

The Biological Basis of Economic Behavior

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1. Introduction

1.1 Initial Motivation

THIS PAPER advocates consideration of the biological basis of economic behavior.² Although human evolutionary history is inherently fascinating and logically must be the foundation of economic behavior, the case is not limited to these observations. Neither do these observations flatly contradict the usual view in economics that preferences can be taken as primitive and that behavior is fully rational. Reductionism for its own sake is not advocated; rather it seems that the marginal product of work on biological foundations now exceeds that of work on more elaborate higher level models of economic behavior. Consideration of the biological basis of economic behavior will, in the long run, help select the leading candidates from the entire slate of standard and nonstan-

dard models of economic behavior. Although some specific implications can be drawn now, the main task is to develop consistent and convincing biological models for the evolution of human economic characteristics.³

1.2 Historical Sketch

The histories of economics and biology intertwine. It is well-known that a key insight for Charles Darwin derived from Thomas Malthus (1803). Malthus' argument that the growth rate of a population would tend to outpace the growth rate of output implied, for Darwin, an inevitable struggle for existence and, hence, natural selection of the fittest. Somewhat less well-known is the influence of Adam Smith (1776), whose Invisible Hand seems to have been a fundamental and pervasive inspiration for Darwin. Unfettered self-interested utility or profit maximization became, for Darwin, the struggle for reproductive success. The efficiency achieved by the market became the prodigious adaptation and balance evident in nature. (See Stephen Jay Gould 1993, pp. 148–51.)

Darwin delayed publishing *The Origin of Species* until 1859, in part because of an awareness of the furor that

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²Jack Hirshleifer (1977 and 1978) was an early advocate of considering such a basis. Gary Becker (1976) also considered the relationship between biology and economics, to some extent taking economics to be more basic.

³Such models should be general and complete, and thus less subject to the criticism of being “just-so” stories—ad hoc explanations of particular phenomena.

would result from describing a complete system in which God was not necessary. Furthermore, Darwin delayed drawing the inevitable implications of evolution for human beings, eventually addressing these directly in *The Descent of Man* in 1871.⁴

The greatest challenge to Darwin's theory then and now is the human mind. Indeed, the codiscoverer of natural selection, Alfred Russel Wallace, came to believe that "a superior intelligence has guided the development of man in a definite direction, and for a special purpose." Although Darwin himself did not shrink from attributing even the human mind to evolution, the question of how evolution could have generated this complex and powerful phenomenon retains much of its mystery.⁵

1.3 Present Aim

The historical trade between biology and economics has not been all one-way. Game theory was recently borrowed from economics and returned in a modified and useful form, for example.⁶ Overall, however, there is a trade deficit favoring economics. Accordingly, the present aim is to ask various questions concerning the biological basis of human economic behavior. The most politically controversial questions often concern the biological basis of differences among various groups of people. Although not innocuous, less controversial and more fundamental questions concern why human beings share particular characteristics. For example,

⁴ *The Expression of the Emotions in Man and Animals* (1872) is more specific, but is a testimonial to Darwin's powers of observation. The essence of his claim for the universality of the expression of emotions has stood the test of time.

⁵ The views of Wallace and Darwin are described by Steven Pinker (1997, pp. 299–300).

⁶ John Maynard Smith (1982) demonstrates the effectiveness of game theory in biology; Michihiro Kandori (1997) and George Mailath (1998) survey evolutionary game theory in economics.

among those taken up here are: Why might utility functions exist? Is utility hedonic? Is it adaptive? What further properties would evolution confer on utility? In particular: Would preferences be purely selfish? Would intertemporal preferences be time consistent? Would behavior under risk satisfy the expected utility theorem? Further: Why did human intelligence and longevity originally evolve together? Why might individuals have a "theory of mind"—a model of the beliefs and preferences of others?

1.4 Overview

Topics in the present paper will be treated in the rough order in which these phenomena might have evolved. Most importantly, utility is taken to have arisen prior to a high degree of intelligence or rationality. That is, although evolution might have substantially modified utility payoffs after their initial appearance and a vestige of rationality is needed to model how preferences first evolved, it is difficult to contemplate increasing rationality without preexisting preferences. This sequence is plausible neurologically, since reward centers can be found in evolutionarily ancient brain structures—the "limbic system," for example—but cognitive decision making occurs in brain structures that were more recently exaggerated in human beings—the frontal lobes.⁷

The following terminology should be clarified: "Utility" has an hedonic cardinal interpretation; "preferences" may

⁷ Joseph Le Doux (1996, pp. 86–87) describes how evolution in mammals has increased the size of the neocortex relative to the limbic system (or "rhinencephalon"). Eric Kandel, James Schwartz and Thomas Jessell (1991, chapters 47 and 48) describe the role of the limbic system in emotional behavior and motivation. The recent growth and "executive function" of the frontal lobes is described by Michael Gazzaniga, Richard Ivry, and George Mangun (1998, ch. 11) for example.

be nonconventional, but otherwise these terms have the usual meaning. “Intelligence” has a general interpretation; “rationality,” more specifically, means the extent to which an individual maximizes utility while using all available information, including appropriate use in strategic settings of opponents’ preferences and beliefs.

Attention will not be confined here to theoretical evolutionary models of the biological basis of economic behavior, but will be given to relevant empirical work and to disciplines other than biology and economics. Neuroscience, for example, a rapidly progressing field that has illuminated the proximate neural causes of behavior, provides evidence here for an evolutionary approach.⁸ (Gazzaniga, Ivry, and Mangun 1998 is a recent text on cognitive neuroscience.) Such evidence does not eliminate the need for theory. For example, more light can now be shed on altruistic behavior towards relatives by considering its evolutionary advantage rather than its neurological basis. It is hard to imagine that knowledge of proximate mechanisms will soon be so complete that evolutionary arguments will become redundant.⁹

The evolution of preferences in distant forebears of human beings will be considered first. It will be argued that the evolutionary rationale for an hedonic internal evaluation system is to permit an appropriate response to novelty and complexity. Such a cardinal

utility function may be over goods that are only intermediate from a biological viewpoint. Utility seems also to be adaptive and an evolutionary advantage of this will be outlined.¹⁰ Adaptive hedonic utility need not, however, produce results that markedly differ from those derived from the usual nonadaptive ordinal view of utility.

A key question about the applications of preferences considered here is: Are these standard selfish economic preferences? Although plausible biological models generate selfish preferences, this is not always true. Specifically, although a simple biological model of the evolution of attitudes to risk generates the expected utility theorem, a more general version of the model produces a particular type of nonstandard, interdependent preferences. An evolutionary perspective thus suggests testable hypotheses that are unlikely to suggest themselves otherwise.

Would evolved preferences be standard in other respects? For example, are intertemporal preferences time consistent? Hyperbolic discounting and the resulting time inconsistency account for a number of otherwise puzzling empirical phenomena. However, although such “excessive” impatience toward immediate rewards may result from systematic error, simple biological models without such error tend to produce consistency. Further: Is there a biological origin for a concern with status? This seems eminently plausible and there are a number of significant attempts to obtain this. Nevertheless, it seems that the definitive treatment of this phenomenon has also not yet been provided.

⁸ There is not yet much detailed evidence on how *genes* affect human behavior. Jonathan Weiner (1999) describes Seymour Benzer’s path-breaking experiments on the genetic basis of fruit fly behavior. Although we are obviously more complex, it is sobering that many of the *Drosophila* genes whose functions were identified have human counterparts.

⁹ Daniel Dennett (1987) discusses why an understanding of the evolutionary “aim” of behavior is more readily attainable than an understanding of its proximate causes.

¹⁰ Randolph Nesse and George Williams (1996) argue persuasively that an organism that was predominantly “happy” might not be motivated in an evolutionarily appropriate way. In particular, they suggest possible evolutionary functions for various symptoms of disease.

Finally, the evolution of two other key characteristics of human beings—intelligence and longevity—will be briefly considered. The ecological intelligence hypothesis is that intelligence arose from dealing with the nonhuman environment. A specific variant of this will be discussed—that the economics of hunting and gathering drove the simultaneous exaggeration of human intelligence and longevity. Not only did economically relevant characteristics of human beings thus evolve biologically, but primitive economic systems may also have provided the impetus.

The social intelligence hypothesis is that intelligence evolved from the need to deal with fellow beings. Relative rationality may matter in strategic interactions, so an arms race and runaway selection could ensue. Another aspect of the social intelligence hypothesis is the “theory of mind,” which concerns the ability of individuals to “put themselves in one another’s shoes.” There is evidence that humans evolved such a specific intellectual capacity, as is fundamental to the notion of Nash equilibrium, and the rationale for this will be discussed.¹¹

2. *Biology of Preferences*

The first and larger part of the present paper is an examination of the biological basis of preferences or utility functions. The working hypothesis here is that the simple choices involved are made rationally. When the biological basis of rationality itself is considered in the next section, the choices involved may be endogenously more complex.

¹¹ The ecological intelligence and the social intelligence alternatives need not be mutually exclusive. Perhaps an ecological niche for highly skilled and coordinated hunting of large game on the African savanna happened to be filled by early humans. This would have created pressure for greater intelligence directly, but also provided an opportunity for the social intelligence mechanism.

2.1 *Why Did Utility Functions Arise? Is Utility Hedonic?*

Although the cardinality of utility is not a theoretical necessity, this section considers evidence that utility actually has emotional or hedonic content. Further, it will be argued that the evolutionary rationale for utility is to deal with novelty and complexity, and it will be shown how utility may be advantageously defined over goods that are only intermediate from a biological viewpoint.

The term “utility” is not popular in biology. Usually, direct appeal is made to the evolutionary optimality of behavior itself without intermediation by preferences. An exception is foraging theory, concerning how animals search for food, which was inspired by economics. (David Stephens and John Krebs 1986 is a textbook treatment of this theory.) For example, a key result of foraging theory, from Eric Charnov (1976), is the “marginal value theorem.” Suppose that an animal forages over patches of a number of different types of food. Time spent searching for a new patch is costly and, furthermore, a searching animal encounters patches of each type of food at differing rates, reflecting the prevalence of that type. Types of food generate differing concave “utility functions” reflecting the net energy gain as a function of the time spent in each patch. Maximization of the overall rate of energy gain is then achieved by quitting each patch when its marginal utility equals the optimal overall rate of gain. This optimal overall rate of gain thus acts as a shadow price guiding the residence time in each patch.¹²

¹² Hillard Kaplan and Kim Hill (1992) apply foraging theory to modern human hunter-gatherers. They emphasize a “prey choice” model, but also consider the patch residence model.

A criticism of foraging theory is that the informational requirements seem excessive. In the patch model, for example, how could the animals know the optimal overall rate of energy gain? John McNamara and Alasdair Houston (1985) consider this issue from a theoretical viewpoint. Although animals do not know the optimal rate of gain initially, there exists a simple rule of thumb that learns this rate and is optimal on average in the long run.

Indeed, animals do seem to apply such rules of thumb in some situations calling for learning. For example, Krebs, Alex Kacelnik, and Peter Taylor (1978) present a two-armed bandit experiment in which “great tits” chose between Bernoulli distributions with unknown probabilities of success. These birds were willing to sacrifice a higher expected payoff in the short run to gain information, as is qualitatively optimal in a bandit problem, and came within 5 percent of the theoretical maximum payoff. Attaining this maximum payoff exactly often requires a strategy of daunting complexity.

What is argued for the present purpose is that the approach of foraging theory should be reversed: Not only can foraging theory be formulated in terms of an implicit utility function, but such problems could explain the evolutionary origin of an hedonic utility function.¹³

Consumption of food is a good place to start, since this generates fundamental choices faced by all animals. Further, an hedonic interpretation of utility

is natural here and the pleasure human beings derive from food need not have changed much for a long time. Many of the specific “reward centers” in evolutionarily ancient structures of the brain also serve to stimulate complex voluntary behavior such as feeding and drinking. In particular, feeding behavior is mediated by the hypothalamus: Electrical stimulation of one part of the hypothalamus induces feeding, while that of another suppresses it.¹⁴

The “somatic marker” hypothesis of Antonio Damasio (1994) builds on such observations to further describe how emotions are intrinsic to rational decision making. The frontal lobes evaluate options by referring to emotions that were associated with relevant previous experiences by the limbic system. Evidence concerning this comes from experiments carried out by Antoine Bechara, Hanna Damasio, Daniel Tranel, and Antonio Damasio (1997). Individuals had to choose from four decks of cards. Two of these decks produced small gains or occasional moderate losses; the other two produced somewhat larger gains but occasional very large losses. The first two decks produced significant expected gains; the second two significant expected losses. Neurologically intact individuals begin to choose from the first pair *before* becoming conscious of the basis for this choice. At this point, their skin conductance responses proved they had an unconscious and perhaps emotional bias against the second pair. Individuals with damage to the “ventromedial prefrontal cortex,” on the other hand, showed no such skin conductance response and continued to choose from the second pair even *after* becoming

¹³ On psychological grounds, Daniel Kahneman, Peter Wakker, and Rakesh Sarin (1997) also advocate a return to the cardinal interpretation of utility due to Jeremy Bentham (1791). Bentham’s pleasure-pain calculus was, in part, a psychological theory independent of his better-known welfare criterion. However, Kahneman, Wakker, and Sarin distinguish hedonic or “experienced” utility from the “decision utility” guiding choices.

¹⁴ See Roger Carpenter (1996, pp. 172–75) and Kandel, Schwartz, and Jessell (1991, ch. 48). Michel Cabanac (1971, 1979) proposes that the biological role of pleasure or pain is motivation.

conscious of the logical case against them. It seems that the emotional response is not only sufficient but also necessary for correct choice, at least in such situations.¹⁵

To consider an evolutionary rationale for a utility function derived from emotional reward and penalty, Robson (1999a) presents a model where individuals must respond appropriately to novel choice situations. There is a two-armed bandit problem where the distributions on the arms are originally unknown. The overall time horizon is finite, but there is a large number of repetitions. Each outcome from the gamble on each arm is a rate of consumption, and each such consumption rate entails a particular arrival rate of offspring according to a biological utility function. There exists a simple rule of thumb using this function that maximizes overall expected offspring. An hedonic von Neumann-Morgenstern utility function, together with a little additional structure, is then sufficient for evolutionary success. On the other hand, given any rule ensuring adaptation to such novelty, this utility function is necessary in a revealed preference sense.

Instead of having a utility function defined over consumption rates, why could an individual not simply observe the actual offspring produced by choice of each arm as a guide to subsequent behavior? After all, consumption is only an intermediate good from a biological point of view; offspring are the final good. One answer is that there is an inevitable small sample problem here, since each individual produces only a small number of offspring. Consider, indeed, a hypothetical type of individual

that relies on offspring produced to evaluate each arm. Such a type must make mistakes with positive probability, since individual experience is limited. However, the procedure based on encoding consumption rates reduces or eliminates such mistakes and so is evolutionarily superior. The appropriate utility function then essentially substitutes the experience of a large number of individuals for that of a single individual.

The above account, by considering a large number of repetitions, de-emphasizes the role of complexity, in the interests of tractability. Consider, instead, an analogy to the chess-playing program "Deep Blue." Given the complexity of chess, such a program can consider all combinations of choices for only a relatively small number of moves ahead. It then must assign scores to each player based on the pieces left and a summary measure of the position. The score for each piece and positional characteristic might be a multiple regression coefficient, obtained from analysis of many complete games and reflecting then the contribution to the overall probability of winning; the total score is analogous to a utility function. This analogy also helps explain why utility could be defined over goods that are intermediate from a biological point of view.¹⁶

¹⁶The following simpler example illustrates a different sense in which a utility function could help address complexity. Suppose there are N possible consumption bundles, strictly ranked in terms of fitness, which are presented in pairs to an individual. One method of choosing appropriately is to specify the optimal choice for each such pair. If the cost of each such specification is $d > 0$, the total cost of this method is then $dN(N-1)/2$, since the number of pairs is $N(N-1)/2$. A second method involves first assigning utilities based on fitness to each consumption bundle. Suppose the cost of each such assignment is $c > 0$. This second method would then choose the bundle from each pair having the higher utility. Suppose this requires

¹⁵Damasio's theory is outlined by Gazzaniga, Ivry, and Mangun (1998, pp. 449–53). Note the contrast with Robert Frank (1988), who suggests that emotions are precommitment devices.

A vivid way of describing the issue here is as a principal-agent problem where nature is the principal and the individual is the agent. (Kenneth Binmore 1994, pp. 151–52 introduces this metaphor. See also Dennett 1987, pp. 422–27.) The principal here has remarkable control over the agent—the possibilities include direct prescription of actions and formulation of utilities over outcomes for the agent.¹⁷ The latter option may be optimal when there are contingencies unforeseen by nature and/or when choice must be guided by intermediate outcomes with a complex relationship to the final outcomes.

Other work bearing on the evolution of utility includes Yew-Kwang Ng (1996), who also defines rationality as flexible maximizing behavior driven by reward and penalty, rather than as automatic hard-wired responses. He argues that such rational behavior may be favored, in an arms race fashion, in environments that are complex due to the presence of such rational species. In situations requiring learning, Dan Cohen and Aviv Bergman (1997) propose a biological role for utility to generate appropriate “reinforcement” from the consequences of actions bearing on fitness. They also stress that utility provides motivation in intermediate states that have a complex relationship to final outcomes.

extra computational capacity at an additional fixed cost of $C \geq 0$. The total cost of the second method is then $C + cN$. For large enough N , constructing utility is preferred; the underlying reason being that this takes advantage of the transitivity of the fitness criterion.

¹⁷If resource limitations are ignored, nature’s objective might be the exponential growth rate of a type. When, more realistically, resources impose ceilings on populations, the criterion might be the long run number of a type. Such more realistic scenarios imply that modelling attention should be paid to the interaction between different species.

2.1.1 *The Adaptive Nature of Hedonic Utility*

There is a large literature in economics on preferences that adapt to experience in an automatic sense, and there is evidence supporting such an approach.¹⁸ On the other hand, such adaptation seems to raise awkward questions if utility is hedonic and hence cardinal. This may help explain why cardinal utility fell out of favor in economics, even if the conceptual difficulty of aggregating such measures of individual welfare was a more important reason. For example, Shane Frederick and George Loewenstein (1999) discuss how intense pleasure derives from winning a lottery, but declines quickly to a level only slightly above that of a control group. At first blush, such effects seem to compromise the conventional successful theory of the consumer.

Adaptation is also of central significance in psychology.¹⁹ For example, David Zeaman (1949) trained rats to run for a goal with a small reward. Suddenly this was replaced by a large reward. The animals ran faster than if the

¹⁸“Automatic adaptation” is meant to contrast with rational Bayesian learning. Becker and Kevin Murphy (1988), also by contrast, present a model of rational addiction in which habit formation is optimal under stable “meta-preferences.” A few papers serve as illustrations of automatic adaptation. Robert Pollak (1970) considers systems of demand functions that yield differing short-run and long-run behavior and represent an exogenous tendency to habit formation. George Constantinides (1990) resolves the “equity premium puzzle” with a similar model of habit formation. Rajeeva Karandikar, Dilip Mookherjee, Debraj Ray, and Fernando Vega-Redondo (1998) invoke endogenous aspiration levels to explain cooperation in the prisoner’s dilemma.

¹⁹Margaret Matlin (1988) illustrates the pervasiveness of adaptation of sensation and perception. “Habituation” is a fundamental property of neural circuits—the magnitude of the reaction to an innocuous stimulus declines when the stimulus is repeated. It can be seen as a simple form of learning. See Kandel, Schwartz, and Jessell (1991, chapter 65).

large reward had been used all along. Similarly, animals that were switched from a large reward to a small reward ran more slowly than if the small reward had been used all along.²⁰

Léon Tremblay and Wolfram Schultz (1999) present direct neurological evidence of the relative nature of preference. (See also Masataka Watanabe 1999.) They examine, in particular, the firing of neurons in the “orbitofrontal cortex” of monkeys. Suppose that preferences over three rewards are $A > B > C$. These rewards are presented in pairs and signals are associated with each reward. If B and C are involved, the signal associated with B causes many of these neurons to be more active than does the signal associated with C . If A and B are involved, A induces similar neurological activity to B in the first choice situation and B has a similar effect to C . That is, this neural activity is not tied to the rewards themselves, but is tied to whichever is the *better* of the two options.

Consider how adaptation of hedonic utility may be biologically advantageous, and how the behavior induced may differ to only a limited extent from that in the usual economic model. The issue is analogous to the use of a voltmeter. To obtain an accurate reading from such a device, it is necessary to first estimate the range in which the unknown voltage falls. If the range is set too high, the needle will not move; if the range is set too low, the needle will jump to the top. Only if the range is chosen so that the needle moves to

²⁰This might result from a nonseparable intertemporal utility function where past consumption affects the marginal utility of present consumption, as in the model of habit formation due to Pollak (1970), for example. It might not be easy to empirically distinguish any of the previous models of automatic adaptation from the present approach; rather, the intention here is to sketch a biological justification for a unified and parsimonious theory accounting for the same observations.

some intermediate position can an accurate reading be established. The underlying reason is that real measuring instruments have limited “sensitivity,” although this is higher for more expensive instruments. Similarly, perceptions by biological organisms must also have limited discriminatory power, although this power can perhaps be increased at a biological cost. Consider, then, the following model in which hedonic utility derives from the position of consumption in a finite grid.

EXAMPLE 1. An individual must make a choice between two alternatives, represented as nonnegative numbers drawn independently according to the same continuous cumulative distribution function F . The individual chooses *after* the draws are made, but can only distinguish whether each realization is above or below some threshold value, c , say. These two draws are experienced as hedonic utility, with such utility being either just “high” or “low.” If both draws have high utility or both have low utility, choice is made randomly, with each possibility having probability 1/2. Incorrect choices can then be made when both draws lie on the same side of c . What is the value of c that minimizes the overall probability of error? The probability of error is $(1/2)Pr\{x_1, x_2 \leq c\} + (1/2)Pr\{x_1, x_2 > c\} = (1/2)(F(c))^2 + (1/2)(1 - F(c))^2$, which is minimized by choosing $F(c) = 1/2$, that is, by choosing c as any median of the distribution given by F . That is, it is *optimal* for utility to *adapt* to the distribution F .²¹

More generally, suppose the organism has N threshold values, given by $c_1 < c_2 < \dots < c_N$. The probability of error is now $(1/2)(F(c_1))^2 + (1/2)(F(c_2) - F(c_1))^2 +$

²¹Although the probability of error criterion is simple to discuss, a more appropriate criterion might be expected fitness. If outcomes are fitnesses, and there is a single threshold, c , it follows that expected fitness is maximized by setting $c = E_F(x)$.

... + (1/2)($F(c_N) - F(c_{N-1})$)² + (1/2)(1 - $F(c_N)$)² and optimal values of c_1 satisfy $F(c_i) = i/(N + 1)$, $i = 1, \dots, N$. Suppose that there is also a component of cost that depends on N and that N is then chosen to minimize the total of the cost arising from the probability of error and the complexity cost. Consider the limit as the cost of complexity tends to zero. Although the utility function remains relative rather than absolute even in this limit, the optimal number of threshold levels tends to infinity and the probability of error tends to zero.

The usual model of absolute (but ordinal) utility approximates this model of relative (but hedonic and cardinal) utility; the lower the cost of discrimination, the better the approximation. Indeed, loosely speaking, evolution faces a problem of the usual economic form where fitness replaces utility; the only “wrinkle” is the cost of discrimination.

2.2 Time Preference

In a key paper, Alan Rogers (1994) outlines a biological model for the formation of standard economic time preference. Each individual has a varying rate of fertility over the lifespan and consumption influences the probability of survival from one instant to the next. The possibility of giving wealth to one’s offspring is a key aspect of the model. Although these offspring may be more fertile, they are only half relatives under sexual reproduction. This is a reason to prefer oneself when young to one’s offspring when one is old, a source of impatience. With zero population growth, this implies a rate of time preference of $\ln 2$ per generation, or about 2 percent a year, an empirically plausible value.²²

²² Becker and Casey Mulligan (1997) also present a model in which time preference is endogenous. However, time preference is modified in a rational way in the light of deep preferences and is not the product of natural selection.

A puzzle concerning actual time preference is that it seems to involve “hyperbolic discounting,” where the discount rate declines with time into the future. (Empirical evidence for such discounting is summarized by Loewenstein and Drazen Prelec 1992.) A preference for an earlier reward over a later reward might be reversed if both rewards are pushed further into the future, but the time difference between them is fixed. David Laibson (1997) notes that this time inconsistency creates a motive for consumers to constrain future choices. If consumers have access to an asset for which a decision to sell must precede receipt of the proceeds, consumption will track income, as is often observed. Financial market innovation may reduce welfare by reducing the precommitment value of the asset.²³

It seems plausible that hyperbolic discounting has a biological basis. Melissa Bateson and Kacelnik (1996), for example, argue that hyperbolic discounting would arise if individuals act *erroneously* as if gambles could be re-taken. An outline of the argument is as follows. Suppose each gamble $i = 1, \dots, I$, say, is characterized by a stochastic reward \tilde{A}_i and a non-stochastic delay, d_i , to obtain this reward. Suppose there is also a non-stochastic time, r , between repetitions that is the same for all gambles. The average reward per unit time for gamble $i = 1, \dots, I$, is then $\tilde{A}_i / (r + d_i)$. If each such gamble could

²³ Robert Strotz (1956) first considered non-exponential discounting in economics. He claimed that individuals following consistent plans would nevertheless act in a way that is consistent with a suitable exponentially discounted criterion. Strotz’s exact proof was shown to be incorrect by Pollak (1968). The work of Douglas Bernheim and Ray (1987) suggested that savings could be discontinuous under non-exponential discounting when they would be continuous under exponential discounting. Stephen Morris and Andrew Postlewaite (1997) provide an example of this, so showing that the two regimes can be sharply distinguished observationally.

be retaken infinitely often, and impatience is ignored, the best gamble maximizes the long run average reward $E(\tilde{A}_i)/r + d_i$, over $i = 1, \dots, I$. If choice between one-time gambles were based on this erroneous perception, that is, hyperbolic discounting would arise.

Without such error, however, evolutionary models typically induce time consistency. Inconsistency can arise here because preferences are relative to the present; as the present varies, reversals can then occur. Biological optimality would militate against such a construction: If some choice is biologically preferred over another initially, preferences should be such that it remains preferred always.²⁴ Indeed, it might be that discount rates for expected offspring that are constant over time support the optimal choice, to this extent mimicking the standard economic criterion for evaluating intertemporal consumption. This is shown by means of the following example.

EXAMPLE 2. Consider an animal which lives for exactly 3 periods, where the expected offspring produced by an individual of age d is $m_d > 0$, $d = 1, 2, 3$. If the age-structured population vector at date t is $n_t = (n_t^1, n_t^2, n_t^3)$, and this population is large, then $n_{t+1} = n_t L$, $t = 0, 1, \dots$, where L is the “Leslie matrix”

$$L = \begin{bmatrix} m_1 & 1 & 0 \\ m_2 & 0 & 1 \\ m_3 & 0 & 0 \end{bmatrix}.$$

Hence $n_t = n_0 L^t$ and the growth rate of population converges to the dominant eigenvalue (“Frobenius root”) of L . The characteristic equation of L can be written

²⁴ Michael Waldman (1994) argues that the first best under sexual reproduction may not be attained. He suggests this may be why normal individuals systematically overestimate their abilities; conceivably this could also help explain time inconsistency.

as $1 = \frac{m_1}{\lambda} + \frac{m_2}{\lambda^2} + \frac{m_3}{\lambda^3}$, where the unique positive root of this is the dominant eigenvalue. (See Brian Charlesworth 1980, Chapter 1.)

Suppose a particular type, having (m_1^*, m_2^*, m_3^*) as its profile of expected offspring, has a dominant eigenvalue λ^* , larger than that of any other feasible type. Such a particular type would then be favored by natural selection, over these other types. Appropriate choices between this optimal type and any other are then supported by the criterion of the present value of expected offspring, using discount rate λ^* .

That is, consider choice between the optimal type and another feasible type with expected offspring profile (m_1, m_2, m_3) and dominant eigenvector $\lambda < \lambda^*$. Since the right hand side of the characteristic equation is strictly decreasing in λ , it follows that

$$1 = \frac{m_1^*}{\lambda^*} + \frac{m_2^*}{\lambda^{*2}} + \frac{m_3^*}{\lambda^{*3}} \\ = \frac{m_1}{\lambda} + \frac{m_2}{\lambda^2} + \frac{m_3}{\lambda^3} > \frac{m_1}{\lambda^*} + \frac{m_2}{\lambda^{*2}} + \frac{m_3}{\lambda^{*3}},$$

as asserted.

This argument relates the rate of time preference supporting the optimal choice to the asymptotic growth rate of population, λ^* . If $\lambda^* > 1$, it is biologically preferable to have offspring sooner rather than later, since these offspring then represent a larger fraction of the population. Alternatively, if $\lambda^* < 1$, it is preferable to delay the production of these offspring, for the same reason. In general, population growth (or decline) is only one of the biological factors influencing time preference. Further, unless current expected offspring is a function only of current consumption, for example, the relationship between present discounted value of expected offspring and the consumption stream need not be straightforward.

Ronald Balvers and Arnab Acharya (1997) discuss the economic implications of expected lifetime maximization. Such a criterion would be appropriate with a constant rate of expected offspring production over each individual's lifetime and zero population growth. Their model also serves to illustrate how consumption in the economic sense could be linked to biological success. Suppose there is a "hazard rate" for death at each point in time as a function of the consumption profile. Although time consistency still holds, the *consumption* discount rates are now endogenous and may vary over time.

Finally, consider the biological efficiency grounds for low time preference in the modern context of a growth model. Ingemar Hansson and Charles Stuart (1990) consider a neoclassical model of growth with a single type of endogenously produced labor but a capacity constraint on overall population. They consider competing "clans," which may differ in savings behavior. The evolutionary outcome is that investment in capital is governed by the unmodified golden rule so that the underlying preferences selected embody a zero rate of time preference.

Robson and Myrna Wooders (1997) also consider a biologically inspired growth model where labor and capital both have various types. The growth rate of each type of labor depends on the per capita income of that type. If the balanced growth rate of society is maximized, income must be distributed in accordance with marginal product pricing, again implying a zero rate of time preference.²⁵

²⁵ Alan Grafen (1998) presents a related growth model. There is a single output, but a number of different types of labor. Each type of labor always has the income implied by marginal product pricing and allocates this over the various types of offspring. Grafen shows that the population genetic equilibrium coincides with a suitable conventional

2.3 Attitudes to Risk

What implications are there of biology for attitudes to risk? Edi Karni and David Schmeidler (1986) present an evolutionary rationale for the expected utility theorem. They consider a multi-period model of wealth accumulation in which an individual chooses a gamble in each period, dying if his wealth becomes non-positive. The probability of survival to the end is the maximand. Although the dynamic programming value function also reflects characteristics of the gambles taken, it inherits linearity in probabilities from this maximand.

William Cooper (1987) considers, more fundamentally, the criterion of expected offspring. There is both aggregate (correlated) risk stemming from the environment and idiosyncratic (independent) risk, but there exists a type that maximizes expected offspring in *every* environment. Although he carries out a detailed verification of the Savage axioms in this biological setting, the desired conclusion is essentially then a consequence of the law of large numbers.

Robson (1996a) considers the expected offspring criterion further, utilizing a model of branching processes in which extinction is possible and the population may start "small." When risk is idiosyncratic, the type that has maximal expected offspring would be selected, conditional on non-extinction of the entire population. This is intuitively clear for a "large" population, where the growth rate of each type is the expected offspring of an individual, by the law of large numbers.

This translates into the expected utility theorem. Suppose there is a number of types, where each type is characterized

economic equilibrium. The focus here is not on time preference but on how utility should be defined over types of offspring.

by a particular simple gamble over commodities. Suppose that q_k^i is the probability that bundle x_k^i is obtained in the gamble taken by type i and these gambles are independent over all individuals. Consumption bundle x induces expected offspring given by $\psi(x)$, for all types. The type i is then selected that maximizes overall expected offspring: $\sum_k q_k^i \psi(x_k^i)$. The attitudes to risk stemming from the concavity and convexity properties of this von Neumann-Morgenstern utility function, ψ , are now biological in origin.

It is not automatic, however, that natural selection will produce preferences of the conventional independent kind. With both aggregate and idiosyncratic risk, the appropriate criterion is as follows. Suppose each type of individual is characterized by some economic gamble as follows. The environment ξ ("aggregate risk") has realization ξ^s with probability π^s . In each environment, each type of individual faces an independent gamble ("idiosyncratic risk") over commodity bundles. Suppose that $q_k^{i,s}$ is the probability that bundle $x_k^{i,s}$ is attained in environment ξ^s by type i . Any commodity bundle x induces the same expected offspring, $\psi(x)$, for all types, so the expected offspring of type i conditional on environment s is then $\sum_k q_k^{i,s} \psi(x_k^{i,s})$. It can be shown that an appropriate biological growth rate for type i is now the expectation over the environments of the logarithm of expected offspring in each environment.²⁶ This yields the following economic criterion:

$$\sum_s \pi^s \ln \left(\sum_k q_k^{i,s} \psi(x_k^{i,s}) \right).$$

The evaluation of risk here depends on how the risk affects others: A gamble

that is idiosyncratic is strictly preferred to one that is aggregate, even if the two distributions are identical.

In the presence of aggregate risk, such a criterion implies it may be biologically advantageous to induce idiosyncratic gambling. Cooper and Robert Kaplan (1982) discuss the following example. Suppose that winters can either be snowy or clear, each with probability 1/2. Animals whose fur changes to white in the fall do well in white winters and badly in clear winters. Animals whose fur remains dark are in precisely the reverse situation, so either pure type does equally well overall. However, a new type that randomizes 50–50 each fall does strictly better than either pure type. To see why this is true, consider the extreme case in which white animals die for sure in clear winters and live for sure in snowy winters and dark animals face precisely the reverse situation. Either pure type is then doomed to eventual extinction. On the other hand, given a large number of the type that randomizes 50–50, half its members always survive the winter.

Theodore Bergstrom (1997) develops this argument further, using a model in which squirrels save nuts for the winter. Gathering nuts incurs a fitness cost, winters have stochastic length, and too little food saved means death. Suppose there is a very small probability of a very severe winter. Any pure type that fails to save enough to cover this is doomed to certain eventual extinction. Surely, however, it is not optimal for the entire species to be held hostage to such a remote possibility? Consider the following example.

EXAMPLE 3. Suppose that long winters occur with probability α and short winters with probability $1 - \alpha$. Type L squirrels store enough for a long winter, but type S squirrels store only enough for a

²⁶ John Gillespie (1991) discusses selection in a fluctuating environment with more realistic models of genetic inheritance than the asexual or haploid model used here.

short winter. Suppose the probability of survival while gathering nuts in the fall is $1/2$ for type L , but is $3/4$ for type S , since fewer nuts need be gathered. Clearly then, no matter how small $\alpha > 0$ might be, type S is doomed, since it cannot survive the first long winter.

Consider a new type where each member randomizes—it stores enough for a long winter with probability π , but only enough for a short winter with probability $1 - \pi$. The growth rate of this type is then $\alpha \ln(\pi/2) + (1 - \alpha) \ln(\pi/2 + (3/4)(1 - \pi))$. The choice of π which maximizes this rate is 3α , as long as $3\alpha \leq 1$. The optimal type then saves enough to cover the unlikely event of an extreme winter with only a correspondingly small probability, but always avoids complete extinction.

The approaches discussed so far obtain risk-aversion from the concavity of a biological production function. Juan Reboreda and Kacelnik (1991) present an ingenious alternative theory, based on Weber's law, which predicts both risk-aversion with respect to quantity and risk-preference with respect to time delay.²⁷ The following example is simple but revealing.

EXAMPLE 4. Consider an individual with a choice between a certain reward of 2 and a gamble with mean 2 that yields 0 or 4, each with probability $1/2$. Suppose 2 is stored in memory as the uniform distribution on $[1,3]$. In line with Weber's law, which is that perception is of relative rather than absolute effects, 0 is remembered accurately (as a degenerate case, to simplify matters) and 4 as the uniform distribution on $[2,6]$. The gamble is remembered with a distribution function that is the average of the distribution functions for the two out-

comes. The individual now makes a draw for each option and chooses accordingly. The probability is then greater than $1/2$ that the draw for the certain option exceeds the draw for the gamble. The animal is then risk-averse in the sense of choosing the certain reward more often than the gamble. For stochastic delay, a similar argument entails risk-preference in the same sense.

Finally, it is worth noting that there are tantalizing puzzles with respect to attitudes to risk that do not seem to have been addressed from an evolutionary viewpoint. One of these is the Allais paradox, the significance of which may be enhanced since it also occurs in experiments on animals. (A key reference from the huge economics literature on the Allais paradox is Mark Machina 1982.) Raymond Battalio, John Kagel, and Don MacDonald (1985) show, for example, that while rats are risk-averse and have transitive preferences over pairs of gambles, they do not seem to maximize expected utility and are subject to Allais-type paradoxes.²⁸

2.4 *Preferences for Status*

One direct implication of biology that many economists would accept is altruism among close relatives.²⁹ This topic is not addressed here since it is treated by Bergstrom (1996), in an admirable survey of family economic interactions from a biological perspective. Consider instead another salient example of interdependent preferences, a concern with status.

²⁸ A treatise on animal behavior under experimentally induced risk is Kagel, Battalio, and Leonard Green (1995), who argue persuasively in favor of an optimization approach to animal behavior to replace the ad hoc matching laws once favored in psychology.

²⁹ A key concept here is "Hamilton's rule." (See William Hamilton 1964.) Bergstrom (1995) demonstrates this rule must be modified to cover general games.

²⁷ Kacelnik and Bateson (1996), who survey the empirical and theoretical biological literature on foraging under risk, also summarize this theory.

Indeed, how could modern preferences over luxuries have an evolutionary basis when such commodities are completely novel in evolutionary terms? One possibility is that such goods enhance social standing, or status, and that a concern with this is evolutionarily “hard-wired.” After all, even food is an intermediate good from a biological viewpoint. Evolution may have utilized status as a more indirect but still informative signal of fitness. (Frank 1985 argues vividly in favor of including status as an argument of utility.)

For an empirical argument in favor of considering status, consider the model of Milton Friedman and Leonard Savage (1948). Although a casual reading suggests they took status as an argument of von Neumann Morgenstern utility, the formal model they present does not do this, raising problems reconciling the model with observation. (Some such problems were raised by Harry Markowitz 1952. One of these is that the Friedman-Savage model implies that individuals of middle income will take large symmetric gambles.) The implications for attitudes to risk of including status in utility are derived in Robson (1992). For example, in contrast to the Friedman-Savage model, a scaling up of all wealth levels may now scale up the lotteries that would be taken. Further, in contrast to Friedman (1953), a distribution of wealth that is stable (in the sense that no fair gambles are taken) need not lack a middle class.

Paul Rubin and Chris Paul (1979) sketch a biological basis for gambling behavior. In their model, young and poor males tend to be risk preferring since they have nothing to lose but much to gain by crossing a wealth threshold. Robson (1996b) generalizes and formalizes this in a model of polygyny where a female chooses a male on the basis of her share in his wealth. Eddie Dekel

and Suzanne Scotchmer (1999) present a winner-take-all game among males in which the prize is reproductive success. The last two models induce gambling based explicitly on a concern with relative wealth among males.³⁰

Harold Cole, Mailath, and Postlewaite (1992) present a model in which a concern with status arises from assortative mating, where this is not a market outcome in the usual economic sense. They interpret this concern as a reduced form phenomenon. That is, basic preferences retain their conventional selfish form, but greater relative income means greater utility, given the marriage market equilibrium. They use this model to consider economic growth, deriving, for example, the effect of status on the evolution of the wealth distribution. (See also Steven Landsburg 1995, and Cole, Mailath, and Postlewaite 1995.) Postlewaite (1998) further argues in favor of this reduced form approach, although he does not doubt that evolution may have hard-wired a concern for status. Indeed, the Cole, Mailath and Postlewaite model lends itself well to biological reinterpretation.

Alberto Bisin and Thierry Verdier (1998) consider a different basis for an interest in status—a wish by parents that offspring share their utility functions. If there are two types of individuals in a population—those who care about status and those who do not—neither pure state is dynamically stable, but there may be a unique stable mixture involving both types. Such a wish for offspring to share one’s preferences is inherently plausible, but it allows rather arbitrary characteristics to be transmitted. It would also be interesting to derive such a motive from evolutionary considerations.

³⁰ Such simple models seem to exaggerate the difference in risk-aversion between the sexes.

The evolution of attitudes to risk is an unexpected source of an interest in status. This can be illustrated with a version of the example due to Cooper and Robert Kaplan (1982), introduced in the previous subsection.

EXAMPLE 5. The probability of a snowy winter is $p \in (0, 1/2)$ and that of a clear winter is $1 - p \in (1/2, 1)$. Animals that turn white in the fall are certain to survive white winters and certain to die in clear winters; those remaining dark have the reverse prospects. Consider a coin-flipping type that chooses a white coat with probability π and a dark coat with probability $1 - \pi$. Allowing for both the aggregate environmental and induced idiosyncratic risk, the growth rate for this type is then $p\ln\pi + (1 - p)\ln(1 - \pi)$, which is maximized at $\pi = p$.

Cooper and Kaplan imply that individuals who end up choosing a white coat here must then be “coin-flipping altruistic.” That is, on a purely selfish basis, they would be tempted to switch after the coin flip since the probability of the circumstance favorable to them is less than with a dark coat. However, Grafen (1999) shows that the correct notion of “reproductive value” implies all individuals here do equally well. This notion derives from the *expected fraction* of the population.³¹ Suppose the population is a continuum of size 1, for simplicity, and consider a small mass, ε , of individuals who choose a white coat. With probability p , these represent ε/p of the population; otherwise they are dead, so the expected population fraction is ε , given $\pi = p$. Similarly, if these individuals instead chose a dark coat they would attain the same expected population fraction of ε .

³¹ McNamara (1995) previously showed that the optimal distribution of types in such a model can be induced as a Nash equilibrium, essentially by using reproductive value as defined by Grafen.

Interpreted from an economic viewpoint, the conceptual difficulty Cooper and Kaplan encountered arose because selfish preferences are inadequate to describe choice here. The difficulty can be resolved with interdependent preferences. As the above example suggests, these have an “expected relative utility” form, for a suitable “selfish” utility function. (See Philip Curry 1999.)

The present paper adopts the hypothesis that preferences derived originally from decision-theoretic problems. An alternative more general hypothesis is that preferences arose in strategic situations, which may shed light on the formation of interdependent preferences. Werner Güth and Menahem Yaari (1992) and Helmut Bester and Güth (1998) discuss how preferences might evolve to be unselfish and thereby generate non-Nash behavior in games. The key assumption is that each player’s type is perfectly “transparent” to his opponents. Under this assumption, choice of type or preferences will be influenced by the effect these have on an opponent’s behavior.

Chaim Fershtman and Yoram Weiss (1998) present a model that generates a concern for status, in particular. There are externalities, the effect of which can be offset by this interest in social standing. Although individuals interact in pairs, their choices have spillover effects on everyone. If types are transparent, an opponent’s equilibrium choice can be affected by a preference for status, so that such preferences can pay in purely selfish terms.

What if types are *not* transparent, as seems plausible? Consider a Nash equilibrium in any game in which all players use fitness payoffs. Would it pay in terms of fitness to deviate to a new set of preferences if these new preferences were not announced to other players? Clearly not. Jeffrey Ely and Okan

Yilankaya (2000) make a similar point under the assumption that although type is not transparent, players know the *distribution* of preferences in the population. Given an arbitrary profile of preferences, a Bayes–Nash equilibrium is achieved. Preferences with higher fitness then grow at the expense of those with lower fitness. Although all preferences need not ultimately reflect fitness, the limiting outcome of aggregate play must be a Nash equilibrium outcome for fitness.

Levent Koçkesen, Efe Ok, and Rajiv Sethi (2000) show interdependent preferences might confer a strategic advantage in a different sense. Take a two-person game where each player has a continuum of actions, $x_i \in \mathfrak{X}$, say, and a “fitness” function $\pi_i(x_1, x_2) > 0$, $i = 1, 2$. The game is symmetric so that $\pi_1(x_1, x_2) = \pi_2(x_2, x_1)$, for all (x_1, x_2) . Player 1 maximizes the payoff function $\pi_1(x_1, x_2)$; but player 2 maximizes $\rho_2(x_1, x_2) = \pi_2(x_1, x_2) / \pi_1(x_1, x_2)$ and so is concerned with *relative* fitness. Player 2 generally then obtains higher fitness than player 1 in any pure strategy Nash equilibrium.

EXAMPLE 6. To illustrate this, suppose $\pi_1(x_1, x_2) = f(x_1) + g(x_2)$ and $\pi_2(x_1, x_2) = f(x_2) + g(x_1)$ where $f > 0$ and $g > 0$ are differentiable; f has a unique maximum at x^* , so that $f'(x^*) = 0$; and $g'(x) < 0$ for all x . In any pure strategy Nash equilibrium, it is immediate that $x_1 = x^*$. If player 2 also chose $x_2 = x^*$, this would yield $\rho_2 = 1$, but player 2 can do better than this. Indeed, since $\frac{\partial \rho_2(x^*, x^*)}{\partial x_2} = -\frac{g'(x^*)}{f(x^*) + g(x^*)} > 0$, player 2 can obtain $\rho_2 > 1$ with a small increase in x_2 , since this reduces player 1’s fitness. On the other hand, consider any (x^*, \bar{x}) which is a pure strategy Nash equilibrium, so that $\frac{\partial \rho_2(x^*, \bar{x})}{\partial x_2} = 0 = \frac{f'(\bar{x})}{\pi_1(x^*, \bar{x})} - \frac{\pi_2(x^*, \bar{x})g'(\bar{x})}{(\pi_1(x^*, \bar{x}))^2}$. Hence $f'(\bar{x}) < 0$, so, although player 2 is maximizing ρ_2 , a mutant player 2 could obtain higher fitness, π_2 , by choosing some $x_2 < \bar{x}$, given $x_1 = x^*$.

3. Evolution of Rationality (and Longevity)

3.1 Ecological Intelligence

This first main hypothesis considered in this section is that the impetus for greater intelligence came from the demands of the ecology, such as the acquisition of plant and animal food, avoidance of predators, dealing with hot and cold, the use of tools, and so on.³²

3.1.1 Coevolution of Intelligence and Longevity

The ecological intelligence hypothesis essentially derives the biological characteristic of human intelligence from the operation of a primitive economy.³³ Hillard Kaplan and Robson (2000) adopt this approach to explain why intelligence and longevity were *simultaneously* exaggerated in humans. Their model has the following motivation.³⁴

Present day hunter-gatherers exhibit a huge intertemporal economic trade-off over the life span. During their childhood and teenage years, hunters, for example, consume much more than they produce; during their twenties, thirties, and forties, they produce a large flow surplus. Hunting is highly skill-intensive and such a trade-off reflects the biological investment in a large brain, as well as the learning-by-doing that exploits this intellectual capacity.

³² Katharine Milton (1981) argues that the cognitive demands of foraging for high quality plant foods were the key impetus for primate intelligence. Thomas Wynn (1988) concludes that it is difficult to correlate the growth in brain capacity with the archaeological evidence on technological evolution.

³³ Karl Marx argued that the economy influences the nature of human beings. (Samuel Bowles 1998, considers this hypothesis from a modern perspective.) The most compelling sense in which this argument is valid derives from about two million years of hunting and gathering.

³⁴ See also Hillard Kaplan, Hill, Jane Lancaster and Magdalena Hurtado (2000).

Not only has human brain size increased dramatically over the last two million years, but human mortality also seems to have fallen substantially. Indeed, if chimpanzee mortality rates approximate those for human evolutionary ancestors, the hunter-gatherer investment in children could not possibly be recouped without such a fall in mortality.

Suppose that the brain is a form of somatic (bodily) capital and that mortality is also subject to natural selection. Energy output is produced from this capital according to a production function. In turn, this output can be reinvested, used to reduce mortality, or for reproduction. The objective is to maximize the expected lifetime energy available for reproduction. An optimal life history entails initial investment in the capital stock until the optimal steady state capital stock is attained. During this initial phase, mortality is decreasing, as a result of the rising value of a life; during the long-run steady state, mortality is constant.

Although the following discrete example is inadequate to represent an optimal life history, it captures the coevolution of longevity and intelligence.

EXAMPLE 7. There are two periods. The individual is endowed with a brain of mass K in the first period so that energy output there is $F(K) + \alpha$, where $F'(K) > 0$; $F''(K) < 0$; and α is a parameter representing a shift in output. Suppose that energy I is invested in the brain and energy M is devoted to mortality reduction. Output in the second period is then $F(K + I) + \alpha$. The probability of survival to the second period is $1 - \mu(M) - \beta$, where $\mu'(M) < 0$; $\mu''(M) > 0$; and β is a parameter representing exogenous mortality. The objective is expected net energy production, $V(I, M) = F(K) + \alpha - I - M + (1 - \mu(M) - \beta)(F(K + I) + \alpha)$. The first-order conditions for maximizing V are

$V_I(I, M) = -1 + (1 - \mu(M) - \beta)(F'(K + I)) = 0$ and $V_M(I, M) = -1 - \mu'(M)(F(K + I) + \alpha) = 0$, assuming an interior solution. The second-order conditions impose the additional requirement that $V_{II}V_{MM} - V_{IM}^2 > 0$. It follows that $\frac{\partial M}{\partial \alpha} > 0$ so that such an increase in output induces greater expenditure on mortality reduction. As a consequence, $\frac{\partial I}{\partial \alpha} > 0$ and such greater productivity also induces greater investment. Alternatively, it follows from the first-order conditions that $\frac{\partial M}{\partial \beta} < 0$, so a decrease in exogenous mortality induces a *reinforcing* decrease in endogenous mortality. As a consequence, $\frac{\partial I}{\partial \beta} < 0$, and such a reduction in exogenous mortality also induces an increase in investment.

Modern education is a huge investment by parents and society, made worthwhile by the intelligence and preferences of humans. These characteristics are presumably products of biological evolution; the present approach suggests they arose because of the investment in brain and the skill required for hunting and gathering. It is not surprising then that modern productivity profiles and intergenerational flows of resources, for example, closely resemble those in hunter-gatherer economies.

3.2 *Social Intelligence*

The second main hypothesis considered is that of social or Machiavellian intelligence. (Byrne and Whiten 1988 and Whiten and Byrne 1997 are collections of readings on this hypothesis.) This is that strategic interactions with other individuals provided the key impetus toward greater intelligence.

Nicholas Humphrey (1988), for example, argues that the intellectual capacities of primates often exceed the demands of their ecology. Chimpanzees, for example, can be shown to realize that an image in a mirror is that of

themselves. If one of them has a spot painted on its forehead under anesthetic, it will immediately touch the spot on itself upon seeing its own reflection in a mirror. (See Gallup 1970.) To what naturally occurring challenge is this intelligence the response? Humphrey suggests that the only strong candidate concerns social interactions with other chimpanzees.

The social intelligence hypothesis raises two more specific issues that are taken up in the next two subsections. First, is it theoretically plausible that humans became more rational, in the present sense of better using all available information to guide decision making, as a result of competitive strategic interactions?³⁵ Are there strategic interactions where individuals set each other problems of statistical inference that are more challenging, for example, given a higher general level of rationality initially? Secondly, why might the human capacity to anticipate one another's desires and beliefs, as is basic in game theory, have evolved?

3.2.1 *Red Queen Effect*

What is then a game where rationality evolves as an arms race? The key feature of such an arms race, or the "Red Queen effect," should be runaway selection, arising since what matters is rationality *relative* to others.³⁶

Robson (1999b) proposes as a candi-

³⁵The empirical plausibility of the Machiavellian intelligence hypothesis is buttressed by the observation that individuals are often more rational in competitive social or economic interactions than in more abstract contexts. Leda Cosmides (1989) demonstrates this with an experiment in which the same problem of logical inference was presented in abstract form and in terms of detecting cheating.

³⁶Matt Ridley (1993) and Pinker (1997) vividly describe the Red Queen effect, although neither of them thinks it is the full story. The ecological hypothesis might also generate such a Red Queen effect between predator and prey, although possibly with weaker force.

date the following infinitely repeated two-person zero-sum game of incomplete information. (This is a modification of a model from Aumann and Maschler 1995.) A long-run player knows the state of the world and hence both payoff functions. There is a *sequence* of short-run uninformed opponents who can only make inferences about the state from observing the informed player. All players use noisy bounded recall strategies. The Red Queen effect arises as long as partial revelation of information is optimal for the informed player. That is: Given any equilibrium with common recall, there is an incentive bounded away from zero for the uninformed players to increase recall. This strategic setting thus provides a "moving target" encouraging greater rationality.³⁷

Ehud Lehrer (1988) and Elchanan Ben-Porath (1993) also obtain an arms race in rationality. They show that greater recall, or a larger automaton, respectively, enables an individual to exploit an opponent in a standard class of repeated games. However, they assume that individuals cannot use behaviorally mixed strategies but can only mix in a normal form sense over the various pure strategies. Lehrer and Ben-Porath emphasize, in addition, that this may take much greater recall or a much larger automaton.

More recently, Dana Heller (1999) also finds an advantage to strategic sophistication. A large population is randomly paired at each date to play a game that is subject to occasional dramatic change. There are naïve individuals whose choice is fixed and individuals

³⁷An alternative suggestion is due to Robert Trivers (1971) in his original biological account of "reciprocal altruism." He argues that maintaining cooperation in the prisoner's dilemma is cognitively demanding and so may (somehow) have driven the evolution of intelligence as an arms race.

who can learn at a cost. Although a naïve type may do best in the absence of changes, Heller shows that the learners may do best in general even as the probability of change tends to zero.

3.2.2 *Theory of Mind*

An individual who attributes states of mind to another has a “theory of mind.”³⁸ Alan Leslie (1987) and (1991) argues that first pretence and then the theory of mind develop in human beings from a capacity for “metarepresentation.” Experiments show that normal four-year old children can understand that another individual holds a false belief, whereas three-year olds apparently cannot. Autistic children have a specific deficit on such theory of mind tasks, even when mental age is controlled for.

Richard Frackowiak, Karl Friston, Christopher Frith, Raymond Dolan, and John Mazziotta (1997, pp. 354–56) examine brain activity associated with such attributions to others. Subjects were asked to read three alternative stories—one involving a theory of mind, another with a similar context but a purely mechanical interpretation, and a third consisting of unlinked sentences. The technique of “functional magnetic resonance imaging,” which maps instantaneous blood flow in the brain, identifies a region in the “left medial dorsal prefrontal cortex” used uniquely for the theory of mind task. This evidence and that on autistic children is suggestive of a specific neurological module for such tasks.

Why might such a capacity have evolved? An analogous evolutionary ra-

tionale to that already given for the existence of a utility function is proposed here. The possession of a representation of another individual’s preferences, for example, permits a flexible optimal response in a class of strategic situations, and so would be evolutionarily favored. Conversely, there is no simpler solution in this class of games, since any solution entails such a representation in a revealed preference sense.

EXAMPLE 8. Consider two players—1 and 2. Suppose that player 1 faces the fixed set of possible outcomes $\{a_1, \dots, a_M\}$ and has preferences $a_1 >_1 \dots >_1 a_M$. Player 2 faces the fixed set $\{b_1, \dots, b_N\}$ and has preferences $b_1 >_2 \dots >_2 b_N$. Both players know their own preferences. Consider the following set of *all* finite two-stage games of perfect information with these outcome sets. Player 1 moves first and player 2 moves second. Player 1’s choices are $\{c_1, \dots, c_R\}$ and player 2’s are $\{d_1, \dots, d_S\}$. For simplicity, player 1’s choices are noisy so that there is at least a small positive probability of choosing any pure strategy. Suppose also that player 2 never faces a tie for any prior move by player 1.

In the first place, if player 1 knows player 2’s preferences and so can predict player 2’s behavior, a Nash equilibrium of the noisy game results. (This approximates a subgame perfect equilibrium of the unperturbed game.) The existence of a representation of player 2’s preferences in player 1’s mind permits player 1 to play in an evolutionarily optimal way.

Conversely, suppose that such a Nash equilibrium is played in *every* noisy game. There is then a “revealed preference” sense in which player 1 must know player 2’s preferences. It is enough to limit attention to choice sets $\{c_1, c_2\}$ and $\{d_1, d_2\}$. Consider player 2’s preference between any pair of distinct

³⁸The term is due to David Premack and Guy Woodruff (1978). Dorothy Cheney and Robert Seyfarth (1990) consider empirical tests of the theory of mind hypothesis. They claim that vervet monkeys are more adept in dealing with one another than in dealing with their predators, thus favoring the general social intelligence hypothesis over the ecological intelligence hypothesis.

outcomes b_i and b_j , say. Let Δ denote the mapping from choice pairs to outcome pairs. Consider the game such that $\Delta(c_1, d_1) = (a_1, b_i)$, $\Delta(c_1, d_2) = (a_N, b_j)$, $\Delta(c_2, d_1) = (a_N, b_i)$, and $\Delta(c_2, d_2) = (a_1, b_j)$. Since the equilibrium implies that player 1 chooses as close to c_1 as possible if $b_i > {}_2b_j$ and as close to c_2 as possible if $b_j > {}_2b_i$, it follows that player 1 must “know” 2’s preferences. There is then no simpler method for ensuring that player 1 optimizes in this entire class of games.

Dennett (1983) proposes an infinite hierarchy of levels of intentionality. A zero-intentionality act is programmed directly by evolution—the wing pattern of an edible butterfly that deters predators by mimicking that of a noxious species, for example. First-order intentionality includes the desires and beliefs of the agent. Second-order intentionality includes knowledge of the desires or beliefs of another agent, and so on. The level of such intentionality could be made empirically meaningful by a generalization of the present revealed preference approach.

4. What Next?

There are a number of promising approaches suggested by the present account, a selection of which follows.

1. The case for food as an argument of hedonic utility is straightforward because the biological value of food is relatively constant. However, emotions are presumably also attached to money, although money is too recent to have *direct* hard-wired significance. For general decision making, then, *how* are emotions attached to experiences?
2. Providing a biological basis for hyperbolic discounting is challenging, since evolutionary models tend to generate time consistency. Perhaps frictions, or costs of complexity, should then be introduced. For example, suppose there are two discrete modules in the mind—one urging grabbing whatever is at hand and another willing to defer gratification. Actual behavior might be a compromise between these two modules yielding a non-constant rate of time preference, but intermediate impatience on average. What are the biological cost considerations that would make two such modules evolutionarily optimal?
3. In the evolutionary account of attitudes to risk, predictions were made that individuals distinguish between idiosyncratic and aggregate risk. Are such theoretical predictions borne out empirically?
4. Although there are a number of attempts to derive a concern with status from biology, there is scope for further work here. In addition, although a basic concern with status may be innate, the exact determinants of status may not be. Some societies identify status with wealth, some with accidents of birth. What can be said about how the determinants of status arise?
5. Present day hunter-gatherer societies yield insight into an economy that shaped human preferences for the last two million years. A conspicuous phenomenon in many of these societies is food sharing, which often seems egalitarian (as well as Pareto-improving). (See Hillard Kaplan and Hill 1985.) What implications might there be for the political preferences of modern human beings?
6. Finally, it is important to analyze the evolution of the theory of mind, since this lies at the foundation of game theory. What kind and degree of sophistication would evolution generate here? What implications are there for the empirical limits on abstract game theory?

REFERENCES

- Aumann, Robert J. and Michael B. Maschler. 1995. *Repeated Games with Incomplete Information*. Cambridge, MA: MIT Press.
- Balvers, Ronald J. and Arnab K. Acharya. 1997. "Optimal Lifetime Utility when Time Preference Depends on Survival Probabilities," West Virginia U.
- Bateson, Melissa and Alex Kacelnik. 1996. "Rate Currencies and the Foraging Starling: The Falacy of the Averages Revisited," *Behavioural Ecology* 7, pp. 341–52.
- Battalio, Raymond C.; John H. Kagel, and Don N. MacDonald. 1985. "Animals' Choices Over Uncertain Outcomes: Some Initial Experimental Results," *Amer. Econ. Rev.* 75, pp. 596–613.
- Bechara, Antoine; Hanna Damasio, Daniel Tranel, and Antonio R. Damasio. 1997. "Deciding Advantageously Before Knowing the Advantageous Strategy," *Science* 275, pp. 1293–95.
- Becker, Gary S. 1976. "Altruism, Egoism and Genetic Fitness: Economics and Sociobiology," *J. Econ. Lit.* 14, pp. 817–26.
- Becker, Gary S. and Casey B. Mulligan. 1997. "The Endogenous Determination of Time Preference," *Quart. J. Econ.* 112, pp. 729–58.
- Becker, Gary S. and Kevin M. Murphy. 1988. "A Theory of Rational Addiction," *J. Polit. Econ.* 96, pp. 675–700.
- Ben-Porath, Elchanan. 1993. "Repeated Games with Finite Automata," *J. Econ. Theory* 59, pp. 17–32.
- Bentham, Jeremy. 1791. *Principles of Morals and Legislation*. London: Doubleday.
- Bergstrom, Theodore C. 1995. "On the Evolution of Altruistic Rules for Siblings," *Amer. Econ. Rev.* 85, pp. 58–81.
- . 1996. "Economics in a Family Way," *J. Econ. Lit.* 34, pp. 1903–34.
- . 1997. "Storage for Good Times and Bad: Of Rats and Men," U. California Santa Barbara.
- Bernheim, Douglas and Debraj Ray. 1987. "Economic Growth with Intergenerational Altruism," *Rev. Econ. Stud.* 54, pp. 227–41.
- Bester, Helmut and Werner Güth. 1998. "Is Altruism Evolutionarily Stable?" *J. Econ. Behav. Org.* 34, pp. 193–209.
- Binmore, Kenneth G. 1994. *Game Theory and the Social Contract, Vol. 1: Playing Fair*. Cambridge, MA: MIT Press.
- Bisin, Alberto and Thierry Verdier. 1998. "On the Cultural Transmission of Preferences for Social Status," *J. Public Econ.* 70, pp. 75–98.
- Bowles, Samuel. 1998. "Endogenous Preferences: The Cultural Consequences of Markets and Other Economic Institutions," *J. Econ. Lit.* 36, pp. 75–111.
- Byrne, Richard W. and Andrew Whiten. 1988. *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans*. Oxford: Oxford U. Press.
- Cabanac, Michel. 1971. "Physiological Role of Pleasure," *Science* 173, pp. 1103–1107.
- . 1979. "Sensory Pleasure," *Quart. Rev. Bio.* 54, pp. 1–29.
- Carpenter, Roger H.S. 1996. *Neurophysiology*. London: Arnold.
- Charlesworth, Brian. 1980. *Evolution in Age-Structured Populations*. Cambridge: Cambridge U. Press.
- Charnov, Eric L. 1976. "Optimal Foraging, the Marginal Value Theorem," *Theoret. Population Bio.* 9, pp. 129–36.
- Cheney, Dorothy and Robert Seyfarth. 1990. *How Monkeys See the World: Inside the Mind of Another Species*. Chicago: U. Chicago Press.
- Cohen, Dan and Aviv Bergman. 1997. "The Evolution of Adaptive Responses and Learning: Linear Production and Utility Functions, R1/R2 Fitness Functions," Stanford U.
- Cole, Harold L.; George Mailath, and Andrew Postlewaite. 1992. "Social Norms, Savings Behavior, and Growth," *J. Polit. Econ.* 100, pp. 1092–125.
- . 1995. "Response to 'Aristocratic Equilibria'," *J. Polit. Econ.* 103, pp. 439–43.
- Constantinides, George M. 1990. "Habit Formation: A Resolution of the Equity/Premium Puzzle," *J. Polit. Econ.* 98, pp. 519–43.
- Cooper, William S. 1987. "Decision Theory as a Branch of Evolutionary Theory: A Biological Derivation of the Savage Axioms," *Psych. Rev.* 94, pp. 395–411.
- Cooper, William S. and Robert H. Kaplan. 1982. "Adaptive 'Coin-Flipping': A Decision-Theoretic Examination of Natural Selection for Random Individual Variation," *J. Theoret. Bio.* 94, pp. 135–51.
- Cosmides, Leda. 1989. "The Logic of Social Exchange: Has Natural Selection Shaped How Humans Reason? Studies with the Wason Selection Task," *Cognition* 31, pp. 187–276.
- Curry, Philip. 2000. "Decision-Making under Uncertainty and the Evolution of a Concern for Status," *J. Econ. Theory* forthcoming.
- Damasio, Antonio R. 1994. *Descartes' Error*. NY: Avon.
- Darwin, Charles. 1859. *On the Origin of Species by Means of Natural Selection*. London: John Murray.
- . 1871. *The Descent of Man, and Selection in Relation to Sex*. London: John Murray.
- . 1872. *The Expression of the Emotions in Man and Animals*. London: John Murray.
- Dekel, Eddie and Suzanne Scotchmer. 1999. "On the Evolution of Attitudes Towards Risk in Winner-Take-All Games," *J. Econ. Theory* 87, pp. 125–43.
- Dennett, Daniel C. 1983. "Intentional Systems in Cognitive Ethology: The 'Panglossian Paradigm' Defended," *Behav. Brain Sci.* 6, pp. 343–90.
- . 1987. *The Intentional Stance*. Cambridge, MA: MIT Press.
- Ely, Jeffrey C. and Okan Yilankaya. 2000. "Nash Equilibrium and the Evolution of Preferences," *J. Econ. Theory* forthcoming.

- Fershtman, Chaim and Yoram Weiss. 1998. "Social Rewards, Externalities and Stable Preferences," *J. Public Econ.* 70, pp. 53–72.
- Frackowiak, Richard S. J.; Karl J. Friston, Christopher D. Frith, Raymond J. Dolan, and John C. Mazziotta. 1997. *Human Brain Function*. San Diego: Academic Press.
- Frank, Robert H. 1985. *Choosing the Right Pond: Human Behavior and the Quest for Status*. NY: Oxford U. Press.
- . 1988. *Passions within Reason: The Strategic Role of the Emotions*. New York: Norton.
- Frederick, Shane, and George Loewenstein. 1999. "Hedonic Adaptation," in *Wellbeing: The Foundations of Hedonic Psychology*. Daniel Kahneman, Edward Diener, and Nobert Schwartz, eds. New York: Russell Sage Foundation Press, pp. 302–29.
- Friedman, Milton. 1953. "Choice, Chance, and the Personal Distribution of Income," *J. Polit. Econ.* 61, pp. 277–90.
- Friedman, Milton and Leonard J. Savage. 1948. "The Utility Analysis of Choices Involving Risk," *J. Polit. Econ.* 56, pp. 279–304.
- Gallup, Gordon G. 1970. "Chimpanzees: Self-Recognition," *Science* 167, pp. 86–87.
- Gazzaniga, Michael S.; Richard B. Ivry, and George R. Mangun. 1998. *Cognitive Neuroscience: The Biology of the Mind*. NY: Norton.
- Gillespie, John. 1991. *The Causes of Molecular Evolution*. Oxford: Oxford U. Press.
- Gould, Stephen Jay. 1993. *Eight Little Piggies*. NY: Norton.
- Grafen, Alan. 1998. "Fertility and Labour Supply in *Femina Economica*," *J. Theoret. Bio.* 194, pp. 429–55.
- . 1999. "Formal Darwinism, the Individual-as-Maximising-Agent Analogy, and Bet-Hedging," in *Proceedings of the Royal Society of London, Series B* 266, pp. 799–803.
- Güth, Werner and Yaari E. Menahem. 1992. "An Evolutionary Approach to Explain Reciprocal Behavior in a Simple Strategic Game," in *Explaining Process and Change—Approaches to Evolutionary Economics*. Ulrich Witt, ed. Ann Arbor, pp. 23–34.
- Hamilton, William D. 1964. "The Genetical Evolution of Social Behavior, I and II," *J. Theoret. Bio.* 7(1), pp. 1–52.
- Hansson, Ingemar and Charles Stuart. 1990. "Malthusian Selection of Preferences," *Amer. Econ. Rev.* 80, pp. 529–44.
- Heller, Dana. 1999. "An Evolutionary Analysis of the Returns to Learning." U. Chicago.
- Hirshleifer, Jack. 1977. "Economics from a Biological Viewpoint," *J. Law Econ.* 20, pp. 1–52.
- . 1978. "Natural Economy Versus Political Economy," *J. Soc. Biol. Structures* 1, pp. 319–37.
- Humphrey, Nicholas K. 1988. "The Social Function of Intellect," in *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans*. Richard W. Byrne and Andrew Whiten, eds. Oxford: Oxford U. Press, pp. 13–26.
- Kacelnik, Alex and Melissa Bateson. 1996. "Risky Theories—The Effects of Variance on Foraging Theories," *Amer. Zoologist* 36, pp. 402–34.
- Kagel, John H.; Raymond C. Battalio, and Leonard Green. 1995. *Economic Choice Theory: An Experimental Analysis of Animal Behavior*. Cambridge: Cambridge U. Press.
- Kahneman, Daniel; Peter P. Wakker, and Rakesh Sarin. 1997. "Back to Bentham? Explorations of Experienced Utility," *Quart. J. Econ.* 112, pp. 375–405.
- Kandel, Eric R.; James H. Schwartz, and Thomas M. Jessell. 1991. *Principles of Neural Science*. Norwalk, Connecticut: Appleton and Lange.
- Kandori, Michihiro. 1997. "Evolutionary Game Theory in Economics," in *Advances in Economics and Econometrics: Theory and Application, Seventh World Congress, Volume I*. David M. Kreps and Kenneth F. Wallis, eds. Cambridge: Cambridge U. Press.
- Kaplan, Hillard S. and Kim Hill. 1985. "Food Sharing among Ache Foragers: Tests of Explanatory Hypotheses," *Current Anthropology* 26, pp. 223–45.
- . 1992. "The Evolutionary Ecology of Food Acquisition," in *Evolutionary Ecology and Human Behavior*. Eric A. Smith and Bruce Winterhalder, eds. NY: Aldine de Gruyter, pp. 167–201.
- Kaplan, Hillard S.; Kim Hill, Jane Lancaster, and A. Magdalena Hurtado. 2000. "A Theory of Life History Evolution: Diet, Intelligence, and Longevity," *Evolutionary Anthro.* 9(4), pp. 156–85.
- Kaplan, Hillard S. and Arthur J. Robson. 2000. "The Coevolution of Human Longevity and Intelligence in Hunter-Gatherer Economies," U. Western Ontario.
- Karandikar, Rajeeva; Dilip Mookherjee, Debraj Ray, and Fernando Vega-Redondo. 1998. "Evolving Aspirations and Cooperation," *J. Econ. Theory* 80, pp. 292–331.
- Karni, Edi and David Schmeidler. 1986. "Self-Preservation as a Foundation of Rational Behavior Under Risk," *J. Econ. Behav. Org.* 7, pp. 71–81.
- Koçkesen, Levent; Efe Ok, and Rajiv Sethi. 2000. "On the Strategic Advantage of Negatively Interdependent Preferences," *J. Econ. Theory* 92, pp. 274–99.
- Krebs, John R.; Alejandro Kacelnik, and Peter Taylor. 1978. "Test of Optimal Sampling by Foraging Great Tits," *Nature* 275 (5675), pp. 27–31.
- Laibson, David. 1997. "Golden Eggs and Hyperbolic Discounting," *Quart. J. Econ.* 112, pp. 443–78.
- Landsburg, Steven E. 1995. "Aristocratic Equilibria," *J. Polit. Econ.* 103, pp. 434–38.
- Le Doux, Joseph. 1996. *The Emotional Brain: The Mysterious Underpinnings of Emotional Life*. NY: Touchstone.
- Lehrer, Ehud. 1988. "Repeated Games with Stationary Bounded Recall Strategies," *J. Econ. Theory* 46, pp. 130–44.

- Leslie, Alan M. 1987. "Pretense and Representation: The Origins of 'Theory of Mind.'" *Psych. Rev.* 94, pp. 412–26.
- . 1991. "The Theory of Mind Impairment in Autism: Evidence for a Modular Mechanism of Development?" in *Natural Theories of Mind: Evolution, Development and Simulation of Everyday Mindreading*. Andrew Whiten, ed. Oxford: Basil Blackwell, pp. 63–78.
- Loewenstein, George and Drazen Prelec. 1992. "Anomalies in Intertemporal Choice: Evidence and an Interpretation," *Quart. J. Econ.* 107, pp. 573–98.
- Machina, Mark. 1982. "'Expected Utility' Analysis without the Independence Axiom," *Econometrica* 50, pp. 277–323.
- Mailath, George J. 1998. "Do People Play Nash Equilibrium? Lessons from Evolutionary Game Theory," *J. Econ. Lit.* 36, pp. 1347–74.
- Malthus, Thomas R. 1803. *An Essay on the Principles of Population*. London: J. Johnson.
- Markowitz, Harry. 1952. "The Utility of Wealth," *J. Polit. Econ.* 60, pp. 151–58.
- Matlin, Margaret W. 1998. *Sensation and Perception*. Boston: Allyn and Bacon.
- Maynard Smith, John. 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge U. Press.
- McNamara, John M. 1995. "Implicit Frequency Dependence and Kin Selection in Fluctuating Environments," *Evolutionary Ecology* 9, pp. 185–203.
- McNamara, John M. and Alasdair I. Houston. 1985. "Optimal Foraging and Learning," *J. Theoret. Bio.* 117, pp. 231–49.
- Milton, Katharine. 1981. "Distribution Patterns of Tropical Plant Foods as an Evolutionary Stimulus to Primate Mental Development," *Amer. Anthropologist* 83, pp. 534–48.
- Morris, Stephen and Andrew Postlewaite. 1997. "Observational Implications of Non-Exponential Discounting," U. Pennsylvania.
- Nesse, Randolph and George C. Williams. 1996. *Why We Get Sick: The New Science of Darwinian Medicine*. NY: Vintage.
- Ng, Yew-Kwang. 1996. "Complex Niches Favour Rational Species," *J. Theoret. Bio.* 179, pp. 303–11.
- Pinker, Steven. 1997. *How the Mind Works*. NY: Norton.
- Pollak, Robert A. 1968. "Consistent Planning," *Rev. Econ. Stud.* 35, pp. 201–208.
- . 1970. "Habit Formation and Dynamic Demand Functions," *J. Polit. Econ.* 78, pp. 745–63.
- Postlewaite, Andrew. 1998. "The Social Basis of Interdependent Preferences," *Eur. Econ. Rev.* 42, pp. 779–800.
- Premack, David and Guy Woodruff. 1978. "Does the Chimpanzee Have a Theory of Mind?" *Behav. Brain Sci.* 1, pp. 515–26.
- Reboreda, Juan C. and Alex Kacelnik. 1991. "Risk Sensitivity in Starlings," *Behav. Ecology* 2, pp. 301–309.
- Ridley, Matt. 1993. *The Red Queen: Sex and the Evolution of Human Nature*. NY: Macmillan.
- Robson, Arthur J. 1992. "Status, the Distribution of Wealth, Private and Social Attitudes to Risk," *Econometrica* 60, pp. 837–57.
- . 1996a. "A Biological Basis for Expected and Non-Expected Utility," *J. Econ. Theory* 68, pp. 397–424.
- . 1996b. "The Evolution of Attitudes to Risk: Lottery Tickets and Relative Wealth," *Games Econ. Behav.* 14, pp. 190–207.
- . 1999a. "Why Would Nature Give Individuals Utility Functions?" *J. Polit. Econ.* forthcoming.
- . 1999b. "The Evolution of Intelligence and the Red Queen," U. Western Ontario.
- Robson, Arthur J. and Myrna Wooders. 1997. "The Growth-Maximizing Distribution of Income," *Int. Econ. Rev.* 38, pp. 511–26.
- Rogers, Alan. 1994. "Evolution of Time Preference by Natural Selection," *Amer. Econ. Rev.* 84, pp. 460–81.
- Rubin, Paul H. and Chris W. Paul. 1979. "An Evolutionary Model of Taste for Risk," *Econ. Inquiry* 17, pp. 585–96.
- Smith, Adam. 1776. *The Wealth of Nations*. London: Strahan and Cadell.
- Stephens, David W. and John R. Krebs. 1986. *Foraging Theory*. Princeton: Princeton U. Press.
- Strotz, Robert. 1956. "Myopia and Inconsistency in Dynamic Utility Maximization," *Rev. Econ. Stud.* 23, pp. 165–80.
- Tremblay, Léon and Wolfram Schultz. 1999. "Relative Reward Preference in Primate Orbitofrontal Cortex," *Nature* 398, pp. 704–708.
- Trivers, Robert. 1971. "The Evolution of Reciprocal Altruism," *Quart. Rev. Bio.* 46, pp. 35–57.
- Waldman, Michael. 1994. "Systematic Errors and the Theory of Natural Selection," *Amer. Econ. Rev.* 84, pp. 482–97.
- Watanabe, Masataka. 1999. "Neurobiology: Attraction is Relative Not Absolute," *Nature* 398, pp. 661–63.
- Weiner, Jonathan. 1999. *Time, Love, and Memory*. New York: Knopf.
- Whiten, Andrew and Richard W. Byrne. 1997. *Machiavellian Intelligence II: Extensions and Evaluations*. Cambridge: Cambridge U. Press.
- Wynne, Thomas. 1988. "Tools and the Evolution of Human Intelligence," in *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans*. Richard W. Byrne and Andrew Whiten, eds. Oxford: Oxford U. Press, pp. 271–84.
- Zeaman, David. 1949. "Response Latency as a Function of the Amount of Reinforcement," *J. Exper. Psych.* 39, pp. 466–83.