, and mammals. Human proteanism is obvious in any competitive sport: good boxers use unpredictable feints and attacks, and good rugby players use unpredictable jinks. Predators can also exploit unpredictability to confuse prey, as when weasels do “crazy dances” to baffle the voles that they stalk, or when Australian aborigine hunters do

behaviors is also revealed in their speed. The neural systems for initiating protean escape are astonishingly fast: a cricket can detect the sound of a predator and effectively alter the rhythmic motor signals to its wings to initiate erratic escape in under 60 milliseconds (May, 1991).

Even if erratic zig-zagging fails, another form of proteanism, convulsive behavior, may succeed. Sudden, unpredictable, vigorous “death-throes”, alternating with puzzling passivity (“playing dead”) is often effective at allowing prey to escape from predators (Driver & Humphries, 1988). Indeed, the adaptive significance of convulsive behavior was first recognized by M. R. A. Chance (Chance, 1957; Chance & Russell, 1959), who initiated the study of protean behavior with his analysis of “audiogenic seizures” in laboratory rats. (When lab technicians accidentally jangle their keys, lab rats have a peculiar tendency to go into convulsions, but if the rats are provided with hiding places in their cages, they simply run and hide when keys are jangled; thus, the convulsions are facultative defensive behaviors rather than pathological oddities.) Adaptive convulsions can also occur in more abstract state-spaces, as when cuttlefish and octopi undergo rapid color changes to defeat the search images (perceptual expectations) of their predators. Additional confusion effects may arise from group flocking and mobbing behaviors that include unpredictable movements, complex motion dynamics, and confusing coloration (zebra stripes or shiny scales on fish); Werner and Dyer (1993) found such confusion effects when simulating the evolution of herding behavior by prey under predation pressure. Unpredictability can also be exploited by divergence between individuals, as when animals within a species evolve “aspect diversity” (polymorphic coloration or behavior) through “apostatic selection” (Clarke, 1962) that favors low-frequency traits (e.g. because predators’ use of search images penalizes common appearances). Indeed, apostatic selection may be a general feature of pursuit-evasion arms races: novel and unexpected tactics may be favored at a variety of levels.

Co-evolution itself can be viewed as a pursuit-evasion contest, operating between lineages rather than between individuals. From this perspective, sexual recombination makes sense as a protean strategy which unpredictably mixes up genes so as to “confuse” pathogens (Hamilton, Axelrod, & Tanese, 1990). Indeed, this proteanism argument is one of the leading explanations for the the evolution of sex (Ridley, 1993). Despite proteanism’s importance, it has been long overlooked in biology, because complex order rather than useful chaos was assumed to be the defining feature of Darwinian adaptations (see Miller, 1993).

### 2.3 The neuroethology of pursuit and evasion

The study of fast pathways for escape and attack forms is one of the major successes of neuroethology (see Beer, Ritzmann, & McKenna, 1993; Camhi, 1984; Ewert, 1980; Ewert, Capranica, & Ingle, 1983; Guthrie, 1980; Kandel, 1976; Hoyle, 1984; Huber & Markl, 1983; Roeder, 1967). Neuroethologists like to study neural circuits for such behaviors because the relevant neurons are so large, the axons are so thick, the circuits are so easy to identify, and the behaviors are so fast, robust, and well-tuned (e.g. see Roeder, 1948; Eaton, 1984). In the tube worm *Myxicola infundibulum* for example, most axons (nerve fibers) are less than 5  $\mu\text{m}$  in diameter, but the median giant fiber for escape can reach 1700

$\mu\text{m}$  in diameter, occupying most of the cross-section of the nerve cord (Guthrie, 1980). Unusually in this case, methodological convenience reflects adaptive importance: large, fast neurons arranged in reliably wired circuits make not only easy work for the scientists, but adaptive sense for the animals. Although circuits for fast attack and escape are probably different from those used for sustained pursuit and evasion, the neuroethology of the former illustrates some relevant principles of speed, robustness, co-evolution, and adaptive specialization.<sup>1</sup>

### 2.3.1 Escape reflexes

Escape circuits are among the best-studied systems in neuroethology (see Eaton, 1984). Unexpected stimuli often provoke startle, escape, or withdrawal in animals, and these reflexes are generally mediated by specialized ‘fast pathways’ (Guthrie, 1980). As far back as 1836, Ehrenberg had identified very large cells in the ventral nerve cords of lobsters and crayfish which were later shown to mediate their escape behaviors. Particularly well-understood are the quick withdrawal of the worm’s head, the tail-flip escape of the crayfish, the escape turn of the cockroach, and the sudden dart of the fish. Aside from whole-body escape, animals with limbs usually have specialized circuits for limb-withdrawl from painful or threatening things. Fast pathways generally use a few large neurons with polarized inputs, long, thick, heavily insulated, low-resistance axons, widely distributed outputs, and electrical rather than chemical synapses. Such neural adaptations permit conduction velocities a couple orders of magnitude faster than normal. Escape reflexes also recruit attention, increase activation, and release hormones, in preparation for sustained evasion if necessary.

Even in colenterates such as sea anemones and jellyfish, there appear to be separate fast pathways for withdrawal reflexes (Guthrie, 1980; MacFarlane, 1969). Similar circuits for gill-withdrawl in sea slugs (*Aplysia*) have been studied by Kandel (1976). The escape-reflex nerve fibers (‘third-order giant fibers’) of the squid *Loligo* are so thick (700  $\mu\text{m}$ ) that they have been widely used in studies of the ionic mechanisms of nerve-fiber conduction. The common earthworm *Lumbricus* has an escape reflex mediated by medial, lateral, and segmental giant fibers and by giant motor neurons, which contact longitudinal body muscles to withdraw the head from danger. The medial giant fibers can attain conduction velocities of up to 45 meters per second, as fast as the myelinated escape-reflex fibers of frogs and fish (Guthrie, 1980). Darwin noted that the worm’s escape reflex rapidly habituates to light or touch, and shows a higher threshold for activation during active locomotion.

The American cockroach *Periplaneta americana* escapes from toad predators (such as *Bufo marinus*) by sensing toad-induced air accelerations with their anal cerci (rear-facing sense organs), turning from the predator, and running away (see chapter 4 of (Camhi, 1984), (see also Camhi, 1980). The sedentary toads generally wait for insects to walk by before striking with their tongues, so a single brief escape suffices; there is rarely sustained pursuit. The cockroach’s seven pairs of giant interneurons (GI) mediate the escape behav-

---

<sup>1</sup>For further relevant readings in neuroethology, see the journals: *Aggressive Behavior*; *Animal Behavior*; *Behavioral Neuroscience*; *Biological Cybernetics*; *Brain, Behavior, and Evolution*; *J. Comparative*



ior, which averages an extremely fast 41 milliseconds (ms) latency (Plummer & Camhi, 1981), but which can occur in an astonishing 11 ms in response to a stronger-than-normal air stimulus (Camhi & Nolen, 1981). The hundreds of wind-receptive hairs on the cerci are directionally tuned and several of the giant interneurons code for predator direction to guide the escape turning behavior (Dowd & Comer, 1988; Liebenthal, Uhlmann, & Camhi, 1994; Westin, Langberg, & Camhi, 1977). This direction information triggers consistent changes in interleg coordination and turning, which have been analyzed with high-speed video, (Camhi & Levy, 1988; Nye & Ritzmann, 1992). Under certain conditions, the same giant interneurons that trigger escape running can trigger escape flying instead (Ritzmann, Tobias, & Fournier, 1980). The entire system is essentially innate, hard-wired, and fully functional in hatchlings, though there is some plasticity to compensate for injury to various components of the system (see chapter 4 of Camhi, 1984). The cockroach's escape system works much like a Braitenberg (1984) vehicle to implement a very rapid predator-avoidance, and could provide a model for further simulation and robotics work.

The escape circuits of the American crayfish *Procambarus clarkii* have also been well-studied (Krasne & Wine, 1987; Edwards, 1991; Olson & Krasne, 1981; Wiersma, 1947) (see also chapter 8 of Camhi, 1984). This animal lives in streams, eats detritus, and is attacked by various large fish. Touches to the crayfish's rear will trigger an abdominal flexion mediated by lateral giant interneurons that somersaults the animal upward and forward; touches to the front will trigger a different kind of abdominal flexion or 'tailflip' mediated by medial giant interneurons that shoots the animal backwards (Wine & Krasne, 1972). In each case, the giant interneurons have rectifying electrical synapses onto large (F1) motor neurons, which, in conjunction with 'segmental giant' cells, activate 'fast flexor muscles'. The escape is an all-or-nothing, highly stereotyped response, which cancels out all other ongoing locomotor activity, requires the coordination of muscles in several abdominal segments, and begins within 20 ms of stimulation. The circuitry underlying this escape behavior has been studied in great detail (Krasne & Wine, 1987; Olson & Krasne, 1981); Stork, Jackson, and Walker (1992) have simulated its evolution from swimming locomotion circuits.

In most teleosts (body fishes), Mauthner cells of the reticulospinal network (Diamond, 1971) mediate a two-stage escape called a 'C-start': turn rapidly, then accelerate axially (Eaton & Emberley, 1991). Within 100 ms, a C-starting fish will have moved around one body length away from the threatening stimulus, and will be pointed in roughly the right direction for further evasion. Rapid escape is especially important for fish attacked by plunge-diving birds such as gannets and kingfishers (Guthrie, 1980), whose appearance is unpredictable, rapid, and lethal. The Mauthner cells as studied in the goldfish *Carassius auratus* guide the basic decision to turn left or right during escape; the exact escape heading is modulated by parallel circuits to produce variations from 15 to 135 degrees change in orientation (Eaton, Didomenico, & Nizzanov, 1988a, 1988b; Foreman & Eaton, 1993). The C-start is fast (initiated within 10 ms), highly ballistic, and is not corrected for threat location once initiated; however, fish seem to avoid facing towards static obstacles during C-starts, so C-starts may be modulated by some environmental information (Eaton & Emberley, 1991). Although Mauthner cells (M-cells) are impor-

tant in triggering C-starts, (Nissanov, Eaton, & Didomenico, 1990) found that M-cell stimulation alone produces a much weaker and less variable C-start. The M-cells seem to determine an initial left-or-right direction of response and a rough stage-1 escape angle; a second group of neurons fires later and modulates the onset time and direction of the stage-2 swimming behavior. Interestingly, Mauthners have also been



(rather than simple attack and escape) has been the work by Kenneth D. Roeder, Asher E. Treat, and their colleagues and followers on interactions between bats and moths (see e.g.



state-conditions, then the optimal pursuit and evasion strategies can be found by applying the tenet of transition.

Isaacs' ideas have proven enormously fruitful (see Basar & Olsder, 1982; Grote, 1975; Isaacs, 1965; Yavin & Pachter, 1987), and initiated a sort of Cold War arms race between American and Russian game theorists concerned with applications

### **3.2 The optimality of mixed strategies**

The key to formal analysis in game theory is for games to be reduced from descriptive form (e.g. rules and heuristics) or “extensive form” (i.e. decision-tree form) to “normal form” (i.e. a

optimal strategies for both pursuer and evader are also mixed. Forte and Shinar (e.g. Forte & Shinar, 1988, 1989; Shinar, Forte, & Kantor, 1992) have shown that in aerial combat scenarios, mixed strategies yield much better performance than any previously known guidance law, and did so for both pursuers and evaders. Moreover, Bernhard and Colomb (1988) showed that the use of mixed strategies by both players can be optimal even when only one player has incomplete information. Other results by Bugnon and Mohler (1988), Imado (1993), and Linder (1991) also illustrate the utility of mixed strategies in pursuit-evasion games. Indeed, some aircraft use systems for “electronic jinking” (Forte & Shinar, 1988) to generate unpredictable flight paths, by analogy to gazelles jinking erratically to evade a predator. Such game-theoretic results support the



non-zero-sum games; (5) the information structure, with games of complete information much simpler than games of incomplete information. Moreover, in differential games with continuous dynamics, the complexity and noisiness of the dynamics has a major influence on the tractability of the game. Anything that complicates the differential state equations complicates the game analysis. Finally, formal application of game theory requires the complete specification of a strategy space. Such a complete specification may not be possible if the strategies are emergent properties of human heuristics, animal brains, or evolved robot control systems, and if the emergent strategies can vary continuously along a number of dimensions, thereby making the game difficult to represent in extensive (decision-tree) form or normal (payoff matrix) form. These problems suggest that differential pursuit-evasion games are difficult to analyze even under the best circumstances, and that the introduction of realistic complexity renders most of them formally intractable.

To avoid these complexities, differential game theory usually assumes that the pursuit-evasion game is one of perfect information between two players with fixed and predetermined roles (one “pursuer” and one “evader”), deterministic dynamics and constant speeds, and a zero-sum payoff structure. Mathematically adept researchers can relax one

terms “perfect” and “imperfect” information conflate the objective information structure of the game (e.g. the state-information available in the world) with the sensory and information-processing capacities of the players. If the latter are limited, then confusion, uncertainty, deception, and protean behavior may prove relevant even if the objective information structure of the game is “perfect”. The great size and speed of escape circuits and muscles in many animals, as reviewed in the previous section on neuroethology, suggests that the speed of both neural processing and motor movement has been under intense selection in pursuit-evasion contests.

In recognition of these problems, some game theorists have recently shifted to numerical and simulation methods to derive near-optimal strategies for more complex pursuit-evasion games (e.g. Jarmark, 1987; Moritz, Polis, & Well, 1987; Rodin, Lirov, Mittnik, McElhaney, & Wilbur, 1987; Tolwinski, 1989). For example, Rodin et al. (1987) used artificial intelligence (AI) methods to simulate players in an air combat maneuvering scenario. Each player derives tactical maneuvers using a world-model based on sensor inputs, an inference engine linked to a database

items, or other goal objects. Much of the work on simulation of collective behavior involves dynamical interactions with other agents that may be similar to the those arising in pursuit-evasion contests. For example, the cooperative behaviors of following, flocking, and aggregation are similar to pursuit behaviors; others such as dispersion and collision-avoidance are more similar to evasion behaviors (e.g. Mataric, 1993). (But note that selection for cooperation rarely favors deception or protean behavior.)

Previous simulation work has usually examined the origins and effects of pursuit-evasion tactics with neither player evolving or with one player evolving; these will be

squad car pursues a slower pedestrian evader on a discrete grid. Most relevantly, Koza (1991) used genetic programming to evolve LISP S-expression controllers for both players in a differential

Individuals from two species played a competitive game where each player attempts to capture a cube and keep it from the opponent. The simulations used realistic physics with gravity, collisions, friction, and momentum. A fascinating variety of tactics evolved for falling, crawling, rolling, and reaching towards the cube, for blocking or pushing away opponents, and for covering or wrapping securely around the cube. This work shows the feasibility of co-evolving complex and diverse behavioral tactics in simulations with realistic physics and open-ended body and brain development methods. Sims' system could be easily extended to studying pursuit-evasion games, since it has already been used to evolve walking, jumping, and swimming capacities (Sims, 1994b).

Other simulation work has evolved forms of pursuit and evasion, or approach and avoidance, without explicitly selecting for them. Yeager's (1994) "PolyWorld" system managed to evolve some simple pursuit-evasion tactics in simulated creatures controlled by neural networks, including running away or fighting back when attacked, and following other creatures in order to attack them. Although not very sophisticated, these behaviors did evolve simply through the ecological interactions such as predation that were permitted in PolyWorld, without any explicit selection for pursuit or evasion abilities. Yeager's work demonstrates not only that pursuit-evasion contests emerge spontaneously given mobile creatures with conflicts of interest, but also that genetically encoded neural networks can evolve to generate adaptive pursuit and evasion behaviors in such contests.

### **4.3 Pursuit and Evasion by Robots**

There is a huge literature on mobile robot control, largely focused on problems of navigation and path-following in unrealistically friendly environments free of anything that requires sustained pursuit or protean evasion (e.g. Brooks, 1989; Cliff et al., 1993; Harvey, Husbands, & Cliff, 1994). Even work on avoiding moving obstacles (e.g. the asteroid avoidance problem (Latombe, 1991) assumes that the obstacles are following predictable courses, which allows long-term path-planning (Canny, 1987; Tychonievich, Zaret, Mantegna, Evans, Muhle, & Martin, 1987). However, many potential robot tasks are essentially pursuit-evasion problems. The same fitness affordance theory that confirms the generality of pursuit-evasion problems for animals also applies to robots, where fitness can be interpreted in economic rather than reproductive terms (see McFarland,

agression<sup>2</sup> try to push one another outside the boundaries of a circular pad, under either radio control or autonomous control. Robot Sumo is a symmetric pursuit-evasion game in which each agent strives for a more central position and for a better application of a centrifugal force vector to the other.

Arkin, Carter, and MacKenzie (1993) reviewed previous work on how robots can avoid moving obstacles, and developed motor schemas for dodging and escape in their reactive mobile robot. Dodging avoids ballistic projectiles by side-stepping; escape by side-stepping;

mal distribution wrapped around a circle, with a null mean corresponding to forwards movement. Varying the step-length and the variance of the direction-change distribution results in changes of a formal measure of movement “sinuosity”  $S$ , which can in turn be used to calculate an expected diffusion path length for foraging. Optimal sinuosity values can evolve for optimal foraging in environments with different food distributions. Although Benhamou and Bovet (1989) did not discuss the utility of this sort of movement unpredictability in pursuit and evasion, their sinuosity measure, or other similar measures, could be useful in analyzing the movement dynamics of pursuing and evading animals. Killeen (1992) has also developed a framework for the dynamical analysis of animate motion based on fields of approach and avoidance vectors.

Other simulation work has shown the utility of co-evolution in evolving strategies for game-like interactions. Work by Hillis (1990) on the co-evolution of sorting strategies and test sets can be viewed as an abstract version of a one-play pursuit-evasion contest, in which the sorting strategies ‘pursue’ optimal sorts while the test sets ‘evade’ the strengths of particular sorting algorithms. Co-evolution of strategies for the simple and iterated prisoner’s dilemma has been particularly well-studied, e.g. by Axelrod (1989), J. H. Miller (1989), and Nowak and colleagues (1992, 1992). Co-evolution has also been simulated successfully in Holland’s (1992) ECHO system, Koza’s (1991, 1992) genetic programming research, Ray’s (1992) TIERRA system, Werner and Dyer’s (1993) Bioland system, and Yeager’s (1994) Polyworld. Angeline and Pollack (1993) demonstrated the utility of co-evolution in genetic algorithms for solving complex problems. Chapter 6 of Kauffman (1993) explores the dynamics of co-evolution in great detail using simulation on N-K fitness landscapes.

## 4.5 Directions for Further Research

This work on co-evolution, along with Koza’s demonstration of entropy-driven evolution through selection for randomness, and previous research on evolution of pursuit and evasion strategies, gave us hope that a co-evolutionary pursuit-evasion scenario could lead to the evolution of protean behaviors. In the companion paper (Cliff & Miller, 1994), we review our simulation methods and results, in which a genetic algorithm evolves pursuit and evasion strategies implemented as dynamical neural networks in simulated robots.

Simple demonstrations that effective pursuit and evasion abilities can evolve in simulation will not prove of much scientific interest (although they may have important engineering applications.) We already know from neuroethology and animal behavior that pursuit-evasion contests result in exquisitely adapted sensors, effectors, neural circuits, and behaviors. To go beyond this, we must address develop and test specific hypotheses about the co-evolutionary dynamics of pursuit-evasion contests, the typical neural mechanisms underlying pursuit-evasion behaviors, the trade-offs between pursuit-evasion capacities and other behavioral capacities, and so forth. For example, researchers could develop hypotheses about variables that might influence the evolution of pursuit-evasion behaviors, manipulate these variables in simulation, and observe the results using relevant measurement tools. In our work, we are currently manipulating the relative physical speed and the relative neural processing speed of pursuers versus evaders, to explore where in this 2D space of parameters various sorts of behaviors (such as dodging, feint-





## **5 Applications and Implications**

By pursuing rather than evading the complexities of pursuit-evasion contests, we

For example, the debate in adaptive behavior research over representational versus dynamical approaches to animal cognition might be illuminated by closer study of pursuit and evasion circuits. Many biologists have cited predator-prey interactions to argue for the special attunement of perceptual systems and internal representations to biologically relevant stimuli and situations; others have cited such interactions to argue for the importance of robust dynamical control. Miller and Freyd (1993) saw no necessary conflict between these positions, and have suggested that pursuit-evasion contests demand 'dynamic mental representations' (Freyd, 1987) that have both a dynamical structure and a representational function.

Implications also arise for our understanding of the general relationship between agents and environments. For those seeking a general theory of environmental complexity (e.g. Wilson, 1991; Todd & Wilson, 1993), the addition of animate agents capable of unpredictable pursuit and evasion in the environment represents a significant conceptual challenge. For example, an environment that contains creatures with continuous-time dynamical noisy recurrent networks as their control systems would be difficult to model as an environmental finite state machine, as proposed in (Wilson, 1991). As in sexual selection (Miller, 1993; Miller & Todd, 1993) and other forms of “psychological selection” (Miller, 1993; Miller & Freyd, 1993), pursuit-evasion contests break down the distinction between environment complexity and agent complexity, because agents become the most important selective forces in each other’s environments.

## 6 Conclusions

Pursuit and evasion behaviors are common because conflicts of interest over approach and avoidance are common, and they

## **Acknowledgements:**

Miller's research was supported by NSF-NATO Post-Doc Fellowship RCD-9255323 and NSF Research Grant INT-9203229. Thanks to Inman Harvey, Alasdair Houston, Phil Husbands, Peter Todd, and an anonymous reviewer for useful comments and

- Benhamou, S., & Bovet, P. (1989). How animals use their environment: A new look at kinesis. *Animal Behavior*, *38*, 375–383.
- Benhamou, S., & Bovet, P. (1991). Modelling and simulation of animals' movements. In Meyer, J.-A., & Wilson, S. W. (Eds.), *From Animals to Animats: Proceedings of the First International Conference on Simulation of Adaptive Behavior*, pp. 135–139. MIT Press/Bradford Books.
- Berkovitz, L. D. (1975). Two person zero sum differential games: An overview. In Grote, J. D. (Ed.), *The theory and application of differential games*, pp. 12–22. D. Reidel.
- Bernhard, P., & Colomb, A.-L. (1988). Saddle point conditions for a class of stochastic dynamical games with imperfect information. *IEEE Transactions on Automatic Control*, *33*(1), 98–101.
- Bovet, P., & Benhamou, S. (1988). Spatial analysis of animals' movements using a correlated random walk model. *Journal of Theoretical Biology*, *131*, 419–433.
- Braitenberg, V. (1984). *Vehicles: experiments in synthetic psychology*. MIT Press.
- Brogan, W. L. (1991). *Modern control theory*. Prentice Hall.
- Brooks, R. A. (1986). A robust layered control system for a mobile robot. *IEEE J. Robotics and Automation*, *2*, 14–23.
- Brooks, R. A. (1989). A robot that walks: Emergent behaviors from a carefully evolved network. *Neural Computation*, *1*, 253–262.
- Bugnon, F. J., & Mohler, R. R. (1988). Structural choices of 2 versus 1 pursuit-evasion differential games. *Journal of Dynamic Systems, Measurement and Control, Transactions ASME*, *110*(2), 160–167.
- Buttazzo, G. C., Allotta, B., & Fanizza, F. P. (1993). Mousebuster: A robot for real-time catching. *IEEE Control Systems Magazine*, *14*(1), 49–56.
- Byrne, R., & Whiten, A. (Eds.). (1988). *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans*. Oxford University Press.
- Camhi, J. M. (1980). The escape system of the cockroach. *Scientific American*, *243*(6), 158–172.
- Camhi, J. M. (1984). *Neuroethology: Nerve*

- Camhi, J. M., & Nolen, T. G. (1981). Properties of the escape system of cockroaches during walking. *J. Comparative Physiology*, *142*, 339–346.
- Canfield, J. G., & Rose, G. J. (1993). Activation of mauthner neurons during prey capture. *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology*, *172*(5), 611–618.
- Canny, J. (1987). A new algebraic method for robot motion planning and real geometry. In *Proc. IEEE Int. Conf. on Foundations of Computer Science*, pp. 39–48.
- Carew, T. J., & Kandel, E. R. (1977). Inking in *Aplysia californica* I and II. *J. Neurophysiology*, *40*, 692–720.
- Chance, M. R. A. (1957). The role of convulsions in behavior. *Behavioral Science*, *2*, 30–45.
- Chance, M. R. A., & Russell, W. M. S. (1959). Protean displays: a form of allaesthetic behavior. *Proc. Zoological Soc. of London*, *132*, 65–70.
- Clark, C. W., & Ydenberg, R. C. (1990). The risk of parenthood I. general theory and applications. *Evolutionary Ecology*, *4*(1), 21–34.
- Clarke, B. C. (1962). The evidence for apostatic selection. *Heredity (London)*, *24*, 347–352.
- Cliff,

- Diamond, J. (1971). The teleost mauthner cell. In Hoar, W. S., & Randall, D. S. (Eds.), *Fish physiology, Vol. 5*. Academic Press.
- Dowd, J. P., & Comer, C. M. (1988). The neural basis of orienting behavior: a computational approach to the escape turn of the cockroach. *Biological Cybernetics*, *60*(1), 37–48.
- Driver, P., & Humphries, N. (1988). *Protean behavior: The biology of unpredictability*. Oxford University Press.
- Dunning, D. C., & Roeder, K. D. (1965). Moth sounds and insect catching behavior of bats. *Science*, *147*, 173–174.
- Eaton, R. (Ed.). (1984). *Comparative neurobiology of startle and other fast escape responses*. Plenum Press, New York.
- Eaton, R. C., Didomenico, R., & Nizzanov, J. (1988a). Flexible body dynamics of the goldfish C-start: Implications for reticulospinal command mechanisms. *J. Neuroscience*, *8*(8), 2758–2768.
- Eaton, R. C., Didomenico, R., & Nizzanov, J. (1988b). Role of the mauthner cell in sensorimotor integration by the brain stem escape network. *Brain, Behavior, and Evolution*, *37*(5), 272–285.
- Eaton, R. C., & Emberley, D. S. (1991). How stimulus direction determines the trajectory of the mauthner-initiated escape response in a teleost fish. *J. Experimental Biology*, *161*, 469–488.
- Edwards, D. H. (1991). Mutual inhibition among neural command systems as a possible mechanism for behavioral choice in crayfish. *J. Neuroscience*, *11*(5), 1210–1223.
- Endler, J. (1991). Interactions between predators and prey. In Krebs, J. R., & Davies, N. B. (Eds.), *Behavioural ecology: An evolutionary approach (3rd Ed.)*, pp. 169–196. Blackwell Scientific.
- Ermolov, A., Kryakovskii, B., & Maslov, E. (1986). Differential game with mixed strategies. *Avtomatika i Telemekhanika*, *47*(10), 1336–1349.
- Ewert, J.-P. (1980). *Neuroethology: An introduction to the neurophysiological fundamentals of behavior*. Springer-Verlag.
- Ewert, J.-P. (1984). Tectal mechanisms that underlie prey-catching and avoidance behavior in toads. In Vanegas, H. (Ed.), *Comparative neurology of the optic tectum*, pp. 247–416. Plenum Press.
- Ewert, J.-P. (1987). Neuroethology of releasing mechanisms: Prey-catching in toads. *Behavioral And Brain Sciences*, *10*(3), 337–368.
- Ewert, J.-P., & Burghagen, H. (1979). Configural prey selection in four species of toads. *Brain, Behavior, and Evolution*, *16*, 157–175.





- Griffin, D. R., Webster, F. A., & Michael, C. R. (1960). The echolocation of flying insects by bats. *Animal Behavior*, *8*, 141–154.
- Grimm, W., & Well, K. (1991). Modelling air combat as differential game: Recent approaches and future requirements. In *Proc. 4th Int. Symp. Differential Games and Applications*, pp. 1–13. Springer-Verlag.
- Grote, J. (Ed.). (1975). *The theory and application of differential games*. D. Reidel.
- Guthrie, D. M. (Ed.). (1980). *Neuroethology: An introduction*. Blackwell Scientific.
- Hamilton, W. D., Axelrod, R., & Tanese, R. (1990). Sexual reproduction as an adaptation to resist parasites: A review. *Proc. Nat'l Acad. Sciences (USA)*, *87*(9), 3566–3573.
- Harper, D. (1993). Communication. In Krebs, J. R., & Davies, N. B. (Eds.), *Behavioral ecology: An evolutionary approach* (third edition). Blackwell Scientific, Oxford.
- Harvey, I., Husbands, P., & Cliff, D. (1994). Seeing the light: Artificial evolution, real vision. In Cliff, D., Husbands, P., Meyer, J.-A., & Wilson, S. W. (Eds.), *Animals to Animats 3: Proceedings of the 3rd International conference on Simulation of Adaptive Behaviour*, pp. 392–401. MIT Press/Bradford Books.
- Hillis, W. (1990). Co-evolving parasites improve simulated evolution as an optimization procedure. *Physica D*, *42*, 228–234.
- Holland, J. (1992). Echo: Explorations of evolution in a miniature world. In Langton, C. G., Taylor, C., Farmer, J. D., & Rasmussen, S. (Eds.), *Artificial Life II*. Addison-Wesley.
- Houston, A., & McNamara, J. (1987). Singing to attract a mate: A stochastic dynamic game. *J. Theoretical Biology*, *129*, 57–68.
- Houston, A., & McNamara, J. (1988). A framework for the functional analysis of behavior. *Behavioral and Brain Sciences*, *11*(1), 117–164.
- Hoyle, G. (1984). The scope of neuroethology. *Behavioral and Brain Sciences*, *7*, 367–412.
- Huber, F., & Markl, H. (Eds.). (1983). *Neuroethology and behavioral physiology: Roots and growing points*. Springer-Verlag.
- Imado, F. (1993). Some aspects of a realistic three-dimensional pursuit-evasion game. *J. of Guidance, Control, and Dynamics*, *16*(2), 289–293.
- Ingle, D. (1991). Control of frog evasive direction: Triggering and biasing systems. In Arbib, M. A., & Ewert, J. P. (Eds.), *Visual structure and integrated functions: Research notes in neural computing*, pp. 181–189. Springer-Verlag.
- Isaacs, R. (1951). Games of pursuit. Technical report P-257, Rand Corporation.
- Isaacs, R. (1965). *Differential games: A mathematical theory with applications to warfare and pursuit, control and optimization*. John Wiley.

Isaacs, R. (1975). The past and some bits of the future. In Grote, J. D. (Ed.), *The theory*

L. A.





Ritzmann, R. E., Tobias, M. L., & Fournier, C. R. (1980). Flight activity initiated via giant interneurons in the cockroach: Evidence for bifunctional trigger interneurons. *Science*, *210*, 443–445.

- Sims, K. (1994b). Evolving virtual creatures. In *Proceedings of 1994 Computer Graphics Conference*, pp. 43–50.
- Stork, D. G., Jackson, B., & Walker, S. (1992). ‘non-optimality’ via pre-adaptation in simple neural systems. In Langton, C. G., Taylor, C., Farmer, J. D., & Rasmussen, S. (Eds.), *Artificial Life II*, pp. 409–429. Addison-Wesley.
- Symons, D. (1978). *Play and aggression: A study of rhesus monkeys*. Columbia U. Press.
- Terzopoulos, D., Tu, X., & Grzeszczuk, R. (1994). Artificial fishes with autonomous locomotion, perception, behavior, and learning in a simulated physical world. In Brooks, R., & Maes, P. (Eds.), *Artificial Life IV*, p. ?? MIT Press.
- Tilden, M. W. (1992). The second international BEAM robot olympics and micromouse competition: Event rules and general guidelines.. Contact [mwtilden@watmath.uwaterloo.ca](mailto:mwtilden@watmath.uwaterloo.ca).
- Todd, P. M., & Wilson, S. W. (1993). Environment structure and adaptive behavior

- Wiersma, C. A. G. (1947). Giant nerve fiber system of the crayfish: A contribution to comparative physiology of the synapse. *J. Neurophysiology*, *10*, 23–38.
- Wilson, S. W. (1991). The animat path to AI. In Meyer, J.-A., & Wilson, S. W. (Eds.), *Proc. First Int. Conf. Simulation of Adaptive Behavior*, pp. 15–21. MIT Press/Bradford Books.
- Wine, J., & Krasne, F. (1972). The organization of the escape behavior in the crayfish. *J. Experimental Biology*, *56*, 1–18.
- Wine, J., & Krasne, F. (1982). The cellular organization of crayfish escape behavior.. In