

# COMPLEX EVOLUTIONARY SYSTEMS AND THE RED QUEEN\*

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## ABSTRACT

Some of the most obvious complex adaptive systems are biological. A key concern in biology is how the overall properties of systems relate to the behavior of their components. Competition between these components in the form of an arms race, the “Red Queen effect”, for example, helps explain the trend towards more complex organisms, perhaps the most dramatic of macroevolutionary trends. The Red Queen effect is then basic to understanding complex biological systems since it helps explain why these became complex and remain that way. An arms race between parasites and a host species may indeed explain why there is sex. Further, a Red Queen effect within our species may well have driven the most distinctive and economically relevant of human biological characteristics—high intelligence. Analogously, competition in the form of the Red Queen effect is a promising avenue of research within economics.

## 1 Introduction and Summary

A revolution in thinking about economic systems began with the publication of Adam Smith’s *The Wealth of Nations*. Smith argued that economies had social efficiency properties that were perhaps unexpected and certainly unintended consequences of the selfish actions of individual participants. (Mandeville in *The Fable of the Bees* had previously argued that public virtues might be the outcome of private vices.) The two modern “Fundamental Theorems of Welfare” capture these efficiency properties in a static sense—in an economy with fixed technology and preferences.

Charles Darwin was strongly influenced by Adam Smith. “The Invisible Hand” inspired Darwin to argue that competition, in the blind sense of natural selection, was the force leading to even complex adaptations like the human eye, thus eliminating the need for divine intervention (Gould, 1993, Ch. 9). There have been reverse borrowings from biology. Recently, for example, economic theory has used evolutionary games as a model of low rationality strategic interactions between individuals (Mailath, 1998). There is an opportunity for more such borrowings.

Section 2 first discusses how competition between species, in a general sense, might have driven the trend towards larger and more complex organisms, the most remarkable of all macroevolutionary phenomena. The economic counterpart of this is Schumpeterian interaction between firms seeking a temporary monopoly edge from innovation, thereby stimulating technological progress and long-run growth. Such dynamic forms of competition are more complex and less perfect than the static forms embodied in the two welfare theorems, but they are bound also to be more important.

The particular phenomenon of interest here is the “Red Queen effect”—an arms race. Section 3 of the present paper first considers the theory of coevolution and the original biological formulation of this effect: A typical species faces an environment that becomes less attractive over time due to the continuing evolution of a number of competing species. Despite its own evolution, the first species may then experience a constant level of adaptation and a constant probability of extinction. The Red Queen from *Through the Looking Glass* gave her name to this effect, since she told Alice, for example:

“Now, *here*, you see, it takes all the running *you* can do to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that!”

It is important that competitive coevolutionary effects, in general, and the Red Queen effect, in particular, have been observed in artificial simulated environments. These phenomena are then best understood as a general property of complex adaptive systems, whether biological or economic. (Markose surveys the relevant literature for Section 3 in her introduction to this Special Issue.)

A specific biological example of the Red Queen effect is the simultaneous exaggeration over time of the ability to run fast in both a predator and a prey species. That is, each species finds it advantageous to evolve to run faster, for a given speed of its opponent. This can be reformulated as an economic example of the interaction between an innovative firm and an imitator. In either case, such arms races appear likely to involve wasteful extravagance. Example A, however, shows how this Red Queen effect might provide a suitable random impetus for a target species or firm to avoid a low-level trap.

Section 4 shows how the Red Queen also helps answer the question: Why is there sex? The mystery about sex in biology results from the modern distinction between the interest of the gene, the individual and the population, combined with a reluctance to use explanations that rely on the last of these. That is, although there seems to be a large individual disadvantage to sex, the advantages seem to accrue mainly to the species. It is difficult then to explain why sexual reproduction would not be displaced by females reproducing on their

own. Perhaps the most popular current explanation of sex argues that, since parasites have short life-spans and so can rapidly adapt to the host, this creates an incentive for the host organisms to keep reshuffling the genetic elements that create resistance, then generating an arms race.

Section 5 considers theories of how the Red Queen effect might have driven the evolution of human intelligence or rationality—an attribute with obvious substantial economic relevance. There are two main categories of explanations for intelligence—the ecological intelligence hypothesis and the social intelligence hypothesis. The former is that the demands of the ecology—the physical and biological environment—drove intelligence up. Even in this case, the Red Queen effect may have been important. That is, humans had an interest in higher intelligence to be more effective hunters; prey species had an interest in higher intelligence to be more effective at eluding such predation by humans and other species. The social intelligence hypothesis, moreover, is essentially identical to the Red Queen effect. In strategic interactions between two human beings, that is, it is not directly advantageous to be smart in absolute terms; rather it pays to be smarter than the opponent. Example B describes a game of incomplete information where this effect arises. One of the players knows the game. This player has an incentive to play so as to conceal some of her knowledge from the other players. In the equilibrium, each of these opponents can derive an advantage from greater recall, no matter how great the common level of recall might have been to start with, thus capturing the Red Queen effect.

Game theory has often concluded that there would be no such arms race. These ar-

guments do not rely on the cost of greater rationality, but would only be reinforced by introducing this factor. That is, there are a number of models in which the advantage nevertheless lies with a less intelligent individual. Since this seems to fly in the face of reality, it is natural to ask: Which of the usual game theoretic assumptions is responsible? In some cases, a suspicious assumption is that, in the same spirit that individuals know an opponent's preferences, they know an opponent's intelligence. This assumption is less compelling when intelligence is subject to evolutionary "choice" and there may be a risk of confusing stubbornness with a lack of intelligence. Finally, it is noted that the Red Queen effect may be inevitable, even when agents are "Turing machines", as rational then as the abstract theory of computation allows.

The persuasive nature of the Red Queen effect is demonstrated by these biological applications. Section 6 concludes by sketching the small amount of research that has applied the Red Queen within traditional economics, that nevertheless demonstrates the promise of this approach.

## **2 The Evolution of Complexity**

A salient feature of the natural world is that some organisms have evolved to be highly complex. Gould (1996, Ch. 13) took a rather agnostic view of such complexity. He invoked the metaphor of a drunk who staggers left or right at random, but is constrained at the left by a wall. That is, if organisms become more or less complex at random, but cannot have negative complexity, there are bound to be highly complex organisms in the long-run.

Although there may be merit to this agnostic view, it ignores the costs and benefits of complexity. First, given two types within a species having the same abilities, the more complex type would be selected against if there were any cost of complexity. Indeed, arbitrary complexity seems likely to fatally restrict the abilities of the type. Presumably for these reasons, the complexity that actual species have evolved is highly specific and directed.

The most obvious kind of biological complexity correlates with physical size. Bonner (1988, Fig. 5, p. 27) presents data on the maximum size of organisms at various ages in the earth's history. Life began 3 or 4 billion years ago with bacteria that were only several thousandths of a millimeter long and culminates in the present with giant sequoias. At the same time, complexity, as measured by the number of different cell types, has increased from 1 in the case of simple bacteria to more than 120 in the case of modern vertebrates (Bonner, 1988, Table 1, p. 122). A key issue here is how various key biological processes scale. For example, since they have a relatively high ratio of surface area to volume, insects can take in enough oxygen by direct transpiration through the cuticle. Larger animals such as humans have needed to evolve specialized internal lungs that expose a relatively larger area of spongy membrane to the air. Thus, in order for an animal to successfully evolve to be bigger, it must first, or simultaneously, evolve more complex organs for breathing.

Bonner proposes that the evolution of complexity was driven by competition, a thesis that is related to but more general than the Red Queen. At first, that is, simple species of animals would become more and more finely adapted to their environment, and grow in number to saturate the corresponding niche. Evolution might then favor a more complex "pioneering"

mutant that would then be the first to exploit a new niche. (See, in particular, Bonner, 1988, pp. 58-59.) Thus this force of competition may have been responsible for the most salient feature of evolutionary history—the evolution of more complex organisms.

### **3 The Coevolutionary Arms Race**

Not merely are species exquisitely well-adapted to their physical environment, they are often finely honed to the characteristics of the other species with which they interact. Not merely, then, do individuals evolve to be complex, but so does the ecological system to which they belong. Ehrlich and Raven (1964) discussed in exhaustive detail how each of a large number of groups of species, or “taxa,” of butterflies feeds on a restricted range of plants, where each such range may include species that are not closely related. However, each range may share a particular natural insecticide, that helps defend the plant from herbivorous insects. Butterflies, for their part, may evolve resistance to such chemicals in the form of biochemical detoxification mechanisms. Once a species of butterfly evolves a new detoxifying mechanism, it can feed on all the plants with the associated insecticide. Natural selection would, in turn, act on plants to produce new or better insecticides. Ehrlich and Raven used the term “coevolution” to describe an arms race in which evolution on each side of such an interaction drives adaptation on the other.

Van Valen (1973) demonstrated that the extinction rates for a wide variety of taxa are remarkably constant over time, although they may vary across such taxa. That is, it seems that species within a given “taxon” with a longer evolutionary history are not



better-adapted to their environments; neither, for that matter, are they less well-adapted. Evolution does not then have a progressive quality. How could this be? The answer that Van Valen proposed was: Older species are not better adapted to their environment because this environment is importantly determined by other species in the taxon, which are also evolving. Despite evolution of the original species, that is, these other species present it with a moving target. With resource limitations, Van Valen suggested that the net effect would be that the net adaptation of each species would remain roughly constant, thus generating roughly constant extinction rates. This phenomenon he named the “Red Queen effect” after the Red Queen in *Through the Looking Glass*.

The theoretical basis of Van Valen’s hypothesis have been challenged. Stenseth and Maynard Smith (1984), for example, question whether resource limitations would play the right role. They investigate a simple general model of an arbitrary number of interacting species. There are various modes of limiting behavior of the dynamical system, but one of them can be identified as a Red Queen regime, with constant rates of evolution, extinction and speciation. Overall, despite such reexaminations, the Red Queen effect has stood the test of time, finding a place in a leading textbook such Ridley (1996, Ch. 22).

Dawkins and Krebs (1979) consider various formulations of the Red Queen that involve one or two species. They argue that important arms races between two unrelated species are likely to be asymmetric. In the first place, the fox wishes to catch the rabbit, but the rabbit wishes to escape. Furthermore, the outcome of a particular fox-rabbit chase is obviously more significant to the rabbit than to the fox—this is the “life-dinner” principle.

If two species instead had a symmetric interest in being dissimilar, this would usually mean they would evolve to be far apart in the relevant characteristics.

Although Van Valen’s formulation of the Red Queen effect suggests it is somehow wasteful, this is not inevitable. The spur of close attention by a predatory species is a random stimulus for a target species. Such evolutionary noise might permit the target species to escape a local maximum, a low level trap, that is, in favor of a preferred global maximum. This is shown by Example A below.

This captures a stylized predator-prey interaction—a plant thriving with an insecticide that is not matched by the detoxification mechanism of the butterfly; a butterfly thriving with a match. In addition, some insecticides may have metabolic cost advantages for the plant. An economic counterpart of this concerns the interaction of an innovative firm and an imitator. Other things equal, the innovator wishes the imitator not to match the technological specification of its product; the imitator wishes to match. Again, some technological specifications have inherent cost or demand advantages.

### **3.1 Example A**

There are two interacting species (or firms). The focus is on the first of these, the “target” species, and on the genotype (or technology) it attains. Abstracting from the second predatory species for the moment, the fitness (or profit) of the target species has two peaks on a scale representing genotype. One of these peaks, a local maximum, occurs at the extreme  $n = 0$ ; the other, the global maximum, at the opposite extreme  $n = N + M + 1$ . Fitness

is decreasing over the range  $n = 0, \dots, N$ ; it is equal at  $n = N$  and at  $n = N + 1$ ; it is then increasing over the range  $n = N + 1, \dots, N + M + 1$ . It is assumed that the slopes of the fitness function leading to the two maxima are the same, so that  $M > N$ , in particular. See Figure 1.

In the absence of the predator, the target species evolves in a deterministic and locally adaptive fashion, so that, for  $t = 1, 2, \dots$ ,  $n_{t+1} = n_t - 1$ , if  $n_t = 1, \dots, N$ ; but  $n_{t+1} = n_t + 1$ , if  $n_t = N + 1, \dots, N + M$ ; and  $n_{t+1} = n_t$ , if  $n_t = 0$  or  $N + M + 1$ . In particular, then, if the species starts in the range  $n = 0, \dots, N$ , it will converge to the local maximum  $n = 0$  and remain there permanently. That is, there is a “low-level trap” at  $n = 0$ . As for the predatory species, its fitness is maximized by choosing a genotype that matches that of the target species. Adopting the simplest possibility, the predatory species chooses  $m_t = n_t$ , where this choice is made at times  $t + 1/2$ , for  $t = 0, 1, 2, \dots$ .

Suppose now the target species has an incentive to move away from the predator. In addition, the underlying fitness continues to matter. Altogether, then, to reflect both effects, suppose that, for  $t = 1, 2, \dots$ , if  $n_t = 1, \dots, N$ , then  $n_{t+1} = n_t - 1$ , with probability  $r \in (1/2, 1)$ , and  $n_{t+1} = n_t + 1$ , with probability  $1 - r$ . If  $n_t = 0$ , then  $n_{t+1} = 0$ , with probability  $r$ , and  $n_{t+1} = 1$ , with probability  $1 - r$ . Similarly, if  $n_t = N + 1, \dots, N + M$ , then  $n_{t+1} = n_t + 1$ , with probability  $r$ , and  $n_{t+1} = n_t - 1$ , with probability  $1 - r$ . If  $n_t = N + M + 1$ , then  $n_{t+1} = N + M + 1$ , with probability  $r$ , and  $n_{t+1} = N + M$ , with probability  $1 - r$ .

This defines a simple Markov chain, which is “regular”, in that it is possible, after at most  $N + M + 1$  periods, to reach any state starting from any other state. Suppose

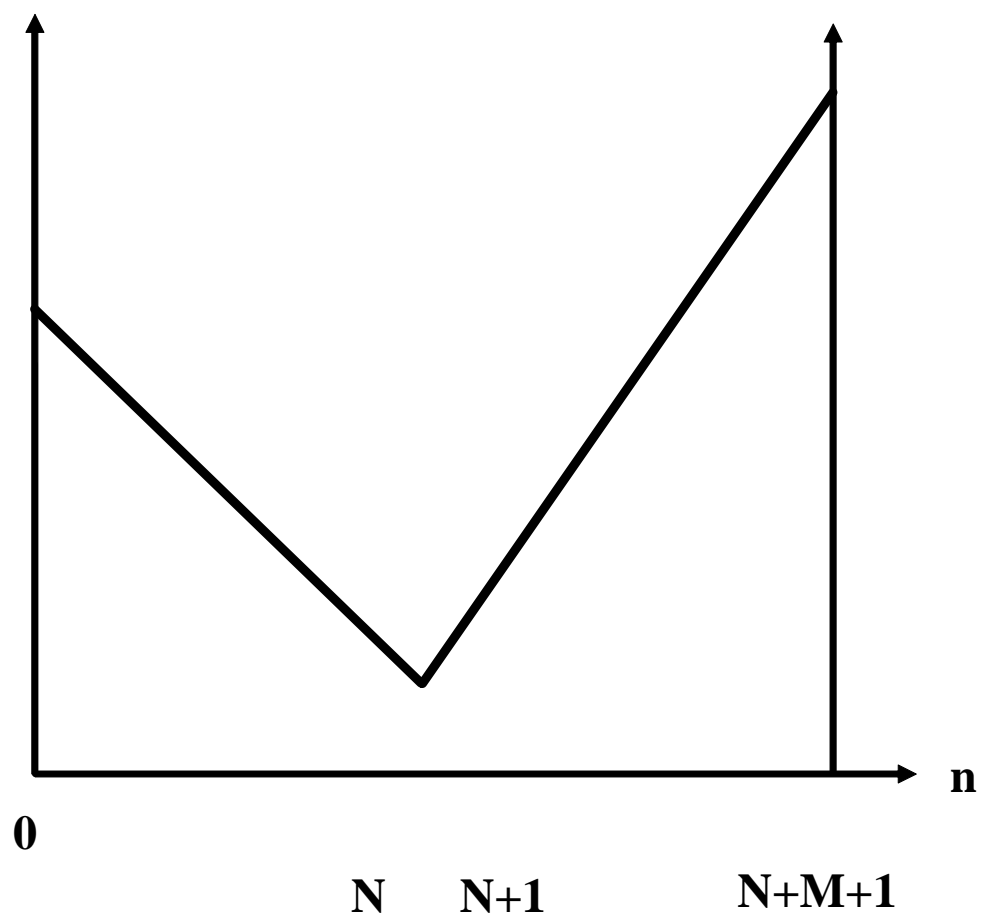


Figure 1: Example A

the stationary probabilities of the chain are given by  $p_n$ , for  $n = 0, \dots, M + N + 1$ . The Appendix shows that these have the following form:  $p_n = \left(\frac{1-r}{r}\right)^n p_0$ ,  $n = 0, \dots, N$ ; whereas  $p_n = \left(\frac{1-r}{r}\right)^{M+N+1-n} p_{M+N+1}$ ,  $n = N+1, \dots, N+M+1$ . It also follows that  $p_N = p_{N+1}$ , so that  $p_{M+N+1} = \left(\frac{1-r}{r}\right)^{-(M-N)} p_0$ . Finally,  $p_0$  is determined by the condition that  $\sum_{n=0}^{N+M+1} p_n = 1$ .

The stationary probabilities of the chain become more and more concentrated near the global maximum, as the number of underlying discrete states increases. Suppose this limit of the discrete model keeps the height of the fitness peaks constant, as well as the position of the underlying fitness minimum, and the one-step transition probabilities. Suppose then that  $M, N \rightarrow \infty$ , but that  $N/(M + N + 1) \rightarrow k \in (0, 1/2)$  also. Since  $\frac{\Pr\{n=0, \dots, N\}}{\Pr\{n=N+1, \dots, N+M+1\}} = \frac{p_0 \left[1 - \left(\frac{1-r}{r}\right)^{N+1}\right]}{p_{M+N+1} \left[1 - \left(\frac{1-r}{r}\right)^{M+1}\right]} = \frac{\left(\frac{1-r}{r}\right)^{M-N} \left[1 - \left(\frac{1-r}{r}\right)^{N+1}\right]}{\left[1 - \left(\frac{1-r}{r}\right)^{M+1}\right]}$ , it follows that  $\Pr\{n = 0, \dots, N\} \rightarrow 0$  and that  $\Pr\{n = N + 1, \dots, N + M + 1\} \rightarrow 1$ , in this limit. That is, the probability of being anywhere on the “hill” with lower peak fitness tends to zero. Further, consider any neighborhood of the global peak of the form  $(\tilde{M}, \dots, M + N + 1)$ , where  $\tilde{M}/(M + N + 1) \rightarrow \tilde{k} \in (k, 1)$ , as  $M, N \rightarrow \infty$ . It then also follows that

$$\frac{\Pr\{n = N + 1, \dots, \tilde{M} - 1\}}{\Pr\{n = N + 1, \dots, N + M + 1\}} = \frac{\left(\frac{1-r}{r}\right)^{M+N+2-\tilde{M}} \left[1 - \left(\frac{1-r}{r}\right)^{\tilde{M}-N-1}\right]}{\left[1 - \left(\frac{1-r}{r}\right)^{M+1}\right]} \rightarrow 0,$$

so that all the probability becomes concentrated near the global maximum of fitness, as claimed. Thus the expected fitness (or profit) of the target species (or firm) must also converge to the maximum possible level in this limit.

## 4 Parasites and Sex

The Red Queen helps answer the question: Why is sex so prevalent? Why is there all the biochemical and behavioral complexity implied by sex? On the one hand, the advantages to the species of sex are reasonably clear. Namely: Sex provides genetic versatility, enlarging the slate of candidates for natural selection. As Medawar and Medawar (1983, p. 238) put it—“Compared with the rival attractions of parthenogenesis and asexual reproduction, sex is clearly a Good Thing—but that, of course, is not explanation enough of its having evolved.” The sticking point is: Why do these overall advantages accrue to individuals?

Maynard Smith (1978) describes the problem as the “two-fold cost of sex.” The issue here, to be more precise, is not the origin of sex, but why its function of “outcrossing”, or genetic mixing, is maintained in the face of asexual alternatives. Suppose then that a mutation occurs in a sexual species. This mutation produces “parthenogenetic” females that reproduce without the need for males. Suppose the number of eggs produced by either kind of female is  $k$  and similarly that the probability of survival to reproductive age,  $S$ , is independent of sex or parthenogenesis. If there are  $N$  adult parthenogenetic females in a given generation, there will be  $SkN$  adult females in the next, yielding a growth rate of  $Sk$ . On the other hand, suppose there are  $n$  males and  $n$  females in one generation of the sexually reproducing type. There will then be  $kn$  fertilized eggs, of which  $(1/2)kn$  will be male and  $(1/2)kn$  will be female. In the next generation, there will then be  $(1/2)Skn$  adult males and  $(1/2)Skn$  adult females. It follows that the growth rate is now only  $(1/2)Sk$ ; thus the two-fold cost of sex. Alternatively put, the disadvantage of sex to an individual female is

a dilution by  $1/2$  of her genetic representation in the next generation. The challenge is to identify an advantage to the individual female that would outweigh such an enormous cost.

This issue only came to forefront recently, along with a renewed insistence that explanations of biological phenomena relying upon “group selection” were to be avoided if at all possible. The insistence that acceptable explanations be on the level of the individual, or better yet, of the gene, also implied that more attention had to be paid to how the various levels—of the group, the individual, and the gene—would interact.

One of the most promising responses to the challenge posed by the “two-fold cost of sex” is that associated with the work of Hamilton, in particular. (See Hamilton, 2001, or, for a popular account, Ridley, 1993, Ch. 3.) This response considers how sexual reproduction serves a host species locked in an arms race with parasites. Parasites have the advantage of short generational times. Within the lifetime of a individual human, a parasite may have several times the generations that humans had in two million years. Thus parasites can adapt to find the chink in the armor of the current population. From the point of view of a host individual, the worst choice of all might be to keep her offspring with the same immune function genes that she currently has. The key element of sexual reproduction is that it permits the retention of genes that might have once seemed disadvantageous, but are now attractive. Thus one would expect parasites and the host species to coevolve, exhibiting the Red Queen effect, with sexual reproduction enabling the host to get temporarily a step ahead, but then the evolution of the parasite enabling it to close the gap. There need be no true innovation here, with old genes in the host and parasite recurring as the system traces

out a possibly complex trajectory, but one that is nevertheless confined to a bounded region.

## 5 The Evolution of Intelligence

Why are human beings so smart? High intelligence is valuable in complex societies that rely on its existence, and economic theory indeed presupposes perfect rationality, but why would such intelligence or rationality have evolved in primitive societies?

Whatever the cause, there has been a remarkable increase in human brain size over the two million years our genus *Homo* has existed. A common measure of relative brain size is the “encephalization quotient”, or EQ, which is the ratio of the actual brain size to the predicted brain size based on body weight, for modern mammals. At the beginning of our history, there was a dramatic shift from an EQ of just over two for our immediate ancestors, represented by *Australopithecus boisei*, to 3.5 for the earliest *Homo*. There was also a rapid continuous increase of EQ in *Homo* in last million years, rising from about 3.5 to about 5.5 in that period (Robson and Kaplan, 2003).

Two main types of hypothesis have been considered as explanations for this increase—the ecological and the social intelligence hypotheses. The ecological hypothesis is that the demands of the non-human environment were a key impetus to higher intelligence. The social intelligence hypothesis, on the other hand, is that a key factor was interactions with other human beings. The ecological and social intelligence hypotheses need not be mutually exclusive. For example, perhaps an ecological niche for highly skilled hunting of large game on the newly formed African savanna some two million years ago happened to be filled



by early humans. This would have created pressure for greater intelligence directly, since hunting is highly demanding cognitively. At the same time, the tight social organization needed for hunting itself and for sharing the resulting risk could have intensified the social intelligence mechanism.

Further, the ecological hypothesis is *consistent* with an arms race between different species. That is, at the same time that it paid for human beings to become more adept at predicting the behavior of their prey, it would have paid for the prey species to become more intelligent and therefore better at eluding such predation. Indeed, perhaps the most striking data presented by Jerison (1973), in his monumental study of the evolution of the mammalian brain, concerns the simultaneous exaggeration, in general, of predator and prey brain size. This was among the earliest, and remains among the most convincing, of the evidence for a Red Queen effect between distinct species.

Jerison's argument is discussed by Gould (1977 , Ch. 23). Gould summarizes Jerison's data on mean EQ's, relative to modern mammals, in the following Table. This renders vividly the apparent arms race of the last 70 million years between predator and prey species, with the predators maintaining a perhaps shrinking net advantage over their prey.

	Herbivores	Carnivores
Early Tertiary (archaic)	0.18	0.44
Early Tertiary (advanced)	0.38	0.61
Middle to Late Tertiary	0.63	0.76
Modern	0.95	1.10

On the other hand, the social intelligence hypothesis has an arms race within the same species as its *essential* feature. (See Byrne and Whiten, 1988, for example.) There have been a number of distinct but related formulations of the strategic interactions that might have been significant here. De Waal (1989), for example, describes extensive observations of a large zoo colony of chimpanzees, focussing on temporary alliances among the males. The largest and strongest male need not become the alpha male. Rather, a coalition of the other males may elevate one of their own to this pinnacle of power and reproductive access. These coalitions dissolve and reform in a manner that would seem likely to tax the cognitive abilities of humans, let alone chimpanzees. Alternatively, Trivers (1971) formulates the theory of reciprocal altruism essentially as conditional cooperation in the repeated prisoner's dilemma. He suggests that the cognitive demands of keeping track of all relevant interactions led to an arms race in intelligence. Finally, Cheney and Seyfarth (1990) present evidence bearing on the related hypothesis that primates attribute mental states to others, perhaps to better deceive them on this basis.

Robson (2003) examines how intelligence might have evolved in strategic interactions with other individuals. The aspect of intelligence focussed upon is rationality—the extent to which an individual maximizes utility in the light of all available information. The model supposes the strategic transmission of information between individuals may have driven the evolution of such rationality.

## 5.1 Example B

Consider the following example from Robson (2003), as inspired by an example in Aumann and Maschler (1995). One of two possible zero-sum games is played in each of an infinite number of stages, where the game is determined once and for all at the start. In state  $A$ , which has probability  $1/2$ , the game is

	$L$	$R$
$L$	$1, -1$	$0, 0$
$R$	$0, 0$	$2, -2$

whereas, in state  $B$ , which also has probability  $1/2$ , it is

	$L$	$R$
$L$	$-2, 2$	$0, 0$
$R$	$0, 0$	$-1, 1$

There is a single long-run player 1, who knows the game, but an infinite sequence of short-run player 2's, who do not, as a minor departure from Aumann and Maschler's model. Player 1 plays each of the player 2's once. The informed player observes both players' choices in each period, but recalls only the last  $M \geq 1$  periods. Such bounded recall is the main departure from Aumann and Maschler. For each state, player 1's strategy is a mixture over  $L$  and  $R$  for each such history of length  $M$ . She then maximizes the limit of the means payoff. Each uninformed player observes the last  $M$  of the informed player's choices. A strategy for each uninformed player is then a mixture over  $L$  and  $R$  for each observed history of length  $M$ . These players maximize the one-shot expected payoff.

The following is then an equilibrium in these bounded recall strategies:

- Every player 2 mixes  $(2/3, 1/3)$ .
- In state  $B$ , player 1 chooses  $R$ .
- In state  $A$ , if player 1 herself chose  $L$  in the last  $M$  periods, she plays  $(2/3, 1/3)$ ; otherwise, she plays  $(p, 1 - p)$ .

Player 1 is then maximizing her payoff, in either state, given player 2's strategy. Each player 2 is also maximizing his payoff if player 1 chose  $L$  in the last  $M$  periods, since the state must then be  $A$ . All that remains is to show is that player 2 is optimizing when player 1 chose only  $R$  for the last  $M$  periods. Robson (2003) shows that  $p \in (0, 2/3)$  can be chosen so that the player 2's are indifferent between  $L$  and  $R$ , in this case, so the above strategies are an equilibrium.

The strategy here for the player 2's ensures that player 1 cannot get *more* than  $1/6$  from any strategy whatever, so player 1 cannot do better with greater recall. On the other hand, suppose each player 2 has unbounded recall, but player 1 still uses the above strategy of recall  $M$ . In the long run, each player 2 can then infer from player 1's behavior which state is in effect. The player 2's can guarantee his equilibrium payoff of  $-2/3$  in state  $A$  and  $2/3$  in state  $B$ , or an average payoff of 0 overall and an improvement of  $1/6$ . This result holds, despite the intrinsically simple setting here, since the informed player always imposes a demanding problem of statistical inference on the uninformed players.

## 5.2 Game Theory and an Arms Race in Intelligence

The contrast between the above result and most of the previous literature in game theory is striking, since this literature often comes to the conclusion that there would be no arms race in complexity. For example, Gilboa and Samet (1989) consider a two-person repeated game between a boundedly rational and a fully rational player. If the former is restricted to particular set of automata, a dominant strategy for the latter is to figure out which automata has been selected. If the game is nonzero-sum, the boundedly rational player can exploit this strategy of the fully rational player, who is then hurt by his rationality. Rationality hurts because it *must* be known by the other individual, who *then* chooses the best boundedly rational strategy. That is, the rational individual is transparent as well as rational, and the other individual is as much stubborn as unintelligent.

Abreu and Rubinstein (1988) consider a two-person infinitely repeated game played by finite automata. Complexity has a cost, but it may be lexicographically less than the payoffs in the game. If an equilibrium exists with endogenous complexity, both players choose common finite complexity. Additional complexity adds nothing to unilateral payoffs. This seems to depend on the assumption of complete information. In the above example with incomplete information, that is, although this property holds for the informed player, additional complexity can increase the payoffs of the uninformed players.

Finally, the Red Queen effect need not spring from bounded rationality in the above simple sense, but may be inevitable if only players are “Turing machines.” Such machines are idealizations of the most powerful computers thought to be possible even in theory. The

following argument based on the “liar paradox” is due to Binmore (1987). Consider a two player game between Turing machines. As the first step, the machines swap Turing machine numbers, where each such number characterizes the particular machine. The machines then predict the mixed strategy of their opponent, and, based on that, produce a recommendation for play. There does not then exist a Turing machine that is rational in that it always correctly predicts the other machine’s strategy. Indeed, suppose that such a machine exists and consider the following opponent. This opponent is a “universal Turing machine”, which can mimic the action of any particular Turing machine, when fed that machine’s number and given the same input. The universal machine can then determine the supposedly “rational” machine’s prediction of the universal machine’s strategy, but then render this prediction false.

Markose (2002*b*) extends this to argue that, relative to any Nash equilibrium, players will have the incentive to choose strategies that “surprise” an opponent. (See also Markose, 2002*a*, Section 3, and her introduction to this Special Issue.) Thus, the Red Queen effect cannot be evaded, even when players are Turing machines, or as rational then as computational theory allows them to be. On the face of it, it is flattering to human beings to model us as Turing machines, so arms races where players are of bounded rationality in the usual sense remain of interest. However, such arms races become even more compelling given that the Red Queen effect is inescapable even as a matter of principle.

## 6 Conclusions—The Red Queen and Economics

There are deep analogies and interconnections between biology and economics. Both disciplines concern how the properties of complex systems relate to the properties of their components. On the one hand, the prevailing orthodoxy in biology is that the individual, or, better yet, the gene is the “unit of selection.” On the other hand, economics is based on an analogous assumption that individuals are selfish maximizers. The Red Queen effect, or arms race, in biology was introduced to explain why species did not seem to become better adapted over time. However, it has a more active role in explaining the most general and long term evolutionary trends, such as the evolution of more complex organisms and systems. The Red Queen may underlie the maintenance of sexual reproduction and might provide an impetus to higher intelligence, despite the difficulty of reconciling this latter phenomenon with standard game theory.

Turning to economics, a famous argument that economies tend to become more complex is due to Schumpeter (1942). He argued, in particular, that allowing temporary monopolies might favor growth despite their static inefficiency. Each firm is spurred to invent more sophisticated technologies by the resulting monopoly profits; the innovative or imitative activities of its competitors may limit these profits to the short run.

However, the Red Queen effect, in particular, has not been applied widely in economics. A key exception is Baumol (2004), who sketches a Red Queen theory of the birth and development of capitalism. In literal arms races, absolute monarchs were compelled to spend ever-increasing amounts on warfare. The rule of law arose from the reflexive need

of the nobles to be protected from the military exactions of these monarchs. But the rule of law provided the foundation for free-market economies, whose economic success led to further military success. Baumol concludes by arguing that the Red Queen effect is still to be found in competition within the high-tech sector of today's economies. Modelling this particular industrial organizational issue in greater analytical detail is an example of a highly promising future application of the Red Queen effect within economics.

## 7 Appendix

Consider the derivation of the stationary probabilities  $p_n$ ,  $n = 0, \dots, N + M + 1$  for Example A. The probability flow into each state must balance the probability flow out. Considering the state  $n = 0$ , it follows that  $(1 - r)p_0 = rp_1$ . Considering  $n = 1, \dots, N - 1$ , it follows that  $p_n = rp_{n+1} + (1 - r)p_{n-1}$ . It follows by induction that  $p_n = \left(\frac{1-r}{r}\right)^n p_0$ , for  $n = 1, \dots, N$ . This was just shown for  $n = 1$ . Suppose then it holds for  $n = 1, \dots, m$ , where  $m < N$ . It follows that  $p_{m+1} = \frac{p_m - (1-r)p_{m-1}}{r} = \frac{\left(\frac{1-r}{r}\right)^m p_0 - (1-r)\left(\frac{1-r}{r}\right)^{m-1} p_0}{r} = \left(\frac{1-r}{r}\right)^{m+1} p_0$ , completing the inductive proof. Similarly, it follows that  $p_n = \left(\frac{1-r}{r}\right)^{N+M+1-n} p_{N+M+1}$ , for  $n = N + 1, \dots, N + M + 1$ . Finally, considering  $n = N$  and  $n = N + 1$ , it follows that  $p_N = (1 - r)p_{N-1} + (1 - r)p_{N+1}$  and  $p_{N+1} = (1 - r)p_N + (1 - r)p_{N+2}$ . Both of these equations are satisfied if and only if  $\left(\frac{1-r}{r}\right)^N p_0 = \left(\frac{1-r}{r}\right)^M p_{N+M+1}$ ; that is, if and only if  $p_N = p_{N+1}$ .



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