Evolution and inequality

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Some scientists remain wary of evolutionary theory because of its supposed genetic determinism and insensitivity to the inequalities often associated with gender, race and class. Our aim is to show that such fears are outdated and to foster a role for evolutionary theory in public health. We use complex adaptive systems theory and the concept of a tradeoff between current and future reproduction to argue that when the future is objectively risky and uncertain the optimal reproductive strategy will often be to reproduce at a young age and/or high rate. Because reproducing early and/or often can lead to ill health and shortened lives, and because inequality is a major source of environmental risk and uncertainty, we argue that any attempt to use evolutionary theory to understand human reproduction, health or wellbeing must include considerations of inequality and social capital.

Keywords   Evolutionary ecology, reproductive strategies, risk and uncertainty, cost of reproduction, social capital

'The political lesson of twentieth-century Darwinian thinking is, therefore, entirely different from that of nineteenth-century Social Darwinism …A Darwinian left, understanding the prerequisites for mutual cooperation as well as its benefits, would strive to avoid economic conditions that create outcasts.'[1 p.53]

Despite its spectacular growth in recent years, the concept of social capital remains obscure; it is said to suffer from a 'lack of clarity'[2] and to have 'little… theoretical rigor.'[3] In this essay we hope to add some clarity by offering a new perspective, that of modern evolutionary theory. We recognise that some are wary of this perspective because of its supposed genetic determinism and insensitivity to the historical contingencies underlying the inequalities often associated with gender, race and class. Such fears are no longer warranted, however, for modern evolutionary theory is far more sensitive than its predecessors to the processes of gene/environment interaction that underlie the development of potentially adaptive individual differences. Evolutionists are nonetheless obliged to address these fears because they prolong the balkanization of knowledge and hamper the use of our only scientific theory of life to improve the quality of life. Our aim is to foster a role for evolutionary theory in public health by showing how and why it is naturally concerned with the inherently biosocial phenomena of inequality and social capital.

Our paper consists of three parts. First we sketch complex adaptive systems theory. This is to make the point that (among

other problems) earlier attempts to apply evolutionary theory to human affairs failed to appreciate that perhaps the major dimension on which ecological niches differ is that of risk and uncertainty. For present purposes the central lesson from complex adaptive systems theory is that the cost of failing to avoid a current 'fitness cliff' (lineage extinction) is always greater than the benefit of setting the stage for some future good fitness move. This is because fitness (reproductive success; leaving descendants) is the currency of evolution. In the face of too much risk and uncertainty the future pales because the most important problem is leaving any descendants at all. Second, after a quick look at the tradeoff between current and future reproduction, we show that when the future is objectively risky and uncertain the optimal reproductive strategy will often be to avoid fitness cliffs by reproducing early and/or often, i.e. by maximizing current reproduction. We then show how maximizing current reproduction in the face of chronic risk and uncertainty can exact tradeoffs in the form of ill health and shortened lives. Third, we outline the developing argument that *Homo sapiens* is not well adapted to inequality. On this basis, and because inequality is now a major source of risk and uncertainty, we contend that evolutionary theory's fundamental assumption of optimality means that any attempt to use the theory to understand human reproduction, health or wellbeing must include considerations of inequality and social capital. We conclude that evolutionary theory has implications for preventing disease because it explains in principle why inequality should lead to disease.

The evolutionary ecology of time

Modern evolutionary theory (specifically, evolutionary ecology) is concerned with how organisms in particular ecological niches solved the adaptive problems that they had to solve in order to leave descendants. It is now accepted that risk and uncertainty

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are among the most pervasive adaptive problems facing all organisms.[4–6] Complex adaptive systems theory helps to illustrate why.

Complex adaptive systems theory grew out of the realisation that there is more to adaptation than Darwinian natural selection. Indeed, it is now widely accepted that the process of adaptation has certain formal properties that can be identified not only in evolving species, but also, for example, in the immune system, ecological and economic systems, and developing embryos and brains. Foremost among these formal properties is the capacity to form what John Holland called 'internal models' for predicting the future.[7] According to Holland (the father of complex adaptive systems theory), internal models are the 'fundamental attribute' of all complex adaptive system because they allow the system 'to look ahead to the future consequences of current actions, without actually committing itself to those actions. In particular, the system can avoid acts that would set it irretrievably down some road to future disaster ("stepping off a cliff"). Less dramatically, but equally important, the (internal) model enables the agent (the complex adaptive system) to make current "stage-setting" moves that set up later moves that are obviously advantageous. The very essence of attaining a competitive advantage, whether it be in chess or economics, is the discovery and execution of stage-setting moves.'[7 p.25]

In short, complex adaptive systems have the remarkable capability of *continuing*, which entails solving at least two very basic adaptive problems. In the terms of evolutionary ecology, continuing requires, first, not stepping off a fitness cliff (i.e. avoiding lineage extinction), and second, setting the stage for future good fitness moves (i.e. *investing* in the future, foregoing short-term fitness benefits in return for greater but delayed benefits). Setting the stage for future good fitness moves is 'less dramatic' than avoiding fitness cliffs because the penalty for stepping off a fitness cliff is immediate, severe and certain, whereas the benefit from setting the stage for some future good fitness move is delayed—and to that extent devalued, relative to the present, because the future is to some extent always uncertain. This is undoubtedly the reason why the probability of lineage extinction is more sensitive to having *few* offspring than it is to having *many* offspring (i.e. why *reducing* number of offspring by a certain amount *increases* the risk of extinction more than *increasing* number offspring by the same amount *reduces* the risk of extinction).[8,9] It is also surely why risk-aversion is 'one of the most robust regularities in experimental psychology [and] is apparently part of the hard wiring of most animal nervous systems.'[10 p.279]

The message from complex adaptive systems theory is the message of the Hippocratic Oath: First, do no harm… to your future! When an organism's future is uncertain, its most pressing adaptive problem has always been making sure that it *has* a future. Avoiding fitness cliffs is downside risk protection; it is the minimax strategy of minimizing the maximum possible damage that can be done. Evolutionary theory's assumption of optimality[11,12] justifies the expectation that selection will tend to favour mechanisms for reducing the risk of lineage extinction in risky and uncertain environments.

We come thus to the tradeoff between current and future reproduction, also known as the General Life History Problem.[5,13] This is a model that predicts an organism's optimal reproductive strategy based on the assumption that there is a tradeoff between current and future reproduction—that is, on the assumption that beyond some threshold, increased reproduction in the short term (current reproduction) is expected to decrease number of descendants in the long term (future reproduction). This can happen for two reasons: (1) because resources consumed for current reproduction would have had greater fitness returns if they had been consumed in the future, or (2) because current reproduction reduces parents' probability of survival into the future. The upshot (and another major difference from earlier evolutionary models) is that selection is no longer expected always to favour mechanisms that simply maximize number of offspring in the short term. This is because consistently producing a small number of offspring of high reproductive value (i.e. high probability of reproducing themselves) can result in more descendants than having a larger number of offspring with low reproductive value (because of reduced intergenerational variance in number of offspring; see Figure 1).

In risky or uncertain environments, however, parents often lack the capability—the material or social capital—to make much difference in offspring reproductive value (health, nutrition, safety, education etc.) Throughout evolution the optimal reproductive strategy under such conditions would generally have been the short-term strategy of maximizing current reproduction, for by maximizing the probability of having *some* offspring who survived and reproduced, organisms minimized the probability of lineage extinction. This is the crux of bet-hedging theory.[4] The take-home message from the General Life History Problem is that contrary to a great deal of popular wisdom, under risky and uncertain conditions producing offspring at an early age and/or a high rate, and investing minimally in each one, *can* be the optimal reproductive strategy.[14–18]

The cost of reproduction

Reproducing at an early age and/or high rate, however, can exact heavy costs, for in order to reproduce, organisms must not only survive, but grow and develop as well. Indeed, fitness itself, although it is *measured* in reproductive terms, actually *consists* of survival, growth and development, and reproduction, which are forms of work. Fitness may thus be thought of as the work that needs to be done to leave descendants.[19] And work, as we know from the Second Law of Thermodynamics, requires resources, which sooner or later are always limited. In the meantime, natural selection presses on inexorably for *greater* fitness (fitness always being relative). This fundamental tension between life's means (limited resources) and ends (unremitting selection for greater fitness—or *continuing* fitness) requires tradeoffs: something has to give. Everything else being equal, when the future is risky and uncertain the optimal reproductive strategy is to take whatever resources are available and quickly convert them into offspring. The cost of maximizing current reproduction may be shocking ill health and shortened lives, for both parents and offspring. But from an evolutionary perspective (i.e. that of continuing), this may be a cost that organisms at the edge of a fitness cliff cannot afford not to pay; extinction, as they say, is forever.

The impossibility of reconciling the conflicting ends and means of life is the rationale for evolutionary theory's bedrock assumption of optimality. We expect that natural selection will tend to favour phenotypic mechanisms that allocate limited resources among the various components of fitness (i.e. the
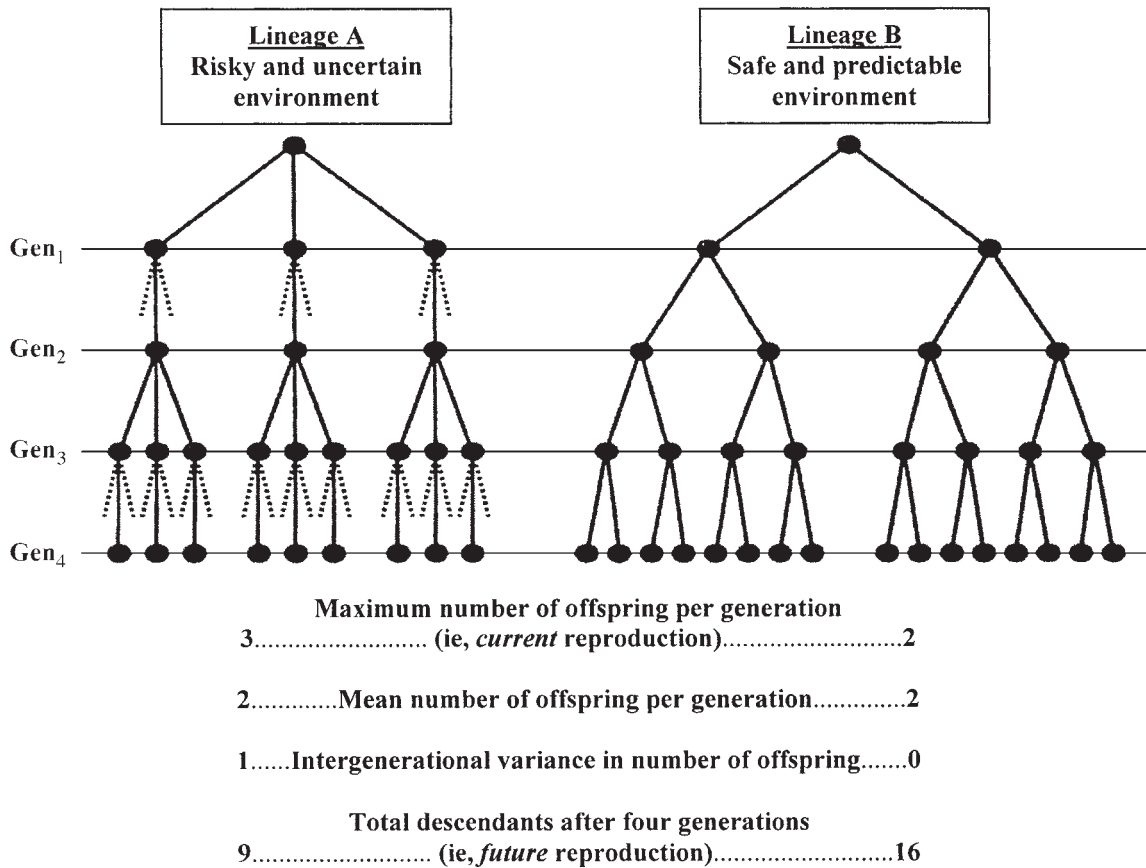
Figure 1 Schematic representation of the General Life History Problem. The diagram depicts the reproductive success of two hypothetical lineages over four generations. Lineage A occupies a risky and uncertain environment and consequently suffers high mortality (dotted lines ending without issue). The optimal reproductive strategy for members of Lineage A is to maximize *quantity* of offspring each generation (*current* reproduction), for this minimizes risk of lineage extinction. Lineage B, on the other hand, occupies a safer and more predictable environment, so all of its offspring survive and reproduce. Facing no immediate threat, the optimal reproductive strategy for members of Lineage B is to maximize the *quality* of their offspring. Even though Lineage B produces only two offspring each generation (versus three in Lineage A) their higher quality means that they are more likely to survive and reproduce. Consistently producing a small number of high quality offspring reduces the between-generation variance in number of offspring who survive and reproduce. Over time this results in more descendants (*future* reproduction) in Lineage B than Lineage A. This consistency, however, comes at the cost of high parental investment. Investment in children increases their social capital.

work of life) in the way that results in the most descendants— but emphatically *not* just in the next generation, for complex adaptive systems are all about continuing *indefinitely*. It follows then, that people, like all complex adaptive systems, are not evolved to maximize health, wealth, happiness, lifespan, vigour, power, prestige, beauty, love, sex, truth, honour, reason or anything else, but to have descendants, which is continuing. It follows, too, that if people, like all complex adaptive systems, find themselves in risky and uncertain environments that threaten their capacity to continue—to leave any descendants at all—we should not be surprised to find that their limited resources are not always allocated to improving their health, wealth, happiness, lifespan, vigour and so forth, or even that of their children. On the contrary, because complex adaptive systems are all about continuing, when people lack the material or social capital to limit risk and uncertainty or to make a difference in their children's reproductive value, their optimal

reproductive strategy will often be to maximize current reproduction—even at the cost of ill health, despair and shortened lives.

The bottom line is that in the face of too much risk and uncertainty optimality can entail pathology. This is because (*ceteris paribus*) the optimal reproductive strategy in the face of chronic risk and uncertainty is to maximize current reproduction. One way to maximize current reproduction is to minimize age at first reproduction. This may help to explain why young women in the world's most disadvantaged societies often have high rates of reproduction (despite generally worse health and nutrition). For example, The Alan Guttmacher Institute[20] (pp.48,52) recently provided data for 18 nations on the proportion of women between the ages of 20 and 24 who gave birth before they were 18 and the United Nations Human Development Index. The HDI is a number which combines three measures of a nation's quality of life: average

life expectancy, years of education, and income; in this sample it ranged between 0.94 (in the USA) and 0.36 (in Bangladesh). The association between early childbearing (which maximizes current reproduction) and HDI (which reflects environmental risk and uncertainty) is highly negative (Figure 2). This is what we would expect if *Homo sapiens* (like other complex adaptive systems) was predisposed to maximize current reproduction in risky and uncertain environments.

Actually doing so, however, entails diverting already limited resources away from the other components of fitness—survival and growth and development (i.e. health, longevity)—and allocating them instead to reproducing early and/or often. How is this done? By what phenotypic mechanisms are risky and uncertain environments identified and resources diverted from future health and longevity and allocated instead to current reproduction? If ill health and shortened lives are the cost of reproducing in the face of risk and uncertainty, as optimality theory suggests, then understanding these mechanisms could have significant public health implications.

One such mechanism is surely the hypothalamic-pituitary-adrenal (HPA) system, which mediates the body's responses to environmental stressors. In chronically risky and uncertain environments the HPA system is chronically active, resulting in prolonged high glucocorticoid levels, with many long-term negative effects on health.[21–23] But what activates the HPA system? How does the body recognize risk and uncertainty? Are all kinds of risk and uncertainty the same? Questions such as these underlie the proposition that the attachment process may be part of a mechanism linking risk and uncertainty, social capital, reproduction, and health.[19]

Attachment theory is an evolutionary theory of the origin and development of individual differences in the subjective experience and internal, mental representation of self and others in close emotional relationships.[24] The major dimension of individual differences in attachment is secure versus insecure. Secure individuals are more likely to have had a history of warm, responsive, and sensitive social relations with others, beginning in infancy. As a consequence they tend to have secure (positive, hopeful) 'internal working models' (mental images and expectations) of important social relations. Insecure individuals tend to have had fewer such relations, thereby developing insecure (anxious, fearful) internal working models of important social relations. Individual differences in attachment security develop in infancy and, barring significant environmental changes, affect romantic, sexual, and parenting relationships in adulthood.[25–27] In keeping with Belsky's[28] original proposal, theory and evidence increasingly suggest that the attachment process is an evolved 'switching' mechanism for entraining the development of alternative reproductive strategies.[19,29]

In effect, the attachment process registers social-emotional risk and uncertainty. Secure individuals, with a history of warm, responsive, sensitive social relations, may be said to have accumulated more social capital than insecure individuals. But this is more than a metaphor, for secure attachment has been shown to buffer children against HPA system activation, apparently because attachment behaviours like cuddling, nuzzling, stroking, and sucking release oxytocin, which reduces cortisol levels.[30–33] This 'anti-stress' effect of warm, sensitive, responsive caretaking may also help to explain the increasing evidence that early psychosocial stress is related to early menarche,[34–39] for chronic HPA activation is believed to accelerate activation of the hypothalamic-pituitary-gonadal (HPG) system, which mediates the onset of puberty.[40–42] In risky and uncertain environments there will tend to be more frequent HPA activation and less consistently warm, sensitive and responsive caretaking. And in such environments, as we have seen, the optimal reproductive strategy is often to reproduce early.

Homo sapiens is not well adapted to inequality

Inequality may also be bad for our health because we are not well adapted to it. This is the intriguing possibility being raised by a disparate group of anthropologists, economists, philosophers and biologists exploring the nature and origin of our capacity for cooperation and egalitarianism. It now seems that the evolution of human social behaviour was characterized by a great, even profound disjunction. Whereas both non-human primate societies (from which we are separated by 5 million years) and modern agricultural and industrial societies (which emerged 10 000 years ago) are characterized by more-or-less obvious dominance hierarchies, existing hunter-gatherer societies tend to be highly egalitarian, with good social capital, in the sense that essentially all social relations are between equals. (This may be more true for males, however.[43,44]) In most hunter-gatherer societies, even if they want to, no individual can rise much above others, to seem better than others, to treat others disrespectfully. This is because no individual can afford to risk alienating others and have them withdraw from exchange relations. Social security and life itself are critically dependent on the reciprocal exchange of everything of value. Just where people place each other in the scale of social relations therefore has a major impact on social and emotional life. Hierarchical social relations are minimized because those who attempt
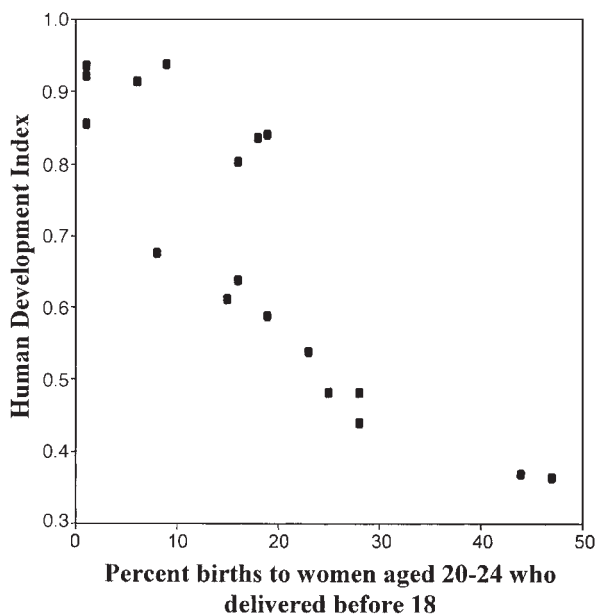

Figure 2 Relationship between United Nations Human Development Index and per cent total births to women under 18 years old in 18 countries (r = –0.87; P < 0.001)[19]

to dominate others are resisted by coalitions of subordinates ('reverse dominance hierarchies'[45]) whose natural loathing of being dominated makes them collectively dominant. Minimizing hierarchical social relations maximizes equality.

Reverse dominance hierarchies were not possible until our hominid ancestors evolved the cognitive-emotional capacity for social exchange and cooperation. If we make the common assumption that the subsistence patterns and social organizations of existing hunter-gatherers are not unlike those of our hominid ancestors, then these reverse dominance hierarchies suggest that inequality was not a major source of risk and uncertainty in the social environments in which *Homo sapiens* evolved.[1,45–51] Since the origin of agriculture, however, and perhaps increasingly in modern times, inequality has been a pervasive source of risk and uncertainty.[52–57]

Thus, on top of the empirical evidence *that* inequality is bad for our health[58–62] we now have an explanation in principle of *why* it is bad: because the optimal reproductive strategy under conditions of inequality is likely to entail tradeoffs in the form of ill health and shortened lives. In addition, because reverse dominance hierarchies tend to minimize inequality it may not have been a major selective force during hominid evolution, suggesting that we are not well adapted to it today. We believe that in explaining in principle why inequality leads to disease our only scientific theory of life has implications for health policy. For example, Kawachi *et al.* claim that 'there is no good theoretical account of how to build social capital.'[61 (p.1497)] On the evolutionary logic advanced here, strategies for building social capital should aim at maximizing the number of people whose subjective experience of risk and uncertainty is sufficiently low that their naturally contingent predispositions to set the stage for the future are given the fullest possible expression.

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