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The Red Tooth Hypothesis: A computational model of predator-prey relations, protean escape behavior and sexual reproduction

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Abstract

This paper presents an extension of the Red Queen Hypothesis (hereafter, RQH) that we call the Red Tooth Hypothesis (RTH). This hypothesis suggests that predator-prey relations may play a role in the maintenance of sexual reproduction in many higher animals. RTH is based on an interaction between learning on the part of predators and evolution on the part of prey. We present a simple predator-prey computer simulation that illustrates the effects of this interaction. This simulation suggests that the optimal escape strategy from the prey's standpoint would be to have a small number of highly reflexive, largely innate (and, therefore, very fast) escape patterns, but that would also be unlearnable by the predator. One way to achieve this would be for each individual in the prey population to have a small set of hard-wired escape patterns, but which were different for each individual.

We argue that polymorphic escape patterns at the population level could be produced via sexual reproduction at little or no evolutionary cost and would be as, or potentially more, efficient than individual-level protean (i.e., random) escape behavior. We further argue that, especially under high predation pressure, sexual recombination would be a

more rapid, and therefore more effective, means of producing highly variable escape behaviors at the population level than asexual reproduction.

Key words: Red Queen Hypothesis, Red Tooth Hypothesis, predation, flight behavior, sex, polymorphic escape sequences, predator-prey, protean escape behavior

Introduction

One of the enduring mysteries of evolutionary biology is the ubiquity of sexual reproduction. If we take as the fundamental postulate of Darwinian evolution that all individuals attempt (unconsciously) to maximize their own genetic material in successive generations, then the cost of sexual reproduction – half of each individual’s genetic material – would seem to be enormous. Williams (1975) famously described this as the “cost of meiosis” and claimed that “Nothing remotely approaching an advantage that could balance the cost of meiosis has been suggested.” Williams traced the origin of the question to Fisher (1930) and, especially, to Muller (1932), who developed a defense of the advantage of sex based on species selection. Muller argued that recombination through sexual reproduction allowed the immediate introduction into the same lineage of favorable mutations occurring in two different individuals. By contrast, in asexual reproduction, one mutation must occur first in some individual and the second mutation must then occur in a descendant of that same individual, a far unlikely event than an individual obtaining both favorable mutations through sexual exchange. In this view, not all the genes acquired through sexual reproduction would necessarily be of immediate

benefit to the individual who acquired them. Rather, were the environment to change, these genes would prove adaptive to the individuals possessing them in the new environment, thereby leading to a more rapid evolutionary adaptation of the species. In short, gene recombination achieved through sexual reproduction would reduce the long-term possibility of extinction of the species in an ever-changing environment.

However, Crow & Kimura (1965) and Maynard-Smith (1971) demonstrated (mathematically) that, while gene accumulation through sexual reproduction might result in increased rates of evolutionary adaptation for very large populations, this would not occur for small populations (e.g., for population sizes smaller than 1000, cf. Crow & Kimura, 1965). We will return to this important point during our discussion of the Red Tooth Hypothesis below.

The Red Queen Hypothesis

Van Valen's (1973) observation that taxonomic survivorship curves (for taxa at or above the level of genera) tended to be log-linear led to a set of new ideas as to why sex and genetic recombination offset the cost of meiosis. He suggested that the observed log-linear species extinction curves were due to co-evolutionary forces among species that were best described as a zero-sum "arms race", the end result of which was no absolute improvement in the average fitness of individuals within a species with respect to the individuals in a competing species. Even though the plausibility of this zero-sum arms race was debated in the literature for a time (e.g., Maynard Smith, 1978; Stenseth & Maynard Smith, 1984), Van Valen's work set the stage for an explicit statement of the

Red Queen Hypothesis and the suggestion that it was responsible for the existence and maintenance of sexual reproduction in essentially all species of higher animals (Hamilton, 1975, 1980; Levin, 1975; Jaenike, 1978; Bell 1982). Bell (1982, p. 143) wrote “...sex is favoured by interaction with other sexual species because the changing spectrum of genotypes among these other species creates a highly uncertain environment, compels an adaptive genetic response which can be supplied only through recombination.” Thus, without recourse to (largely discredited) theories of species selection, RQH specifies the benefits provided by sexual reproduction that would offset its elevated genetic cost to individual organisms. Bell (1982, p.157) named this the Red Queen Hypothesis of sex and recombination, after the Red Queen in Lewis Carroll’s *Through the Looking Glass* who runs as fast as she can to remain in the same place.

Jaenike (1978) first introduced the idea of a parasite-based theory of the maintenance of sex and Burt and Bell (1987) refined this idea into what is currently the most common construal of RQH – namely, that “crossing-over [i.e., recombination through sexual reproduction] may function to combat antagonists with short generation times.” Burt and Bell’s focus was specifically on host-parasite relations and the fact that genetic mixing was essential to allow individuals to successfully combat assaults by parasites. In other words, since the reproductive rates of some parasites are four to five orders of magnitude faster than those of their hosts, for each generation of their host, the parasites have hundreds of thousands of generations of mutation-engendered opportunities to unlock its defense mechanisms. But each individual host is the potential target of many, different parasites and, while a fortunate mutation might provide that individual with an effective defense against one particular parasite, mutation alone would not be sufficient to protect

that individual from the range of parasites likely to attack it. Consequently, RQH posits that only the exchange of genetic material via sexual reproduction would allow some individuals to acquire the full range of protective mechanisms required to fend off a large number of different and ever-changing parasites. So, while the cost of sexual reproduction is half of one's genetic material, at least the half that is sent into the next generation has a better chance of surviving attacks by parasites. In other words, while asexual reproduction would ensure the transmission of all of an individual's genes, the bearers of these unchanging genes would eventually succumb to parasites.

The Red Tooth Hypothesis

The present article fully acknowledges the role of RQH in the emergence and maintenance of sexual reproduction, but, in addition, suggests that sexual reproduction might also have evolved, and would continue to be maintained, because of predator-prey relations alone, even in the absence of classic parasite-host relations characterized by highly different reproduction rates. (Predation, in this context, will refer to the capture and consumption of one animal by another.) Hereafter, we will refer to this hypothesis as the Red Tooth Hypothesis (RTH), after Tennyson's characterization of nature as being "red in tooth and claw."

Assumptions of RTH

Four main assumptions underlie RTH. These are:

- 1 i) Virtually all higher animals are in predator-prey relationships with other animals.
- 2 ii) There are reflexive (i.e., innate) behavioral components in prey escape patterns.
- 3 iii) Predators have sufficiently developed neural hardware to allow them to learn from
- 4 their hunting experiences.
- 5 iv) Building dedicated neural circuitry for protean (i.e., random) escape behavior
- 6 comes at an evolutionary cost.

7 The argument for RTH can be summarized as follows. Protean escape behavior (Chance
8 and Russell, 1959; Driver and Humphries, 1988; Miller, 1997) – i.e., random,
9 unpredictable escape behavior – is clearly adaptive in that, if a predator cannot learn to
10 predict its prey's escape trajectory (ET), the prey's chances of escape improve. However,
11 the development in individuals of specialized neural circuitry capable of producing
12 protean escape behavior would come at some evolutionary cost. Further, any decision-
13 making (e.g., looking back to determine where the predator is) during escape would
14 likely be more time-consuming, and hence less adaptive, than a purely reflexive sequence
15 of escape movements. Thus, during escape, the number of these decision-points must be
16 kept as small as possible. Consequently, the optimal situation from the prey's standpoint
17 is to have a small number of highly reflexive, largely innate escape patterns, but ones that
18 would be unlearnable by the predator. One way for nature to have achieved this would be
19 to equip each individual in the population with a limited set of hard-wired escape patterns
20 for various escape contexts, but which were different for each individual. In this way,
21 individuals are protected since the “protean escape behavior” would be, to a large extent,
22 at the population level, while each individual in the population would have its own small
23 set of optimally rapid, reflexive escape patterns.

We assume, like Zheng et al. (2005), that a small number of innate elementary escape-movements (EEMs) make up more complex escape patterns and that there are low-level neural correlates for these innate EEMs. There are two basic ways to generate a variety of escape patterns from these innate EEMs at the population level: mutation and recombination. In this paper we will argue that the most efficient way to rapidly generate a wide range of complex escape patterns at the population level – thereby producing what appears to the predator to be protean escape behavior at the individual level (because the predator does not chase the same individual twice) – is by recombination of these EEM genes through sexual reproduction.

Clearly, complex, rapid escape patterns made up of sequences of more elementary behaviors are not the only efficient means of escaping from predators that prey have developed. Tortoises, for example, have no need for rapid escape patterns, nor do individual fish in schools, at least until the predator is very close at hand. Some animals never venture far from their refuges and need only to make a straight-line dash for the safety of their refuge whenever a predator threatens. Nevertheless, a great many animals *do* flee from predators and remain in the open long enough for protean escape patterns to contribute to their survival. These are the animals for which RTH applies.

Justification of RTH assumptions

We will discuss each of the assumptions of RTH in turn and then will present a computer simulation that illustrates these principles and, at the same time, makes a certain number of predictions.

1 The first assumption concerning the ubiquity of predator-prey relations, of course,
2 needs no justification.

3 Concerning the second assumption, we begin with the observation that a great many
4 animal behaviors are hard-wired. These include stereotyped courting and mating
5 behaviors (e.g., Boyce, 1990; Diamond, 1991), aspects of web-building in spiders,
6 cocoon-building in butterflies, nest-building in birds, and even long, complex sequences
7 of seemingly intelligent actions, such as those of the *Sphex* wasp when it places
8 paralyzed prey in its burrow to provide food for its grubs (Wooldridge, 1965, pp. 82-84).
9 There is, therefore, no a priori reason to assume that escape behaviors would not also
10 depend, at least in part, on reflexive, innate neural control.

11 Bolles (1970) has argued convincingly in favor of species-specific defense reactions
12 (SSDRs). He writes: “Neither the mouse nor the gazelle can afford to *learn* to avoid;
13 survival is too urgent, the opportunity to learn is too limited and the parameters of the
14 situation make the necessary learning impossible. The animal which survives is one
15 which comes into its environment with defensive reactions already a prominent part of its
16 repertoire.” Bolle’s point about escape-behavior learning is a consequence, in part, of an
17 obvious, but often overlooked, asymmetry – namely, that the failure on the part of a
18 predator to capture its prey means that it goes hungry, presumably having learned how to
19 be a slightly better predator for its next attack; failure on the part of the prey to escape its
20 pursuer has far more dire consequences. This asymmetry, dubbed the “life-dinner
21 principle” by Dawkins and Krebs (1979), plays a prominent part in the predator-prey
22 simulation described in this paper.

23 A number of examples illustrate Bolles’ point. For example, four closely related

species of (asexually reproducing) whiptail lizards in the American Southwest can be distinguished by an experienced observer solely on the basis of their highly stereotyped escape behavior (Schall and Pianka, 1980). In an aquatic environment, Burdick, Harline and Lenz (2007) have shown a similar result for calanoid copepods. Four co-occurring species of these zooplankton can be distinguished by their escape patterns to simulated predators.

Arnott, Neil, and Ansell (1999) have shown that for certain predator-approach angles, the brown shrimp (*Crangon crangon*) has a highly predictable escape region. In addition, they showed that there were certain escape regions that these shrimp never use, even though they are physically capable of doing so. Pongráz and Altbäcker (2000) have recently shown that the predatory escape-patterns of European rabbits (*Oryctolagus cuniculus*) do not require any previous experience with predators, further supporting the idea of innate (i.e., genetically engendered) escape patterns. Zheng et al. (2005) have developed a model based on empirical data of the collective evasion behavior of schooling fish that emerges from innate escape behavior patterns of the individual fish. Domenici and Blake (1993) suggest that angelfish (*Pterophyllum eimekei*) have innate preferential escape trajectories modulated by sensory feedback. Jablonski (1999) has shown that certain predators take advantage of their prey's stereotyped escape behavior. For example, the painted redstart (*Myioborus pictus*) uses various displays specifically designed to evoke a hard-wired escape response in its prey, thereby facilitating capture of the prey. Krasne and Wine (1984) discuss the neural correlates of the innate tailflip escape response in crayfish. Eaton (1984) documents the neural mechanisms underlying the startle responses that initiate escape-behaviors in animals ranging from annelids to

mammals. Recently, Domenici, Booth, Blagburn & Bacon (2008) have shown that inbred (i.e., genetically highly similar) individuals in a population of cockroaches (*Periplaneta americana*) have a small number of preferred escape trajectories. And finally, anecdotally, the archeologist Louis Leaky (1969) claimed that, as an adolescent, he was able to catch fleeing hares by being able to predict when and in what direction they would jink! We will return to this point in the discussion following the presentation of the simulation results when we discuss the behavioral polymorphisms engendered by the genotype of an individual.

Is there an inherent contradiction in our being able to have a measure of predictive accuracy for the escape patterns of a particular species and the claim that individuals within a population have highly variable escape patterns? No, because, while a degree of predictability by us humans, does, indeed, imply reduced variability in escape patterns compared to truly random escape patterns, this still leaves a lot of room for population-level escape-trajectory variability. The degree of variability among individuals must only be enough to outwit predators, which is all that counts. (Outwitting field evolutionists studying animal escape patterns isn't necessary.) In other words, the fact that we humans can detect reduced escape-pattern variability in a particular species of animals does not mean that there is no longer enough variability in these patterns to escape from common predators. A simple example might make this point clear. The escape pattern of rabbits fleeing their burrow involves their making a large circle that returns them to their burrow. So, if all rabbit predators had the cognitive resources of human hunters, they would presumably flush out the rabbit from its hole and simply wait, as hunters do, for its return and then pounce. This is clearly a far more efficient strategy than embarking on a tiring,

energy-intensive chase that might well end up not catching the rabbit. But, presumably, animals other than humans don't have the cognitive facilities to make escape-trajectory predictions that far in the future. As a result, the reduced variability of rabbits' escape trajectories, which allows us humans to make predictions about their escape behaviors, is, nonetheless, usually sufficient to allow them to avoid their common predators. This principle, applied to prey animals in general, is all that is needed for the hypotheses of this paper.

Our third assumption is that predators have sufficiently developed neural hardware to allow them to learn from their hunting experiences, both their successes and their failures. Like the first assumption, this one, too, needs little justification. All animals with neural circuitry are capable of learning from their various interactions with the world, including predatory interactions. The capability of predators to predict escape trajectories of prey has often been invoked as the driving force behind the emergence of protean escape behaviors in animals. As Miller (1997) says, "...while the Poker Face [hiding intentions] and KGB [deceit] Strategies remain vulnerable to the coevolution of smarter intention-sensing and deception-foiling capacities, there is no real defense against genuine unpredictability." In short, if prey escape patterns did not vary, predators could, in many cases, learn them, or at least parts of them, thereby gaining a significant adaptive advantage over their prey.

It would, therefore, be advantageous for prey to be able to have "unpredictable elements" in their escape response to prevent predators from gaining this advantage. This behavioral unpredictability has been called "protean behavior" (Chance & Russell, 1959; Driver & Humphries, 1988; Miller, 1997). Arnott, Neil, & Ansell (1998), in discussing

1 escape patterns of the brown shrimp *C. crangon*, comment that, “Unpredictable elements
 2 of the escape response have been shown to be a prominent feature of *C. crangon* escape
 3 swimming and are probably important in preventing predators from learning a fixed
 4 pattern of response.” A detailed chronicle of the near ubiquity in nature of protean escape
 5 behavior has been given by Driver and Humphries (1988).

6 The final assumption underlying RTH is that there is an evolutionary cost associated
 7 with equipping individuals with the ability to produce protean escape behavior. There are
 8 several related issues here. First, the requirement of making choices during escape would
 9 be cognitively more costly, and therefore slower, however slightly, than purely reflexive
 10 movements. Second, protean behavior in an individual does not come for free. Some
 11 neural mechanisms must exist to produce it and those mechanisms would have come at
 12 an evolutionary cost. As Driver and Humphries (1988, p. 177) have pointed out,
 13 “Organized – through overtly erratic – variations of direction and speed in prey animals,
 14 i.e., protean flight, necessitate the evolutionary development of special control
 15 mechanisms.” The problem is that it is not clear how these mechanisms might work.
 16 Driver and Humphries invoke the possibility of mechanisms involving lowered inhibition
 17 of motor control neurons and suggest that individual-level protean escape patterns might
 18 be generated in a manner similar to epileptic-like convulsions. What is needed, then, is a
 19 neural mechanism that would provide feedback-controlled, escape-movement specific,
 20 convulsions and it is far from clear how this might work. Further, while epileptic-like
 21 convulsions may appear to be random, they may well not be. As Miller (1997) has
 22 pointed out, the question of whether animals can actually produce truly random behavior
 23 at all is still open to debate.

1 **Escape behaviors: hard-wired and protean**

2 This brings us to our explanation of how can animals can have escape behaviors that
3 are both hard-wired and protean.

4 Since a given predator rarely, if ever, attacks the same animal twice, nature would
5 not have had to go to the trouble of equipping individuals with any specific,
6 evolutionarily costly, mechanisms for protean escape behavior, as long as there was
7 protean escape behavior at the *population level*. In short, an individual prey animal is best
8 served by having a largely fixed, reflexive – and therefore, maximally rapid – escape-
9 sequence (or small set of these sequences to be used in different escape contexts), whose
10 unlearnability is ensured because other similar animals have randomly different escape-
11 sequences.

12 This is, of course, not to deny the existence of neurally encoded protean escape
13 behavior in individuals. Rather, RTH suggests that, just as there are polymorphisms for
14 characteristics like cryptic coloration, there are also *behavioral* (in this case, escape
15 pattern) polymorphisms among individuals. An important challenge for empirical
16 research, then, is to distinguish the extent to which protean escape behavior within a
17 given species is at the individual versus population level.

18 It has been suggested (J. Endler, personal communication) that even if the neural
19 circuitry designed to produce escape patterns was essentially identical for all individuals
20 in a population, minute changes in environmental conditions, hormonal levels, etc. could
21 produce different firing patterns of this circuit that could, in turn, produce radically
22 different, even chaotic, escape behavior, thereby achieving, at essentially no additional
23 cost, the desired protean escape behavior at the individual level. This is certainly

possible, but small neural changes leading to chaotic, or quasi-chaotic, behavior is –
 fortunately – not a general property of most neural circuitry. Small changes in the
 environment do not, for example, cause us to speak in a chaotic manner or to act in
 radically unpredictable ways. Thus, if all individuals did have identical neural escape
 circuitry, one would have to ask what mechanisms would allow these circuits -- and only
 these circuits -- to be hyper-sensitive to minute environmental changes, when most neural
 circuitry is not. Secondly, escape patterns only have to show certain general regularities
 over time and in certain contexts to allow the predator to learn, however imperfectly,
 something about its prey escape patterns, thereby giving the predator a significant
 adaptive advantage over its prey.

Prey escape-patterns and their relation to sexual versus asexual reproduction

The conundrum of mutation-driven evolution, as Williams (1975) realized, is that
 evolution, which relies on mutation-driven variability, has evolved myriad mechanisms to
 keep mutation rates as low as possible. He writes (Williams, 1975, p. 148), "... all
 observed mutations rates should all be regarded as approximations of zero." This would
 imply that the innate (i.e., genetically engendered) escape patterns of prey animals would
 evolve only very slowly if mutations occurring during asexual reproduction were the sole
 means of modifying them. This would increase the likelihood that predators could learn
 them. By contrast, sexual reproduction would produce a population of different – and
 therefore unlearnable by predators – escape patterns at no extra evolutionary cost, while
 allowing mutation rates to remain as low as possible.

The simulations presented in the next section compare survival rates of prey under sexual reproduction versus mutation. They will show the clear advantage of sexual reproduction over mutation alone, especially where predation pressure is high. These simulations also show that high mutation rates can, by themselves, generate escape-pattern randomness at the population level. But high mutation rates have other, almost invariably deleterious effects on individuals in the population, which is why nature keeps them as low as possible. In humans, for example, genome mutation rates are on the order of 10^{-8} per base pair per generation (Nachman and Crowell, 2000).

Red Tooth Hypothesis Simulations

In what follows, we will present a set of simple predator-prey simulations in which predators are modeled by neural networks designed to learn sequences. Over time these predator networks learn short segments of the prey escape-sequences by successive encounters with the prey. Each instance of pursuit constitutes a learning trial for the predator. In contrast, a prey's failure to escape a predator is (obviously) not a learning experience for the prey. Escape patterns of prey therefore evolve, not during the lifetime of the animal, but over evolutionary time. Each individual in the prey population is modeled as a sequence of "elementary escape-movement (EEM) genes" that determine how it will escape from a predator.

We then compare evolution in the prey population achieved through mutation alone with evolution produced by a combination of mutation and crossover.

1 **Details of the simulation**

2 In all simulations reported here, we begin with an initial population of 100 prey
3 individuals and a single predator. During each generation, we assume that the predator
4 attacks each member of the prey population once, thereby allowing the fitness of each
5 prey individual's escape behavior to be calculated. Reproduction occurs at the end of
6 each generation based on a standard genetic algorithm.

7 We used a standard genetic algorithm (Holland, 1975; Mitchell, 1996) to model the
8 evolution of escape patterns through sexual reproduction. There is a clear description of
9 the algorithm used in Mitchell (1996, pp. 10-12). A population of 100 individuals was
10 maintained at each generation. Single-point crossover was used and both of the newly
11 created offspring were included in the new population. None of the "fittest animals"
12 from the prior generation were explicitly retained in the succeeding generation.

13 We manipulated mutation rates and predator speeds. Each simulation ends either
14 after 30 generations or earlier if the prey population has become extinct. In order to study
15 RTH without, in addition, having to model the dynamics of two interacting populations,
16 we chose to have a single predator which encounters all of the prey each generation.

17 For each simulation the initial population contained 100 prey animals, each with one
18 of two randomly chosen escape-sequence genotypes. A single predator pursued all of the
19 prey individuals during the course of each generation. The fitness of each prey individual
20 was determined by how far it was from the predator after 20 jinks in its escape trajectory.
21 If an animal was caught, it was eliminated from the population. Reproduction was based
22 on fitness with fitter individuals producing more offspring (see Holland, 1975). A new
23 population of 100 individuals was produced at each generation in order to ensure that the

predator had an equal number of learning cycles per generation, thereby allowing the same amount of predator learning across generations. The simulation was stopped after 30 generations or earlier, if all of the prey in the population were caught by the predator.

Prey

Each individual in the prey population is modeled as a string of 80 bits, corresponding to a sequence of twenty 4-bit “EEM genes,” each of which codes for a jink angle with respect to the current line of flight. (The length of the escape sequence was arbitrarily chosen and does not affect the conclusions of the RTH simulation.) Each of the 16 possible EEM genes corresponds to what Zheng et al. (2005) refer to as fixed (innate) “behavior patterns”. The fitness of an escape-sequence, and its corresponding gene sequence, is measured by how far apart the prey with that sequence is from an attacking predator after 20 jinks. Escape patterns for prey that are caught by the predator are assigned a fitness of zero. It seemed reasonable to suppose that the farther an animal was from its pursuer after a given amount of time, the “fitter” its particular escape behavior. For this reason we adopted a continuous measure of fitness, rather than a coarser, all-or-nothing measure of fitness where “fit” corresponded to escape and “unfit” to capture. We did, however, test the all-or-nothing fitness measure and the pattern of results is globally similar to that which is obtained using the continuous measure, the only difference being that the rise in entropy of the population (see Figure 7 and the discussion of entropy) occurs more slowly.

In a real environment, of course, escape trajectories are produced by an interaction between underlying behavior patterns and environmental influences on those patterns.

1 The terrain over which an escape occurs is invariably uneven and strewn with obstacles,
 2 such as rocks, trees, and bushes, and no escape pattern would be executed independently
 3 of this environment. Animals, even if their escape patterns were completely innate, do not
 4 run into trees while escaping. In the interest of simplicity, however, we did not attempt to
 5 model these environmental factors. We made the assumption that a given innately-driven
 6 escape pattern would give rise to responses in particular environmental contexts that were
 7 still learnable. All that is required for predators to improve their prey capture rate is to
 8 learn, in general, what its prey is likely to do in a particular context. So, for example, if
 9 its prey is approaching a dense thicket, knowing that it will, on average, veer to the right
 10 significantly more often than to the left is very valuable -- and learnable -- information
 11 for the predator, even if it does not allow for perfect prediction. The response, “veer right
 12 when approaching a thicket,” we assume to be a product of the underlying escape
 13 encoding.

15 **Predators**

17 Predators are modeled by a simple three-layer backpropagation neural network whose
 18 inputs correspond to the current jink angle of the prey, as well as the previous two jink
 19 angles, which provide context information. The network attempts to predict the next jink
 20 angle of the prey. If it is able to accurately predict the upcoming jink angle, it
 21 stochastically begins to make attempts to learn a two-jink prediction. If it is able to learn
 22 this, as well, it attempts a three-jink prediction.

23 The network, therefore, has 12 input nodes (plus bias nodes on the input and hidden

layers), corresponding to the present jink angle and the previous two jink angles. There are 12 hidden nodes. There are also 12 output nodes, the first four of which correspond to the prediction of the next jink, the second set of four corresponds to a two-jink prediction, and the final group of four corresponds to a three-jink prediction. The hidden layer is fully connected to the first set of four output nodes (representing the immediately following jink angle), fully connected to the second set of output nodes (representing a two-jink prediction), and fully connected to the third set of output nodes (representing a three-jink prediction). The learning rate was 0.01 and momentum 0.9. Both the hidden and output layers were fed activation from a bias node in the preceding layer. The hidden and output layers used standard sigmoid squashing functions. A standard sum of squares error function on output was used to drive learning. A generalized delta learning rule was used for all weight changes. (See Rumelhart & McClelland, 1986, vol. 1, pp. 45-54 for implementation details for a standard backpropagation neural network.)

Initially, the network attempts to predict the next jink of the prey. As it gets better and better at doing this (i.e., when the network error is low for the next jink in the sequence), it will (stochastically) start to make two-jink predictions. If it gets good at two-jink predictions, it will try to make three-jink predictions. The better the predator's predictive look-ahead is, the more likely it will be to catch its prey. The less of any given individual prey's escape-sequence it can predict, the harder it will be to catch that individual.

The predator pursues all 100 individuals in each generation of prey. The learning acquired during previous generations remains with the predator as it pursues prey in future generations. In other words, the predator will have a total of 3000 learning

experiences during the course of the simulation. (This corresponds to 3000 learning “epochs” of the neural network that constitutes the predator.)

Figure 1 shows a typical predator-prey chase. After 20 jinks, the distance remaining between the predator and its prey is used as a measure of the fitness of the prey’s escape-sequence. If the predator catches the prey before the end of the escape sequence, the fitness of the sequence is set to 0.

<Figure 1 here >

Figure 1. A typical predator-prey chase. The fitness of the escape-trajectory is determined by the distance between predator and prey after 20 jinks.

In a real predator-prey interaction, a number of factors are crucial in determining the probability that the prey will escape, most importantly, the animals’ maximum speed, acceleration, maneuverability, and endurance (Alexander, 2003). In the present simulation we chose to model only one of these parameters, maximum speed. We felt that the inclusion of the other variables was unnecessary to make the main point of the paper – namely, the advantages of sexual reproduction in producing the emergence of protean escape patterns at the population level which hinder the predator from catching its prey.

In the constant evolutionary arm-races between species of prey and their predators, the maximum speed of a given predator is generally not too far above that of its prey (Alexander, 2003). For this reason, the ratio of prey-to-predator speeds in our simulations varies from 1:1.1 to 1:1.5.

In our simulations, we did not explicitly model the differences in the centripetal

forces involved when a larger predator turns compared to its smaller prey. This difference in forces means that, at close quarters, it is inherently advantageous for prey to turn tightly (Alexander, 2003) to avoid a heavier predator. The main points of our model are about prediction and learning on the part of the predator and evolution on the part of the prey and, for this reason, we made no assumptions about the relative size of the predators and prey. As a result, the forces involved in turning were not modeled explicitly. However, there is no a priori reason that this could not have been done. Had we done so, it is likely that we would have seen the systematic emergence of tight turning behavior when the predator is close to the prey.

Predator and prey position calculations

Predators begin their pursuit at the origin of a grid. Each prey individual starts at (0,2) on that grid. Prey are assumed to have a speed of 1 at all times. Predators have a fixed speed that is some factor of the prey's speed (e.g., 1.1, 1.2, 1.5). A fixed "reaction time" for the predator is associated with each jink of the prey. If the predator correctly predicts the next jink direction, this reaction time is decreased by a fixed amount. The predator predicts where its prey will go on its next jink (or jinks) and heads in the direction of its prediction. Given that we know the current position of the predator, its direction, its speed, and its time to react to the prey's jink, we can calculate its next position. As the predator learns and gets better at one-jink predictions, it will (stochastically) occasionally make two-jink predictions and, ultimately, sometimes, three-jink predictions (directly heading towards the spot the prey will be after two or three jinks). From its starting

point, the prey simply executes the fixed escape trajectory defined by its sequence of twenty EEM genes.

Evolution of survival rates for sexually versus asexually reproducing populations

In what follows we compare survival rates in sexual versus asexual populations. We will begin by showing (Figure 2) survival-rate curves over 30 generations for a given predator pursuit speed (in this case, 1.4, compared to the prey's speed of 1) and a given mutation rate ($\mu=0.0001$).

Figure 2 shows median and average survival rates for sexually and asexually reproducing populations when the prey-predator speed ratio is 1:1.4. The data were averaged over 20 runs. The average data was calculated only for non-extinct populations at each generation (i.e., if, say, at generation 23 there were only five runs in which the prey population had survived, the average survival rate for that generation was calculated based on those five populations).

<Insert Figure 2 here>

Figure 2. Evolution of survival rates of sexual and asexual prey populations over 30 generations (average and median data)

A key result of our simulations is illustrated in Figure 2. We have a low mutation rate of $\mu=0.0001$ and a prey-predator speed ratio of 1:1.4. Under these conditions, the median survival rate for the sexually reproducing population climbs rapidly to above 80% and

1 levels out around 90%. In contrast the median survival rates for asexual populations drop
 2 to 0 by 20 generations. In other words, most of the time they will become extinct before
 3 30 generations.

5 **Survival rates, mutation rates, and predation pressure**

7 What happens if we vary mutation rates and predation pressure? The graphs in Figures
 8 3a, 3b, and 3c show that if predation pressure is low (i.e, predators run only 10% faster
 9 than their prey, Figure 3a), low mutation rates can be maintained in both sexual and
 10 asexual populations and prey survival rates will remain high. However, as predation
 11 pressure increases (up to a prey-predator speed ratio of 1:1.5 in Figure 3c), sexual
 12 reproduction becomes essential to simultaneously maintain both low mutation rates and
 13 high prey survival rates. Of course, high mutation rates in asexual populations also
 14 produce the variety of escape patterns that sexual reproduction produces at low mutation
 15 rates. Even with high predation pressure (prey-predator speed ratio = 1:1.5), if the base
 16 mutation rate of 0.0001 is increased by a factor of 50 to 0.005, there is no difference in
 17 survival rates of asexual and sexual populations. But of course, high mutation rates
 18 almost invariably have other deleterious effects on the organisms, as we have discussed
 19 above.

20 In the original population, if the two original escape-sequence genotypes differ only
 21 slightly (e.g., by no more than 20%, rather than both being random), we obtain essentially
 22 the same results as in Figures 3a, 3b, and 3c.

<Figure 3a here>

Figure 3a. The prey-to-predator max.-speed ratio is 1:1.1

<Figure 3b here>

Figure 3b. The prey-to-predator max.-speed ratio is 1:1.3

<Figure 3c here>

Figure 3c. The prey-to-predator max.-speed ratio is 1:1.5

In short, for environments of low predation pressure, asexual reproduction is as effective as sexual reproduction in producing effective polymorphic escape-behavior. However, under heavy predation pressure, sexual reproduction becomes much more important. This corresponds to what is commonly observed in certain heterogamous animals. For example, the freshwater crustacean *Daphnia* generally reproduces parthenogenically, then switches to sexual reproduction as competition and predation increase. Williams (1975) and Bell (1982) document numerous cases of this shift to sexual reproduction when the environmental conditions, such as climate, increased predation, etc., become harsher.

Prey-predator first encounters

Our simulations (Figure 4) also show that when a founder population of prey animals first encounters a new predator, initially, the predators will kill a significant number of them, frequently leading to the extinction of the prey. However, if extinction does not occur in

the first few generations, the counterbalancing effects of sexual reproduction producing a wide variety of prey escape trajectories will rapidly become evident. Two things happen: i) prey with better escape-sequences survive the initial onslaught of the predator and transmit to future generations their more effective escape-sequences and ii) more escape sequences are generated, thus making it impossible for predators to learn prey escape movements.

In simulations with asexually reproducing populations with a low mutation rate and low predation pressure, if the population does not go extinct early on, we see the same general evolution of survival rates, only with a much more gradual slope. In other words, asexual populations are more vulnerable than sexual populations to initial predatory attacks, but if the population manages to survive long enough, the effects of mutation alone will ultimately be the same as those of recombination – namely, the population-level escape trajectories will become varied enough to afford individual-level protection from the predator.

<Figure 4 here>

Figure 4. Prey are initially vulnerable to attack by predators learning their escape-behaviors. Evolutionary forces gradually reduce the effectiveness of these attacks.

Sexual recombination of escape-sequences makes the predator's chase harder

Figure 5 compares how easy or difficult it is for a predator to follow its prey. We assume that the prey will jink 20 times in its escape-sequence. The predator pursues all 100 of

prey in each generation once, which gives a total of 3000 encounters with prey. This means that the neural network that models the predator has 3000 learning cycles to predict where the prey will be after each jink. Accurately predicting where the prey will be means that the predator can take shortcuts during pursuit of the prey. The graph compares the evolution of the number of direction changes that the predator needs to make when pursuing asexually reproducing prey compared to sexually reproducing prey. After 3000 learning cycles, the predator requires only 10 changes of direction to successfully track its prey, whereas for a sexually evolving prey population, where population-level protean escape-behavior is established, very little anticipatory prediction (i.e., learning of escape patterns) is possible and the predator requires an average of 17 to 18 changes of direction to pursue its prey.

<Figure 5 here>

Figure 5. The evolution of the number of changes of direction during pursuit of its prey in populations of asexually and sexually reproducing prey. For 20 jinks of the prey in an asexual population the predator needs only 10 changes of direction, whereas 17 to 18 are required for when pursuing sexually producing prey.

Protean escape-patterns versus good escape patterns

An escaping animal can be protected in at least two different ways when fleeing an attacker. It can either have an excellent escape-sequence that is intrinsically hard for the predator to follow, even taking into consideration the predator's ability to learn segments of

it. Or, even if its escape-sequence is only moderately effective by itself, it can be protected by the fact that the predator cannot predict its escape-patterns because of the random nature of escape patterns at the population level. This would imply that in sexually reproducing species individual protection is likely to be provided by a great many escape patterns of varying intrinsic quality. By contrast, in asexual populations there will be less escape-pattern entropy at the population level, which will mean that, in general, (parts of) these escape sequences will be easier to learn by the predator. Consequently, those asexual populations that do survive will have escape sequences that, even though parts of them can be learned by the predator, are, nonetheless, still good enough to escape the predator. This implies that escape trajectories of asexual populations will have to be, on average, intrinsically better than those of sexual populations under equivalent predation pressure.

Variability of escape patterns in sexual and asexual populations

In Figures 6a and 6b we can see the results of a simulation where the mutation rate was 0.0001 and the predator-to-prey maximum speed ratio was 1:1.4. It is clear that in the case of the sexually reproducing population (Figure 6b), the range of escape-patterns is considerably more varied than in the asexually reproducing population (Figure 6a).

<Figure 6a here>

Figure 6a. A random selection of 36 escape-patterns in an asexually reproducing population with a mutation rate of 0.0001 after 30 generations.

<Figure 6b here>

Figure 6b. A random selection of 36 escape-patterns in a sexually reproducing population with a mutation rate of 0.0001 after 30 generations.

A quantitative measure of population-level escape-trajectory variability

It seems clear from a visual examination of Figures 6a and 6b that after 30 generations sexually evolving populations have more highly varied escape trajectories than asexually evolving populations. But it would be very useful to have a measure of this variability. In particular, this would allow us to trace the evolution of variability of escape trajectories within a population over time. If RTH is correct, this evolution of variability should correlate closely with the evolution of prey survival rates.

To measure population-level escape-trajectory variability, we used a standard conditional entropy measure (MacKay, 2002) taken from information theory. Conditional entropy is calculated as follows:

$$H(S) = - \sum_{i \in I} p(i) \sum_j p(j|i) \log_2 p(j|i)$$

In our simulations this measure is interpreted as follows. For a given population S , we consider a set of randomly chosen escape trajectories (in this case, the escape trajectories of 36 individuals in the population). Since there are 16 possible jink angles and the predator uses the most recent jink, along with the two previous jinks before that, to predict the upcoming jink, this means that there $16^3 = 4096$ different “jink contexts”. However, in fact, there are only a relatively limited number of different jink contexts encountered by the predator (the fewer that are actually encountered, the lower the variability of the population of escape-trajectories). The probability of each of the jink

context actually encountered (indicated by $i \in I$ in the entropy formula) with respect to all possible jink contexts is indicated in the formula above by $p(i)$. The conditional probability of the upcoming jink angle, j , given the context, i , is designated by $p(j|i)$. We calculate these values over the set of all escape trajectories in our sample population to arrive at an entropy value of H_1 for single-jinks, H_2 for double-jinks, and H_3 for triple-jinks. The final value H for the population of escape trajectories is the average of these three values.

< Insert Figure 7 here.>

Figure 7. Evolution of the entropy (i.e., randomness) of escape trajectories of individuals from asexually reproducing and sexually reproducing populations.

Figure 7 is a graph of the evolution of H at each generation. In particular, this graph illustrates the rapidity with which sexual evolution creates variability in the escape trajectories at the population level compared to asexual evolution. In the first 5-7 generations, the entropy of the sexual population's escape trajectories (i.e., SEX 0.0001) increases rapidly and by 12 generations it has reached its maximum variability. By contrast, the entropy of the escape trajectories of the asexual population with the same mutation rate (i.e., ASEX 0.0001) increases only very slowly over the course of the 30 generations of the simulation. These values are drawn from a population where the predator is only slightly faster than the prey (predator-prey speed ratio: 1.1) with a low rate of mutation ($\mu = 0.0001$). In this way, very few populations went extinct during any

given run of the simulation. The graph also shows that as the mutation rates in asexual populations increase from 0.0001 to 0.005 (i.e., a 50-fold increase), the escape-trajectory entropy curves approach those of a sexually reproducing population with a mutation rate of $\mu = 0.0001$. These graphs show how sexual reproduction can ensure high variability at the population level of escape trajectories, all the while keeping the mutation rates very low.

Discussion

The simulations presented in this paper show that, if there are underlying innate behavior patterns comprising escape behavior, then sexual reproduction would be a more effective means than asexual reproduction of producing protean escape behavior at the population level, while allowing faster, reflexive behavior to be maintained at the individual level. In other words, evolution may well have endowed individuals with neural mechanisms to produce random behavior, but this would have been a far more evolutionarily costly process than producing this behavior at the population level. This is not to deny the existence of individual-level protean behavior, of course, but it is hard to see what forces would have caused evolution to develop it in individuals if, in fact, equivalent protection from predators had already been achieved by population protean behavior that emerged from sexual reproduction. It could have been that sexual reproduction was evolution's response to the need for rapid emergence of population-level protean escape behaviors. In any event, once sexual reproduction was in place, generating protean escape-behavior at the population level would have incurred almost no extra cost to prey but would have provided significant adaptive advantages.

It would be interesting to attempt to tease apart the extent to which observed protean escape-behaviors are individual-level behaviors or population-level polymorphic behaviors. Almost all studies of escape behaviors to date have been done on groups of individuals. It would be interesting to begin with two animals with an identical genetic makeup (i.e., identical twins), raised from conception in an identical environment and then placed in an experimental apparatus similar to that used by Arnott et al. (1999) in order to determine the extent to which their respective escape behaviors differed. This would give us a better idea of the degree to which escape behaviors are innately engendered. Empirical studies of this kind on a small naturally occurring clonal fish species *Kryptolebias marmoratus* are currently under way in Britain in the Animal Behaviour Group in the Psychology Department of the University of Exeter (D. Croft, personal communication).

Crow & Kimura (1965) and Maynard-Smith (1971) proved that one of the fundamental flaws with theories that suggested that sexual reproduction resulted in increased rates of evolutionary adaptation through gene accumulation was that they only applied to populations whose size approached infinity. For small populations, for example, populations with less than a thousand individuals, they showed there was essentially no advantage to gene accumulation through sexual reproduction.

But as the above RTH simulations show, this does not apply to the hypothetical jink genes. This is because mutations of these genes, unlike most genes, do not have deleterious consequences for the individual in which they occur. On the contrary, their expression simply leads to a different escape-trajectory in that individual. This contributes to population-level protean escape behavior which protects not only the individual in which

the mutation occurred, but the other individuals in the population.

In other words, if EEM genes that are linked to elementary escape-behavior patterns do, indeed, exist then the mutations of these genes and their subsequent accumulation and recombination through sexual reproduction will be highly advantageous to individual prey, however small the population.

Our simulations demonstrate a manner in which learning can drive evolution. Further, RTH gives rise to a number of predictions, such as, the entropy of prey's population-level escape-patterns should be proportional to the intelligence of their predators; the diversity of escape patterns should tend to be larger in sexually reproducing populations, the diversity of escape patterns in asexually producing animals should be smaller, but they should be of better quality; the greater the predation pressure, the more important and prevalent recombination by sexual reproduction becomes; etc.

Although we have not modeled this here, it is clear that simulations of this sort could, and should, be extended to include the co-evolution of multiple generations of predators. The quasi-impossibility of learning the escape behavior of its prey because of its population-level protean nature would presumably stymie the effects of Baldwin-like learning (Baldwin, 1896; Morgan, 1896; Hinton & Nowlan, 1987; French & Messinger, 1994) on the predator genome. In other words, the impossibility of learning during hunting would have meant that hunting would not have driven improved learning capacities in predators over evolutionary time. This might help explain why "...true co-evolution ... seems remarkably rare in predator-prey systems." (Endler, 1991) Once a sufficient degree of randomness in escape behavior was achieved (either at the individual or at the population level), the predator would no longer be able to learn prey escape

patterns from prior encounters with that prey.

Empirical tests using heterogamous animals, similar to those designed to explore RQH (e.g., Lively, 1987), could be run for RTH as well. RTH would, for example, predict that heterogamous animals in asexual reproductive mode would tend to switch to sexual reproduction when the predator pressure in their environment increased, something which is known to be the case for the freshwater crustacean *Daphnia* (Bell, 1982). This water flea reproduces by parthenogenesis then switches to sexual reproduction as competition and predation increase.

In the simulations presented in this paper there is a one-to-one correspondence between EEM genes and their expression as primitive escape-movements. Sequential combinations of these primitive escape movements are assumed to determine more complex escape patterns. However, it may be that other genes regulate these EEM genes, whose expression would, therefore, not be identical in all animals of the species. This does not, however, affect the central point of the paper – namely, that each animal will have a small number of escape patterns that are *fixed (i.e., innate)* and that the degree of similarity of these patterns across the population determines how learnable they are by predators. But regardless of how the genotype-phenotype mapping is achieved, RTH suggests that the least costly way for evolution to produce unlearnable individual-level escape patterns is to ensure the randomness of these escape sequences at the population level via sexual recombination.

Conclusion

The goal of this paper has been to suggest that, given the ubiquity of predator-prey relations in nature, sexual reproduction would likely produce polymorphic escape behavior more rapidly and more effectively than asexual reproduction. This leads to the suggestion that protean escape behavior, heretofore taken to be an individual-level phenomenon, is, to a significant extent, actually population-level behavior.

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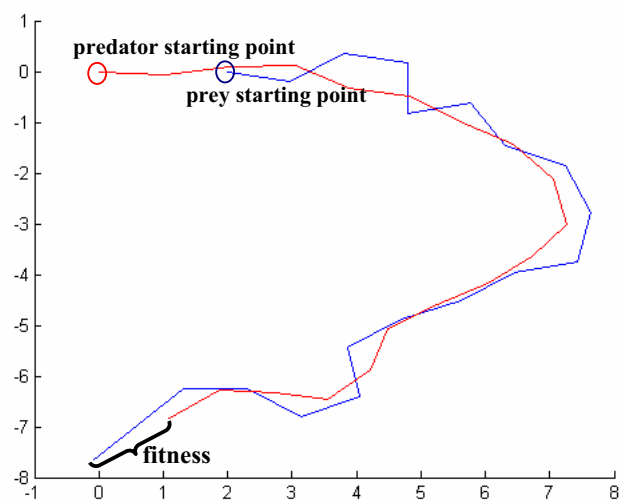


Figure 1

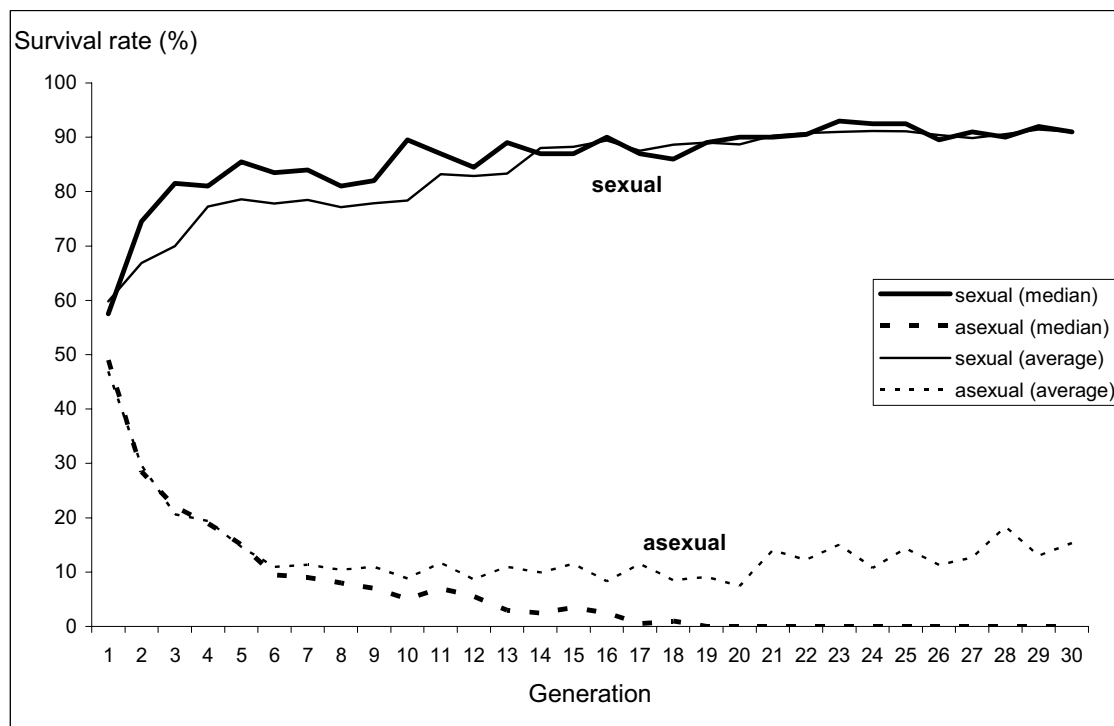


Figure 2.

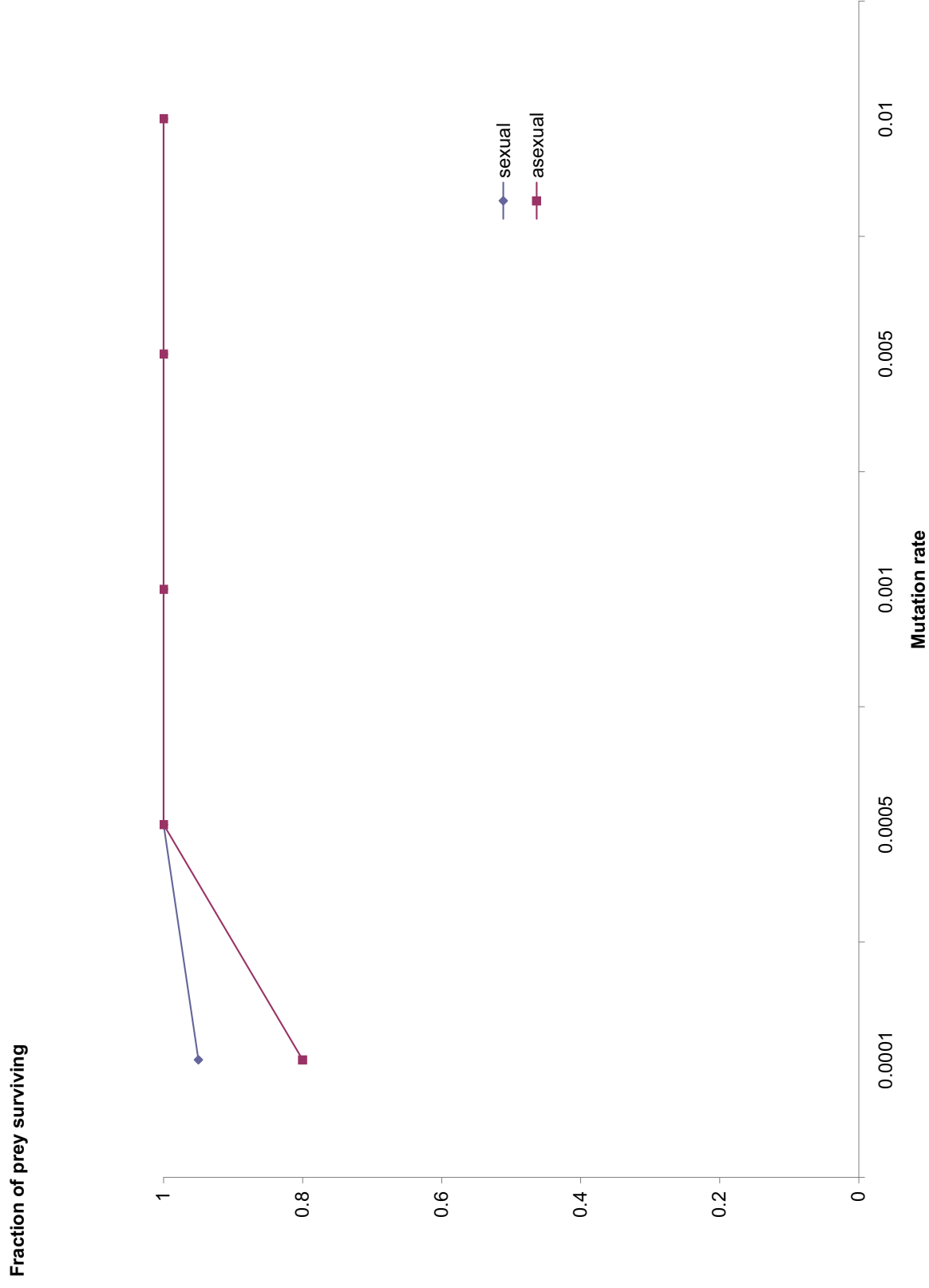


Figure 3a

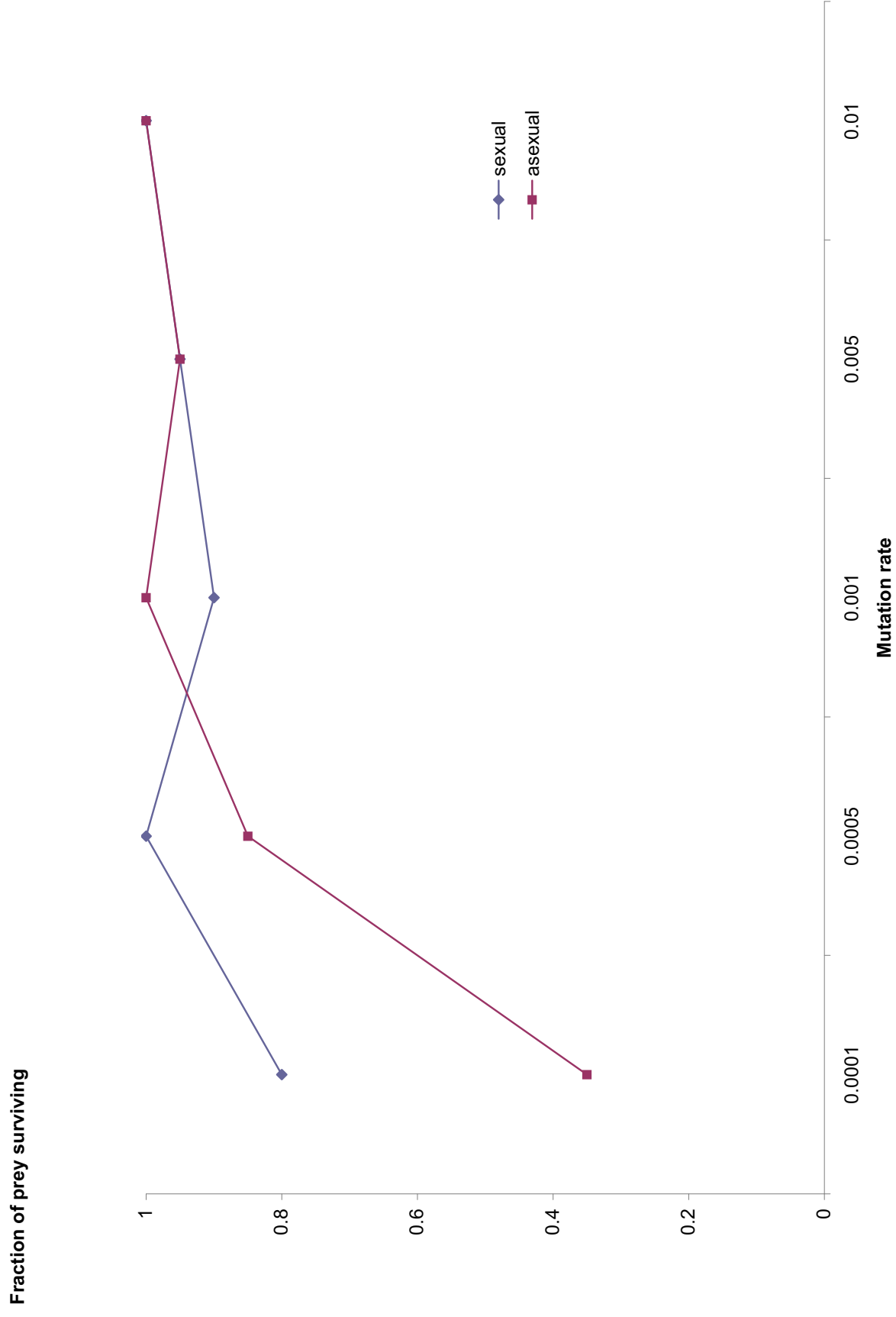


Figure 3b

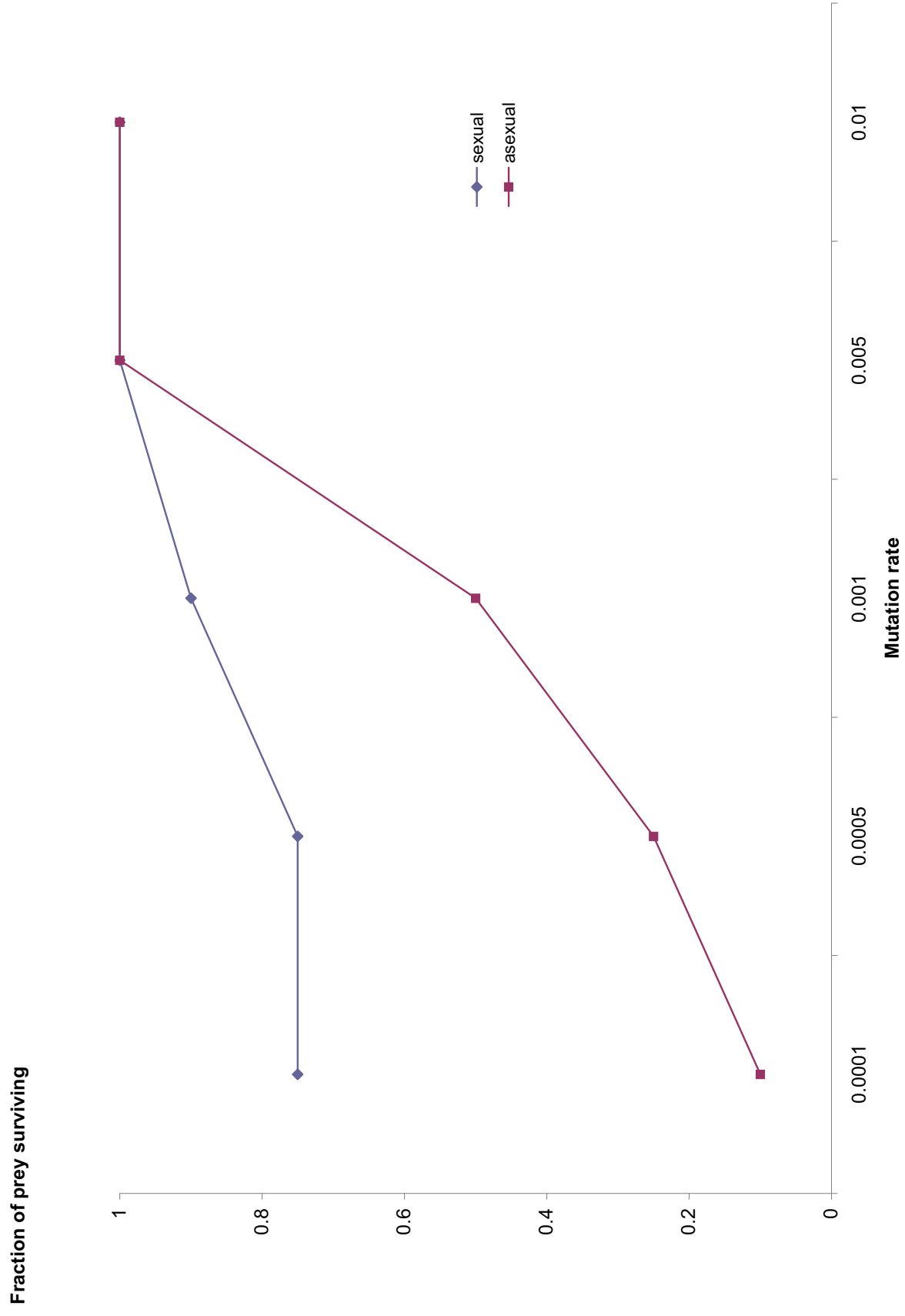


Figure 3c

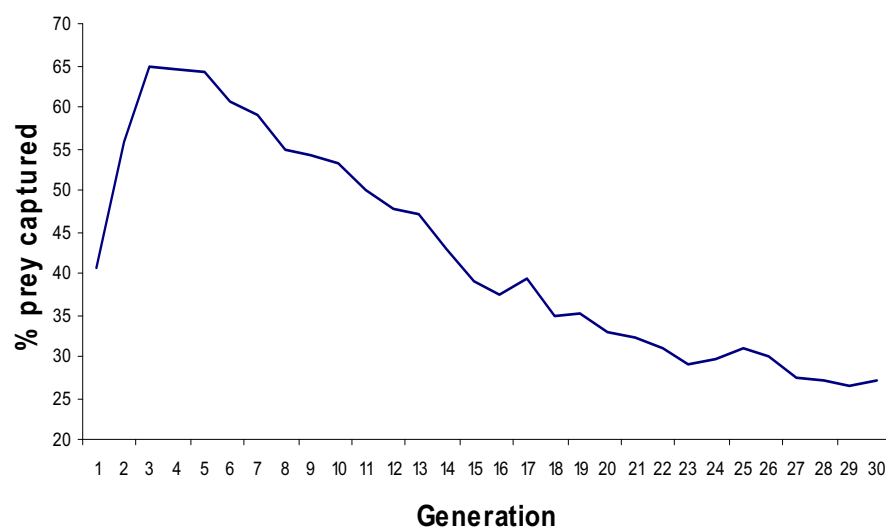


Figure 4

No. of predator
direction changes

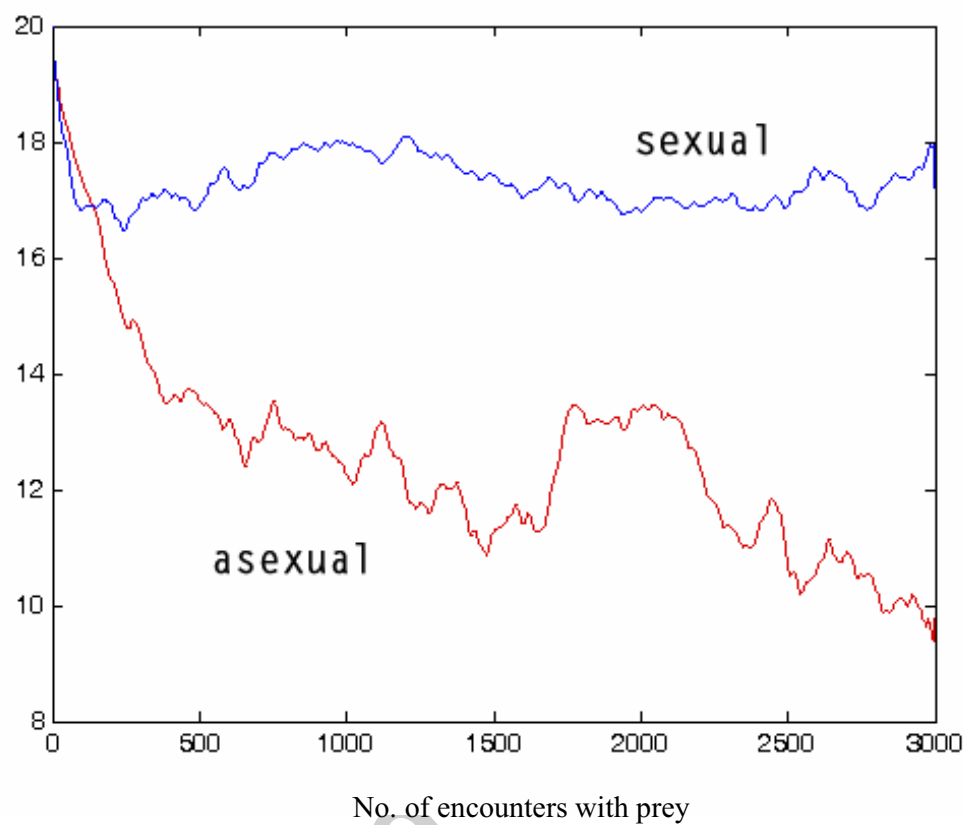


Figure 5

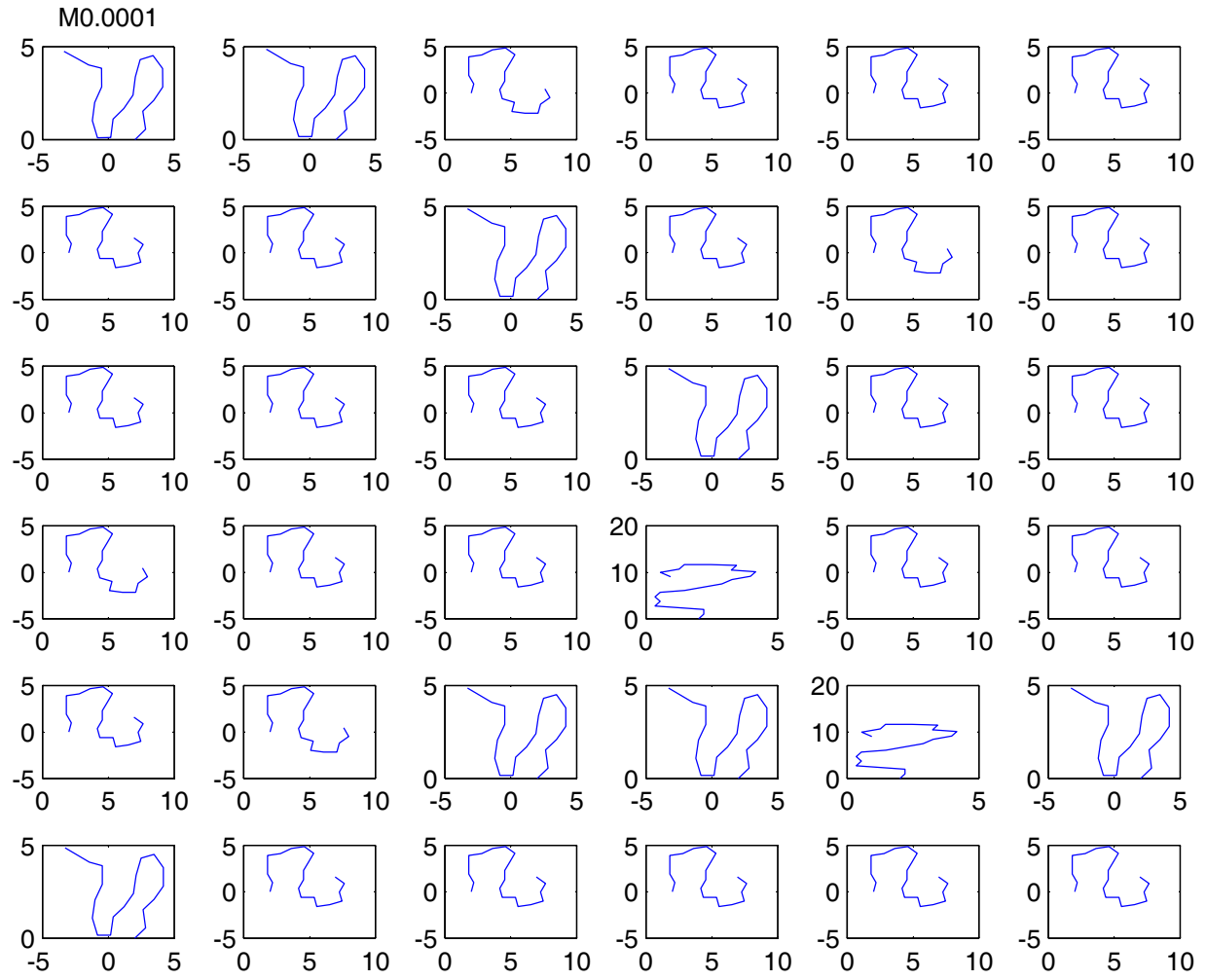


Figure 6a

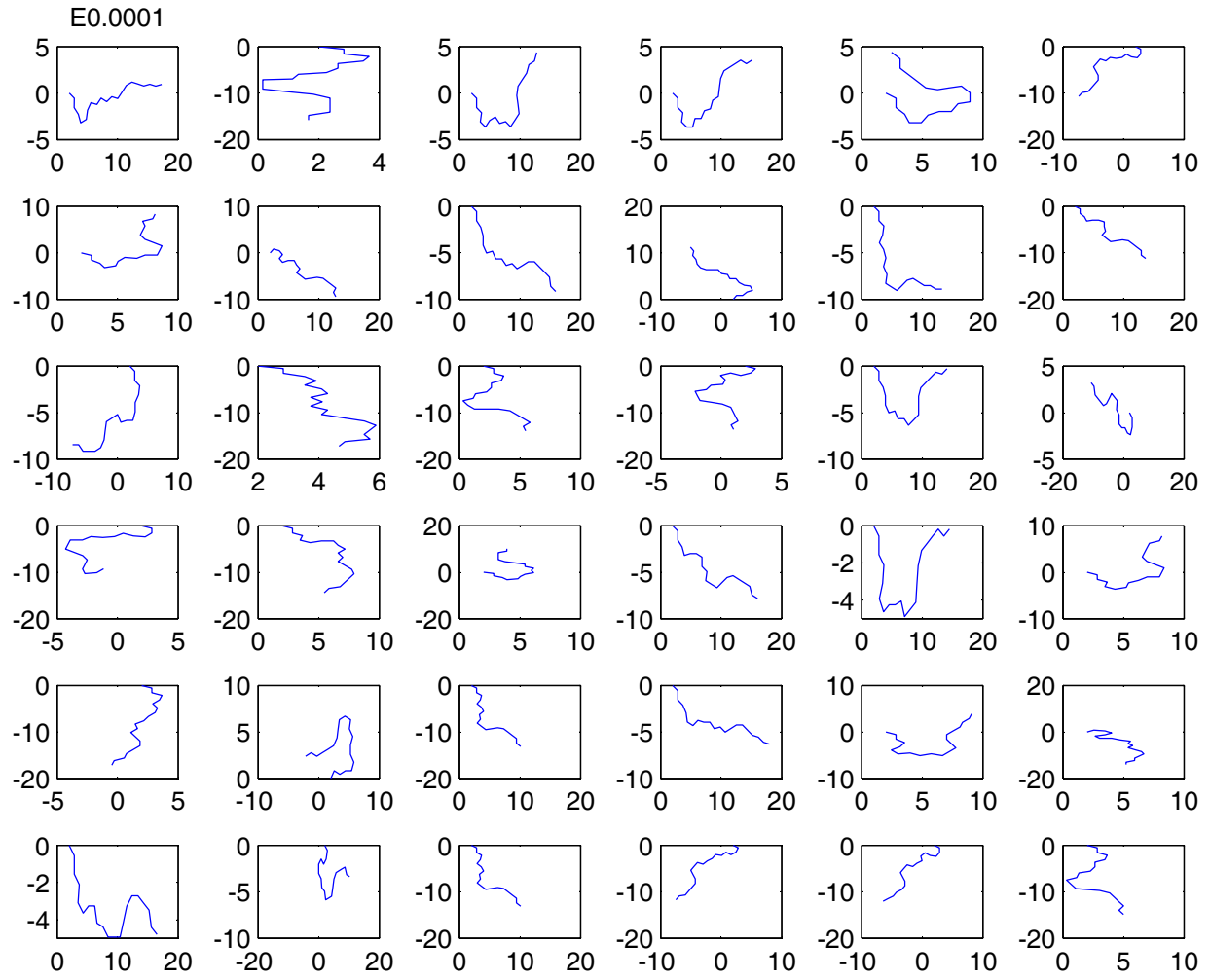


Figure 6b

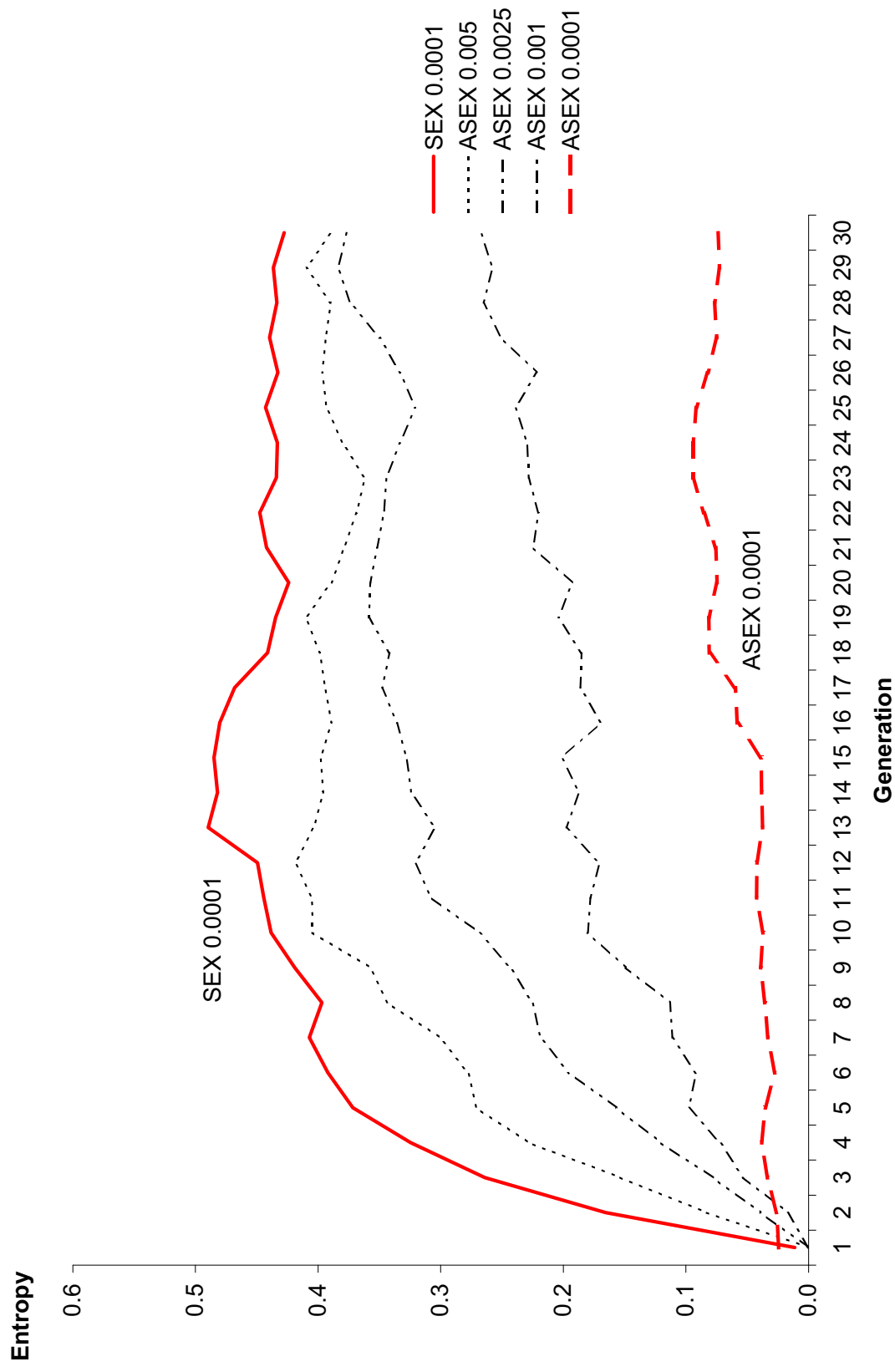


Figure 7