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Robert M. French. The red tooth hypothesis: A computational model of predator-prey relations, protean escape behavior and sexual reproduction. *Journal of Theoretical Biology*, 2009, 262 (1), pp.165. 10.1016/j.jtbi.2009.09.016 . hal-00559158

HAL Id: hal-00559158

<https://hal.science/hal-00559158>

Submitted on 25 Jan 2011

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Author's Accepted Manuscript

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PII: S0022-5193(09)00436-6
DOI: doi:10.1016/j.jtbi.2009.09.016
Reference: YJTBI5707



www.elsevier.com/locate/jtbi

To appear in: *Journal of Theoretical Biology*

Received date: 6 February 2009
Revised date: 4 August 2009
Accepted date: 10 September 2009

Cite this article as: Robert M. French, The red tooth hypothesis: A computational model of predator-prey relations, protean escape behavior and sexual reproduction, *Journal of Theoretical Biology*, doi:[10.1016/j.jtbi.2009.09.016](https://doi.org/10.1016/j.jtbi.2009.09.016)

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

3

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

6

7 **Introduction**

8

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

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

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

13 **The Red Queen Hypothesis**

14
15 Van Valen's (1973) observation that taxonomic survivorship curves (for taxa at or above
16 the level of genera) tended to be log-linear led to a set of new ideas as to why sex and
17 genetic recombination offset the cost of meiosis. He suggested that the observed log-
18 linear species extinction curves were due to co-evolutionary forces among species that
19 were best described as a zero-sum "arms race", the end result of which was no absolute
20 improvement in the average fitness of individuals within a species with respect to the
21 individuals in a competing species. Even though the plausibility of this zero-sum arms
22 race was debated in the literature for a time (e.g., Maynard Smith, 1978; Stenseth &
23 Maynard Smith, 1984), Van Valen's work set the stage for an explicit statement of the

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

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

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

9

10 **The Red Tooth Hypothesis**

11

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

20

21 **Assumptions of RTH**

22

23 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.

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

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

18

19 **Justification of RTH assumptions**

20

21 We will discuss each of the assumptions of RTH in turn and then will present a computer
22 simulation that illustrates these principles and, at the same time, makes a certain number
23 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

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

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

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

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

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

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

20 It would, therefore, be advantageous for prey to be able to have "unpredictable
21 elements" in their escape response to prevent predators from gaining this advantage. This
22 behavioral unpredictability has been called "protean behavior" (Chance & Russell, 1959;
23 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

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

11

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

13

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

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

10 **Red Tooth Hypothesis Simulations**

11
12 In what follows, we will present a set of simple predator-prey simulations in which
13 predators are modeled by neural networks designed to learn sequences. Over time these
14 predator networks learn short segments of the prey escape-sequences by successive
15 encounters with the prey. Each instance of pursuit constitutes a learning trial for the
16 predator. In contrast, a prey's failure to escape a predator is (obviously) not a learning
17 experience for the prey. Escape patterns of prey therefore evolve, not during the lifetime
18 of the animal, but over evolutionary time. Each individual in the prey population is
19 modeled as a sequence of "elementary escape-movement (EEM) genes" that determine
20 how it will escape from a predator.

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

23

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

1 predator had an equal number of learning cycles per generation, thereby allowing the
2 same amount of predator learning across generations. The simulation was stopped after
3 30 generations or earlier, if all of the prey in the population were caught by the predator.

4

5 **Prey**

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

22 In a real environment, of course, escape trajectories are produced by an interaction
23 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.

14 15 **Predators**

16
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

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

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

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

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

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

7

8 <Figure 1 here >

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

11

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

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

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

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

10

11 **Predator and prey position calculations**

12

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

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

3

4 **Evolution of survival rates for sexually versus asexually reproducing populations**

5

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

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

16

17

<Insert Figure 2 here>

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

20

21 A key result of our simulations is illustrated in Figure 2. We have a low mutation rate of
22 $\mu=0.0001$ and a prey-predator speed ratio of 1:1.4. Under these conditions, the median
23 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.

4

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

6

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.

23

1 <Figure 3a here>

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

3
4 <Figure 3b here>

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

6
7 <Figure 3c here>

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

9
10 In short, for environments of low predation pressure, asexual reproduction is as
11 effective as sexual reproduction in producing effective polymorphic escape-behavior.
12 However, under heavy predation pressure, sexual reproduction becomes much more
13 important. This corresponds to what is commonly observed in certain heterogamous
14 animals. For example, the freshwater crustacean *Daphnia* generally reproduces
15 parthenogenically, then switches to sexual reproduction as competition and predation
16 increase. Williams (1975) and Bell (1982) document numerous cases of this shift to
17 sexual reproduction when the environmental conditions, such as climate, increased
18 predation, etc., become harsher.

19
20 **Prey-predator first encounters**

21
22 Our simulations (Figure 4) also show that when a founder population of prey animals first
23 encounters a new predator, initially, the predators will kill a significant number of them,
24 frequently leading to the extinction of the prey. However, if extinction does not occur in

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

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

15

16

<Figure 4 here>

17 Figure 4. Prey are initially vulnerable to attack by predators learning their escape-

18 behaviors. Evolutionary forces gradually reduce the effectiveness of these attacks.

19

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

21

22 Figure 5 compares how easy or difficult it is for a predator to follow its prey. We assume

23 that the prey will jink 20 times in its escape-sequence. The predator pursues all 100 of

1 prey in each generation once, which gives a total of 3000 encounters with prey. This
2 means that the neural network that models the predator has 3000 learning cycles to
3 predict where the prey will be after each jink. Accurately predicting where the prey will
4 be means that the predator can take shortcuts during pursuit of the prey. The graph
5 compares the evolution of the number of direction changes that the predator needs to
6 make when pursuing asexually reproducing prey compared to sexually reproducing prey.
7 After 3000 learning cycles, the predator requires only 10 changes of direction to
8 successfully track its prey, whereas for a sexually evolving prey population, where
9 population-level protean escape-behavior is established, very little anticipatory prediction
10 (i.e., learning of escape patterns) is possible and the predator requires an average of 17 to
11 18 changes of direction to pursue its prey.

12

13

<Figure 5 here>

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

18

19 **Protean escape-patterns versus good escape patterns**

20

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

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

13 **Variability of escape patterns in sexual and asexual populations**

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

18

19 <Figure 6a here>

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

22

23 <Figure 6b here>

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

3
 4 **A quantitative measure of population-level escape-trajectory variability**

5
 6 It seems clear from a visual examination of Figures 6a and 6b that after 30
 7 generations sexually evolving populations have more highly varied escape trajectories
 8 than asexually evolving populations. But it would be very useful to have a measure of
 9 this variability. In particular, this would allow us to trace the evolution of variability of
 10 escape trajectories within a population over time. If RTH is correct, this evolution of
 11 variability should correlate closely with the evolution of prey survival rates.

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

15

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

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

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

8

9

< Insert Figure 7 here.>

10

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

13

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

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

8 **Discussion**

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

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

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

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

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

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

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

13 Although we have not modeled this here, it is clear that simulations of this sort
14 could, and should, be extended to include the co-evolution of multiple generations of
15 predators. The quasi-impossibility of learning the escape behavior of its prey because of
16 its population-level protean nature would presumably stymie the effects of Baldwin-like
17 learning (Baldwin, 1896; Morgan, 1896; Hinton & Nowlan, 1987; French & Messinger,
18 1994) on the predator genome. In other words, the impossibility of learning during
19 hunting would have meant that hunting would not have driven improved learning
20 capacities in predators over evolutionary time. This might help explain why "...true co-
21 evolution ... seems remarkably rare in predator-prey systems." (Endler, 1991) Once a
22 sufficient degree of randomness in escape behavior was achieved (either at the individual
23 or at the population level), the predator would no longer be able to learn prey escape

1 patterns from prior encounters with that prey.

2 Empirical tests using heterogamous animals, similar to those designed to explore
3 RQH (e.g., Lively, 1987), could be run for RTH as well. RTH would, for example,
4 predict that heterogamous animals in asexual reproductive mode would tend to switch to
5 sexual reproduction when the predator pressure in their environment increased,
6 something which is known to be the case for the freshwater crustacean *Daphnia* (Bell,
7 1982). This water flea reproduces by parthenogenesis then switches to sexual
8 reproduction as competition and predation increase.

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

21

22 **Conclusion**

23

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

6

7

8 **Acknowledgments**

9

10 This work was supported in part by grants FP6-NEST-029088 and FP6-NEST-516542
11 from the European Commission. Thanks to Gray Clossman, Darren Croft, John Endler,
12 Stephen Lea, Joah Madden, Michael Thomas, and Mark Weaver for their contributions to
13 the ideas and emphasis of this paper. Particular thanks to three anonymous reviewers and
14 the editor for their careful reading of this paper and their insightful comments on how to
15 improve it. The author would also like to thank the Firestone Library at Princeton
16 University for permission to use their collections.

17

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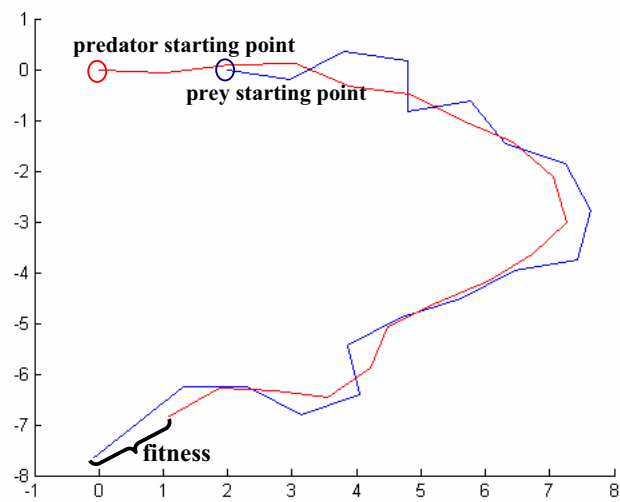


Figure 1

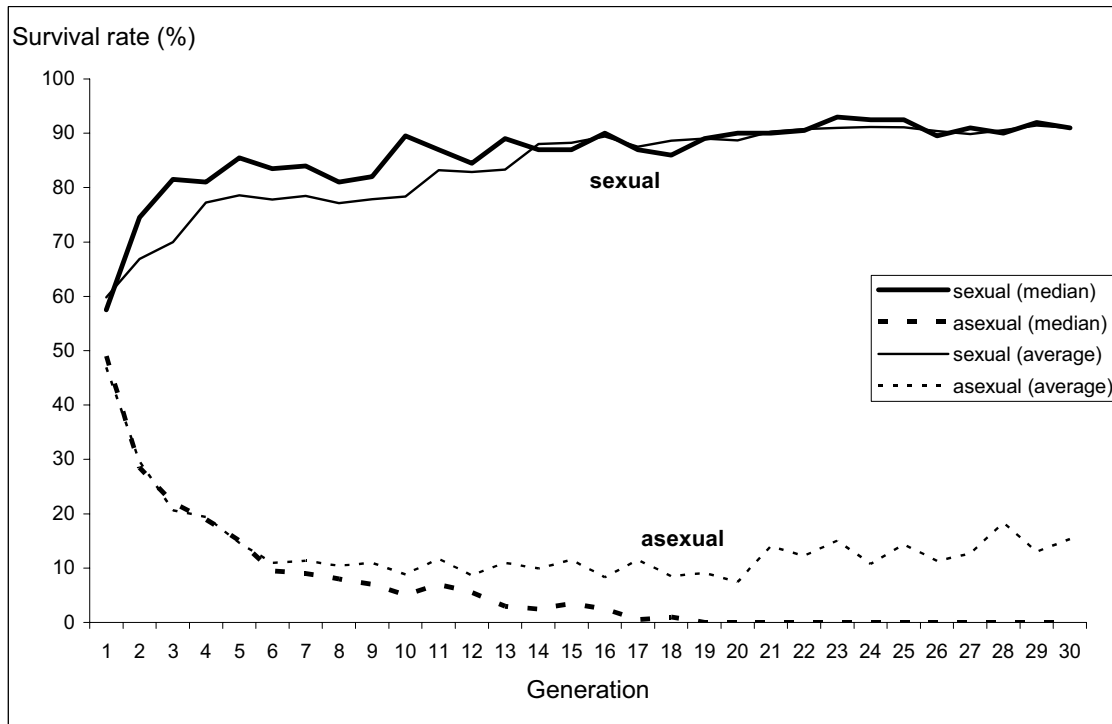
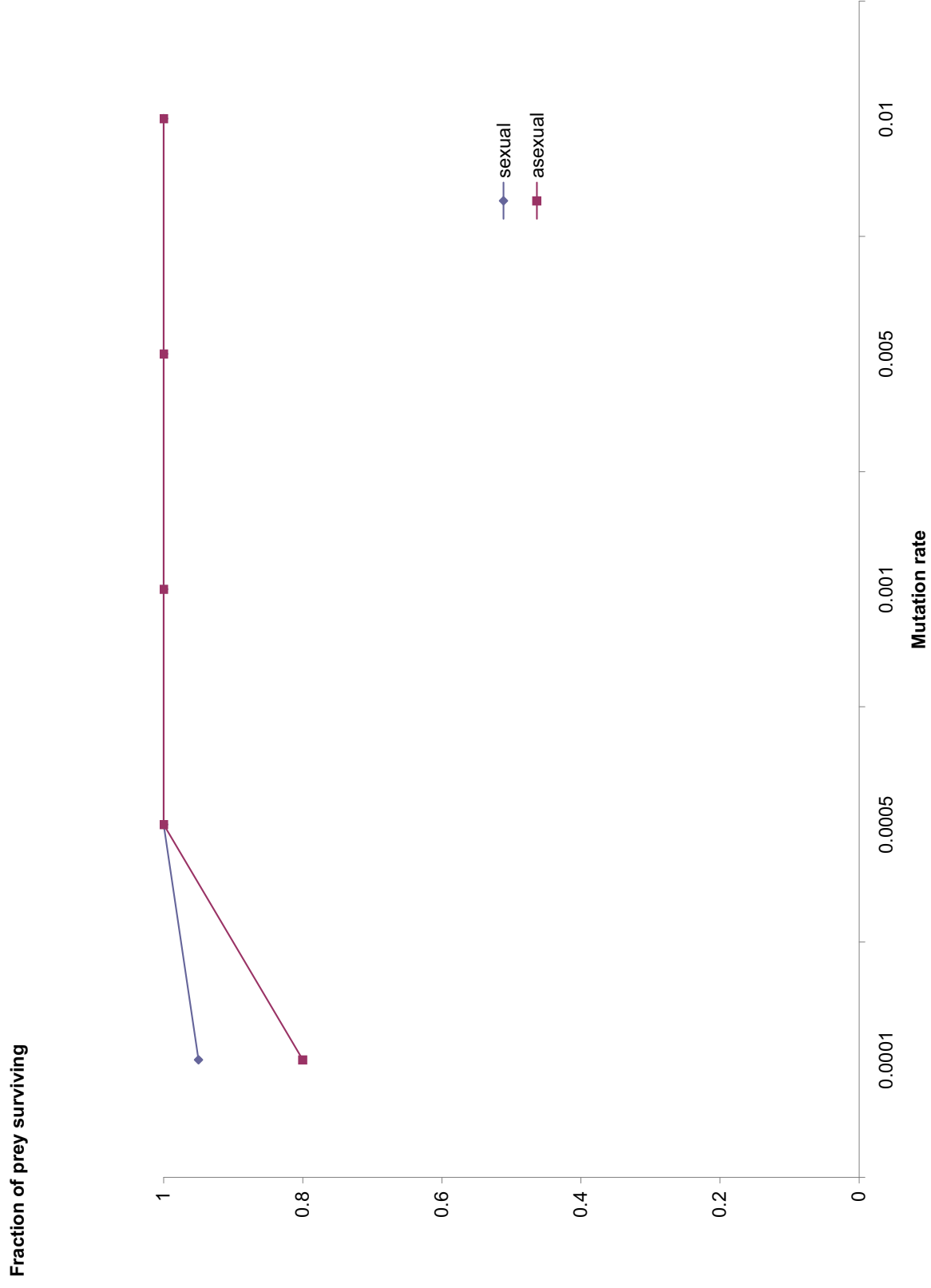
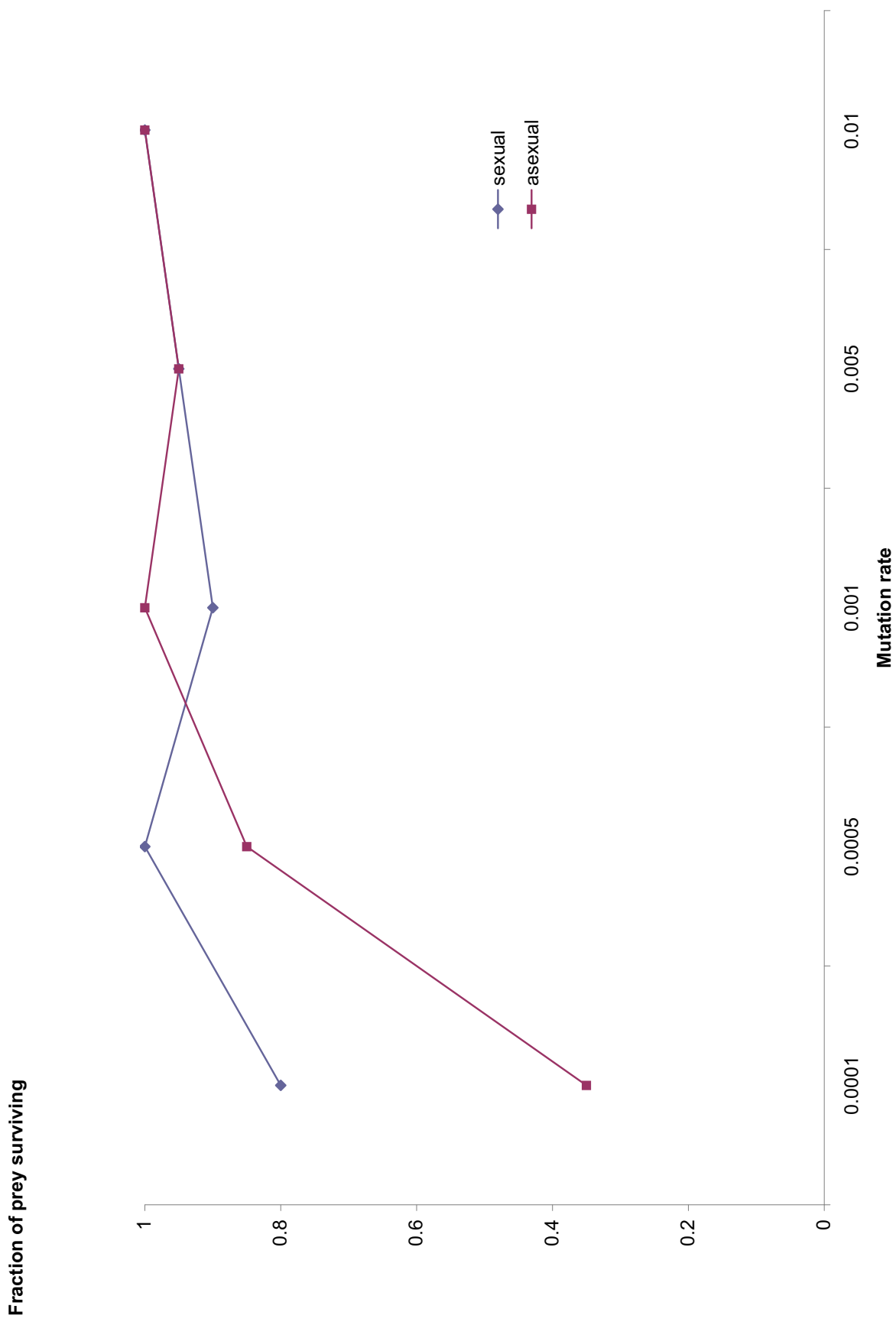


Figure 2.



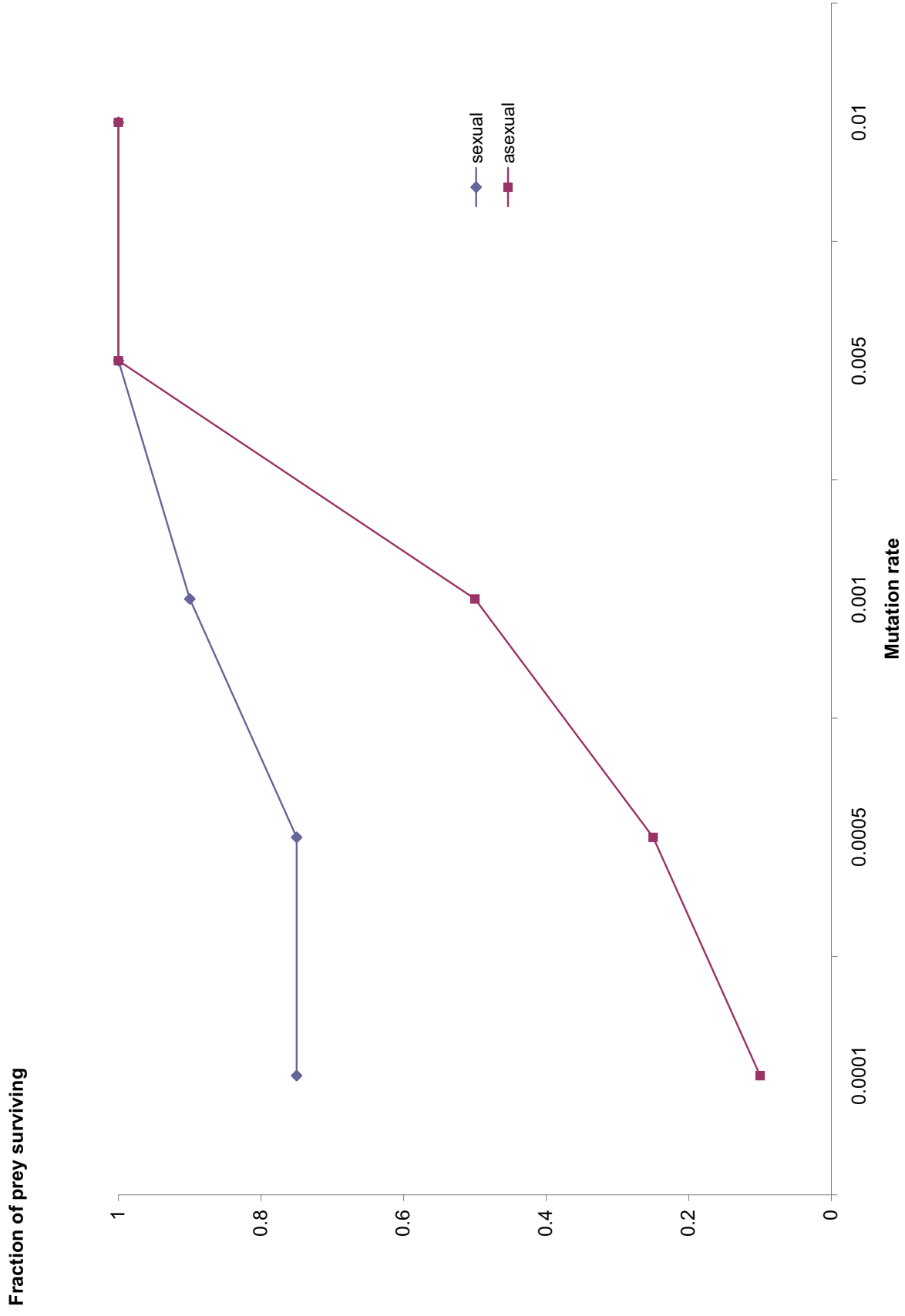
4. Figure

Figure 3a



4. Figure

Figure 3b



4. Figure

Figure 3c

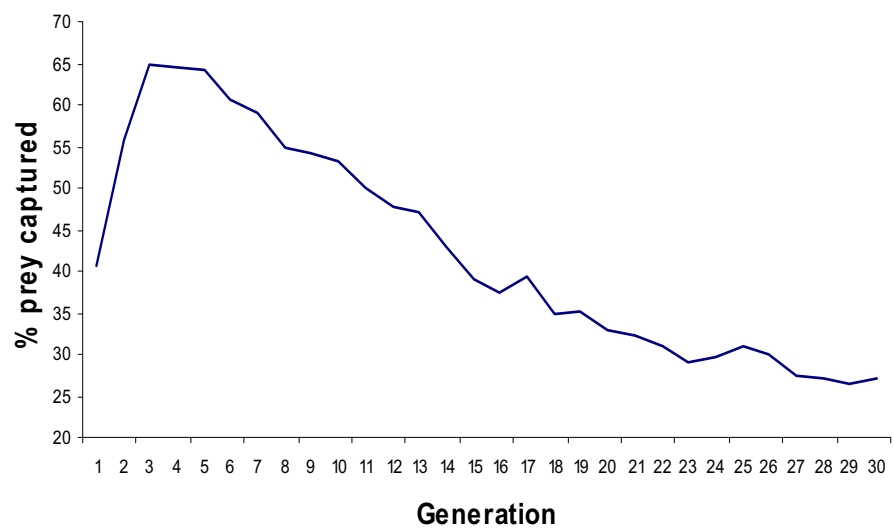


Figure 4

Accepted manuscript

No. of predator
direction changes

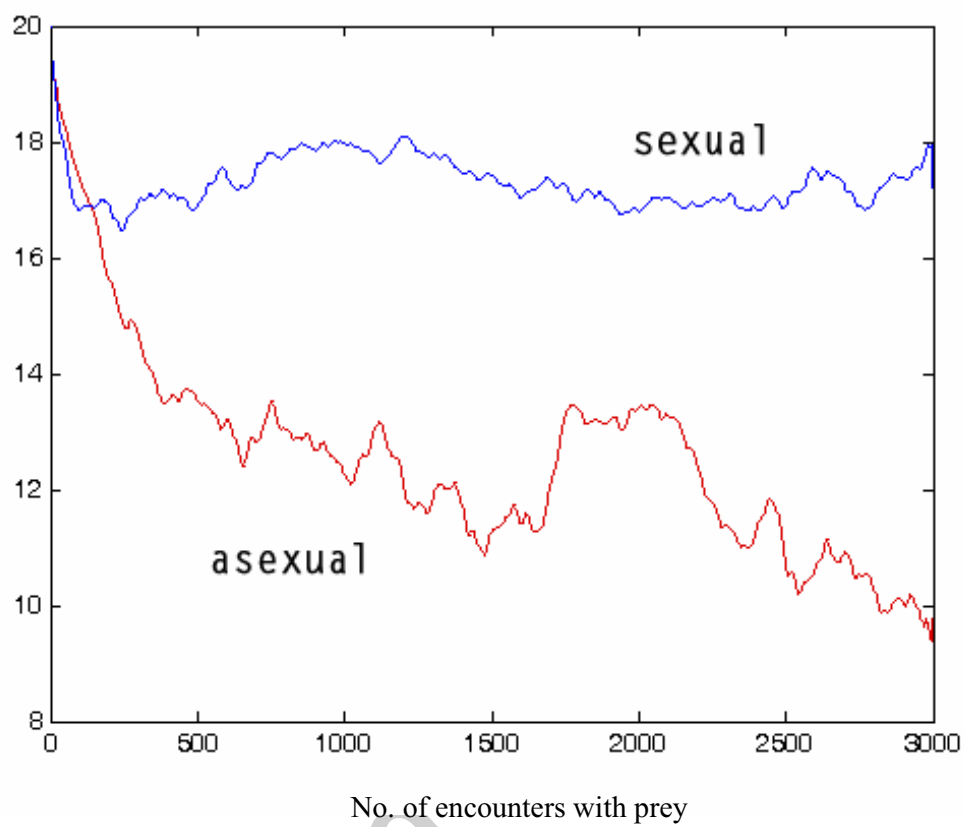


Figure 5

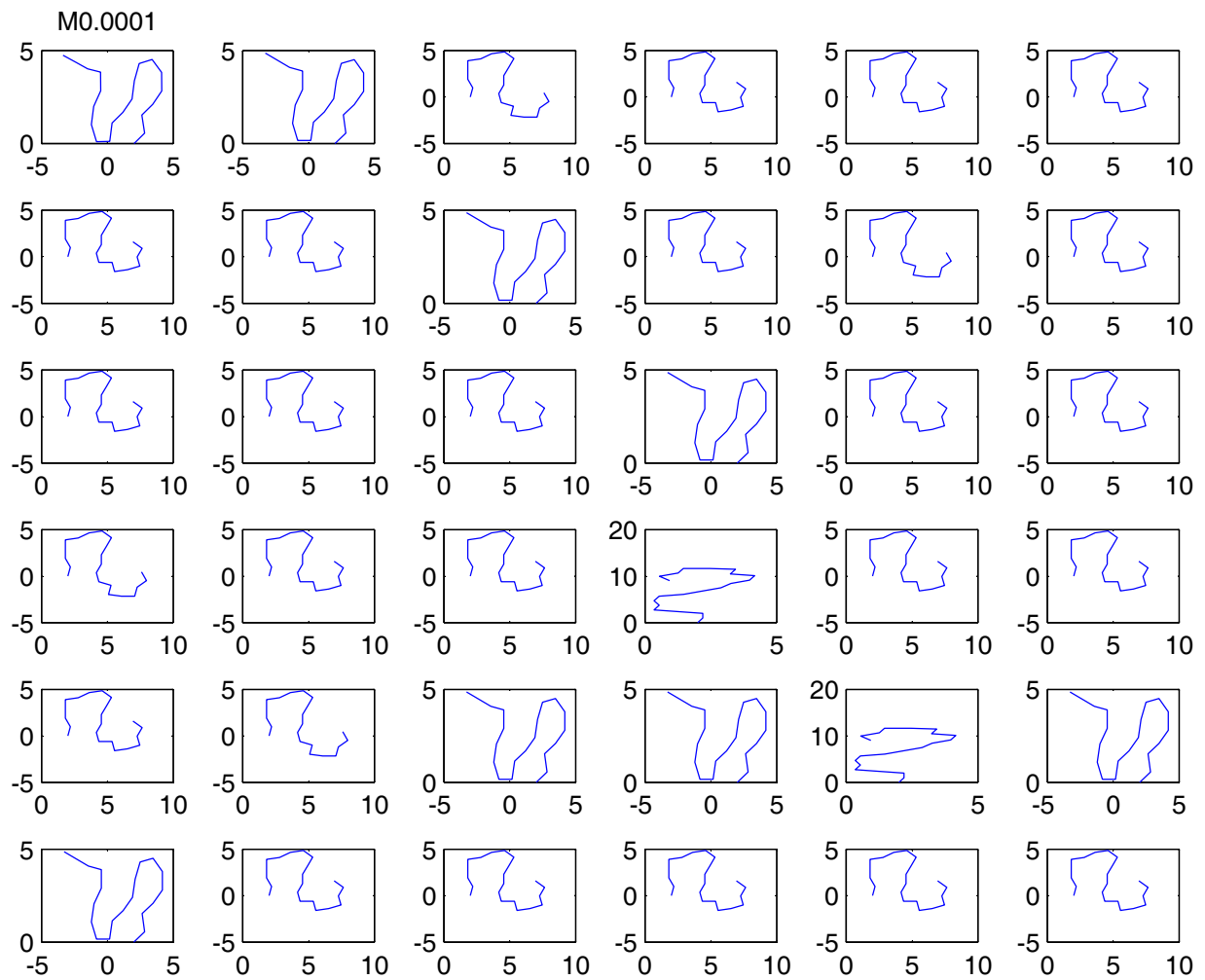


Figure 6a

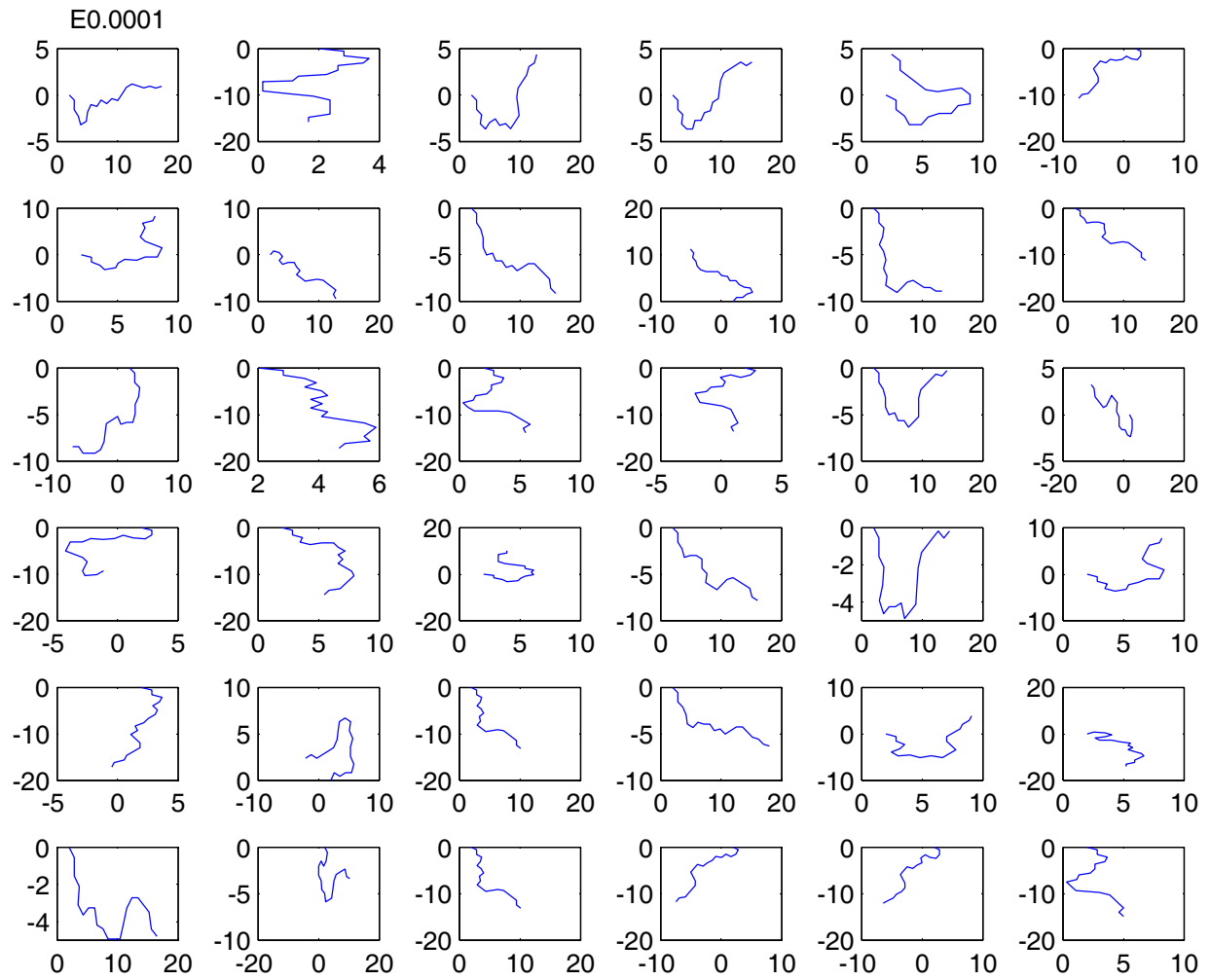
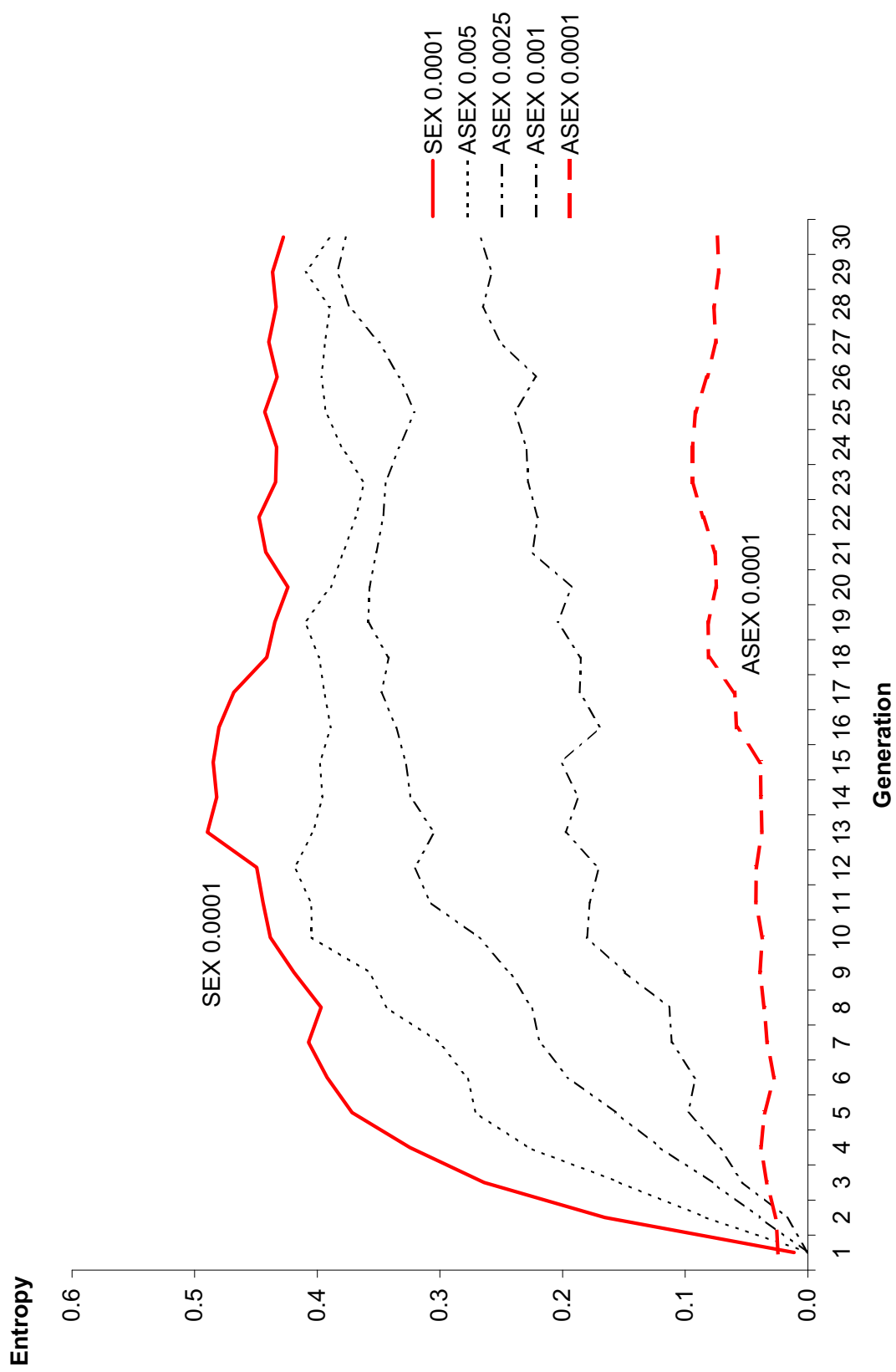


Figure 6b



4. Figure

Figure 7