Evolutionary Psychology and Development Economics

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Abstract. Contemporary development economics have provided much empirical evidence to suggest that democracy and other institutions that promote equity are good for growth and development. Why should this be the case? In this paper it is argued that Evolutionary Psychology (EP) can greatly enrich development economics, specifically in adding to our understanding of the micro-foundations of the family unit and the explanations of long-run economic growth and development. In this paper, emphasis was placed on the evolutionary foundations of the family unit, on the understanding of human co-operation, and how these result in institutions, such as monogamous family units with positive male parental investment, where a switch from preference for quantity of children towards the quality of children leads to improved technology and learning. Given that monogamy is more prevalent in a more egalitarian society, institutions such as democracy and an equality sensitive state may have biological roots. Human mate choices influence co-operation, conflict and competition, and the existence and nature of the family unit depend on such biologically determined choices. In particular, the argument is made that human choice, competition for mates, and the resulting sexual selection, lead to different forms of pair-bonding such as monogamy or polygyny. Each of these has different institutional repercussions, with different development outcomes since the family / kinship environment in which children grow up may have important implications for technology adaptation, innovation and learning.

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JEL Classification Numbers: E11, O11, O3

"Human beings are animals…we are governed by the laws of biology, and even our thoughts and emotions are the result of electrochemical processes in the brain"
- (Scruton, 2004:18).

"In a strict sense, all economic activity must involve the human brain" - (Camerer, Loewenstein & Prelec, 2004 : 555)

1. INTRODUCTION

Economics can benefit from the insights of Evolutionary Psychology (EP). Economics is still, to a large degree, suffering from a lack of consistency and multidisciplinary compatibility with other behavioural and social sciences as well as the natural sciences. How can such greater consistency be achieved? This paper argues that development economics could benefit from greater use of the insights of EP, especially with regard to the theory of long-run economic growth and development. The paper contributes by adding to the small but growing number of contributions that highlight the need for economics to be more consistent with biological evolution. The dominant tradition in evolutionary economics is to focus on complexity and technologically induced change, following Nelson and Winter (1982). As such, evolutionary economics focuses more on economic dynamics than on the economic actors and their institutions as the results of biological evolution. Two recent and important contributions that have started to shift the focus towards economic actors and their biology are Van den Bergh and Gowdy (2003) and Robson (2001). The former addresses the micro-foundations of macro-economics and the relevance of biology, whilst the latter deals extensively with the issue of preferences. Preferences may not be treated usefully in micro-economics. In the economics of the household, preferences are assumed to be given (exogenous), and fixed, without specifying the mechanisms through which these preferences are shaped. Consumers are assumed to maximize expected utility subject to (budgetary and other) constraints. Most of these assumptions have been shown to be tenuous in recent years, through large numbers of empirical and experimental studies (see also Robson, 2001). The problem is partly that economics attempts to explain "how" the household functions without understanding "why' households exhibit the behaviour and preferences that they do.

This paper adds to the above mentioned literature by arguing that evolutionary psychology (EP) can provide important insights into answering this "why' question of preferences. Moreover, given that the there is a rich tradition of "psychology" in economics wherein it will not be novel to argue why and how preference are established, and also given the fact that the idea that economics can be improved by giving attention to the psychology of choice is not new, the present paper attempts to contribute by showing how EP can be important to provide a link of economic development thinking with biology (and go beyond mere psychology as is exemplified in research published in such journals such as Journal of Economic Psychology and Journal of Socio-Economics. At the minimum, any theory of economic growth and development must be consistent with biological evolution. In this, the paper attempts to support the relatively modest, but growing, literature on evolution and biology in economic development, for example such as Galor and Moav (2002), Zak (2002), and Camerer, Loewenstein and Prelec (2004). It also aims to complement growing literature on the implications of EP for other branches of economics and management (see e.g. Ben-Ner & Putterman, 2000; Earl & Potts, 2000; Hoffman, McCabe & Smith, 1998; and Kazanawa, 2004)

The paper is structured as follows: Section 2 provides a short background on the relevance of biology and EP for economics as a science. In section 3, the concept of evolution is introduced (it is assumed most economists are unfamiliar with the basic tenets of evolutionary theory). In section 4, the contribution of Evolutionary Psychology is discussed with specific references to its applicability in illustrating how co-operation and conflict on the level of the

household can provide micro-foundations for understanding institutions. Section 5 draws some implications for answering the question as to the explanations of the features of growth and development posed in section 2. Section 6 concludes.

2. ECONOMICS, BIOLOGY AND EP

Economics studies the behaviour of people, as they interact as consumers, firms and other organizations within particular institutional frameworks. If economic theory is to offer consistent explanations of long-term economic growth and development, it ought to be more consistent with other fields of social and natural sciences, especially psychology, sociology, anthropology and other behavioural sciences. Moreover, economics ought to be more consistent with biology, specifically evolutionary biology. Evolution by natural selection, as put forward in the Neo-Darwinian Synthesis, offers a framework for integration of economics on the one hand with biology and on the other hand. This is perhaps obvious, since human behaviour sciences must ultimately be consistent with human beings' biological nature[1] (Robson, 2001:11). Hodgson (1999:74) has pointed out that ideas from biology are relevant to economics because both economic and biological systems are complex, involve continuous change and contain wide variety.

In economics, this need to have roots consistent with biology has been expressed in various forms since the early days after Darwin published his "Origin of Species" in 1859 (Hirshleifer, 1977). Alfred Marshall claimed that "the Mecca of the economist lies in economic biology" (Marshall, 1949:xii) and Thorstein Veblen posed the question "Why is economics not an evolutionary science?" (Veblen, 1898). Despite these insights, development economics appears to be largely isolated and distanced from biology and evolution. With the formulation of the Neo-Darwinian Synthesis in the late 1940s, and the discovery of the structure of DNA in the early 1950s, there were a number of economists and others who started to see the implications for the social sciences. In 1951, Tinbergen argued that some of human behaviour may be instinctive. Alchian (1950), Enke (1951), and Penrose (1952) are amongst those who broadly explored various implications of evolution by natural selection for broad economic systems. For an extensive review see Hodgson (1995).

Although Darwin's (1859; 1871) theory of evolution by natural and sexual selection was originally developed to explain the evolution of biological organisms, the theory has a more general application, particular to the social sciences and humanities – and to development economics as this paper argues. Indeed, over the past decade there has been a significant growth in the application of evolutionary principles and biology in the social sciences. Natural and sexual selection have, for instance, been fruitfully applied over the past decade or so to the study of human culture, to the development of language and computer science, and to the understanding of how the brain functions. In philosophy Karl Popper adopted an explicit evolutionary approach to understand and explain the process through which human knowledge is generated (Popper, 1972). Today, the core of neo-Darwinism (the theory of DNA-based reproduction and evolution) is "*now beyond dispute amongst scientists…the hope that it will be refuted by some shattering breakthrough is about as reasonable as the hope that we will return to a geocentric vision and discard Copernicus*" (Dennett, 1995:20).

Within psychology, it is only recently that the need to root the discipline in human biology has taken off, in the multidisciplinary approach known as Evolutionary Psychology (EP). EP "*seeks to apply theories of evolutionary biology in order to understand human psychology*"

[1] The neo-Darwinian basis is already functioning to integrate the social sciences in many areas, as witnessed in the growing integration and overlaps between areas as formerly diverse as evolutionary biology, cognitive science, behavioural ecology, psychology, hunter-gatherer studies, social anthropology, biological anthropology, primatology and neurobiology.

(Tooby & Cosmides, 1992). EP offers much to economics, and vice versa; EP also contributes towards raising the standards of psychology as science, in view of the recognition by Trivers (2002: 257) that (standard) psychology is "not, in fact, a real discipline, but rather a competing set of hypotheses about what was important in human behaviour". The biological underpinning that EP provides to psychology thus provides it with a foundation as a discipline, as well as a possible common and consistent foundation with economics. The focus of EP on the human consisting of a complex and modular system of subroutines, called adaptations, for solving problems faced by humans over evolutionary time can be useful, and Potts (2000:196) remarked that "*The very abilities that make an economic system possible are adaptations of the mind*". These adaptations are potentially important in economics since human preferences are generally taken as exogenous in economics.

Given that these preferences are characterized by self-interest, altruism towards kin, and social distinction amongst others, an EP approach may be useful in explaining these preferences as the "selection over time of traits having greater genetic fitness and survival value" (Becker, 1976:826). The relevance of EP in this case for understanding long-run economic development will be shown in this paper to lie in its ability to provide insight on the way human preferences influence co-operation, conflict and competition, and how core institutions such as family units can develop given such human interaction.

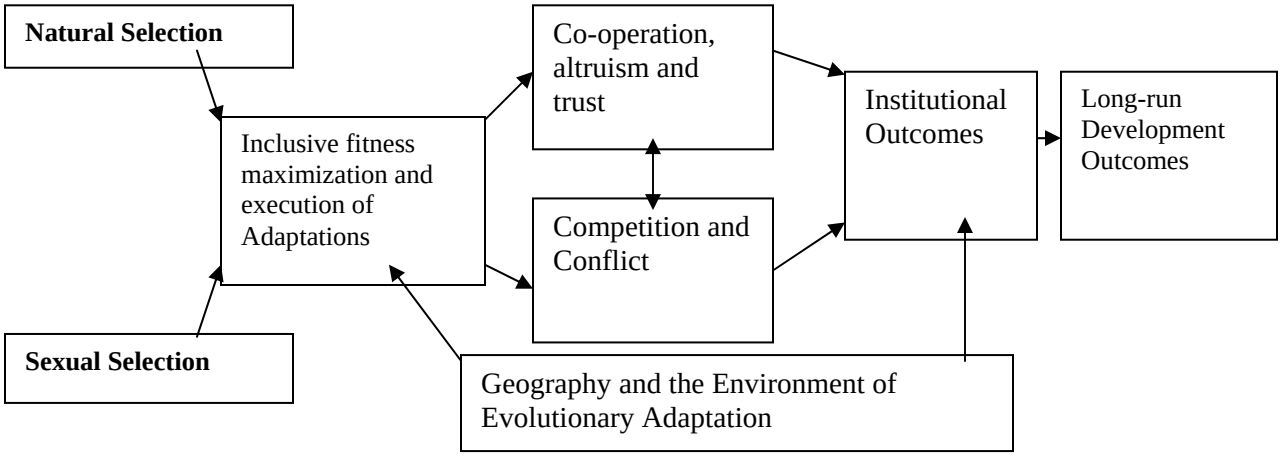
In the current understanding of long-run economic growth and development there is a consensus that institutions matter for economic growth and development, specifically since good institutions are seen to ensure both political stability and good economic policies – in particular policies that encourage and facilitate investment and innovation (North, 1991; Acemoglu, 2003). A key "institution" vital for economic growth and development (through, for instance, technological progress) is property and contract rights (Keefer and Shirley, 2000; Rodrik & Subramanian, 2003). The security of property and contract rights is reflected in a country's governance. The World Bank has identified more than 300 indicators of various aspects of governance[2]. According to Kaufman et al (1999) these can be categorized under headings such as voice and accountability; political stability/lack of violence; government effectiveness; regulatory framework; rule of law and corruption and graft.

From the types of categories that define governance, it can be concluded that good institutions can only exist where there is co-operation and trust in a society. It can also be seen that mechanisms to regulate and mediate conflict and competition in society are important. How do co-operation and trust come about? How can conflict and competition be harnessed for economic growth and development? Unless there is greater unity and consistency between the social sciences, and between economics and natural sciences, the ultimate explanations for economic growth and development might not be properly understood. In particular, by using evolutionary sciences such as evolutionary biology and evolutionary psychology, more consistent underpinnings for economic development can be provided.

The thesis of this paper, which will be elaborated below, is depicted in the following diagram.

[2] See www.worldbank.org/wbi/governance/wphtm#governance

Diagram 1: Relationship between evolution and economic development outcomes



In Diagram 1, evolution by natural and sexual selection applied over human populations generates "inclusive fitness" maximization (concepts will be explained below) and human brains consisting of domain-specific modules of adaptations to the problems frequently encountered by humans over the period known as the Environment of Evolutionary Adaptation (EEA). Given this EEA, humans developed adaptations towards co-operation, apparent altruism and trust, all of which are important to generate gains from trade and specialization - key requirements of economic development. Evolutionary Psychology (EP) is the social science that studies these elements of human adaptations, and is clearly important for providing foundations for the science of economic development.

However, given that resources are scarce, humans also have adaptations for conflict, for competition and for selecting amongst strategies (say between co-operation and conflict) the most appropriate for the circumstances. Even in apparently co-operative ventures such as the family unit there are always underlying tensions and conflicts, as will be shown later. This is why game theory, the field of economics development that models human strategic interaction and which is fruitfully used in evolutionary biology (see e.g. Maynard Smith, 1982; Sigmund, 1995; Sigmund & Novak, 2000) is important in understanding the balance between conflict and co-operation, and in understanding that positive economic development outcomes are by no means guaranteed, nor necessary, dependent on the absence of conflict and competition. The institutions that come into being to harness this interaction with positive results should be institutions that recognize that human behaviour has a biological basis, shaped by evolution, and driven by competition for scarce resources. In the sections that follow, the various elements of this argument will be set out in greater detail.

3. EVOLUTION

Economists do not normally encounter the concepts of evolution by natural and sexual selection in their studies. Therefore, before illustrating how evolution by natural selection can assist explanations of long-run economic growth and development, it may be useful to summarize the concept of evolution and the theories of evolution by natural selection and sexual selection. This section deals firstly with the concept of evolution, and with natural selection. The next section (section 3.2) explains sexual selection and section 3.3 briefly outlines the salient tenets of EP.

3.1 The Concept of Evolution

In 1859 Charles Darwin published an influential book, the result of decades of research. Known as "The Origin of Species", Darwin explained how selective pressures could result in evolution over millennia. Today, evolution is a fact of nature and the theory of evolution by natural selection is one of the most widely supported and accepted scientific theories[3]. Dennett (1995:21) declared that "*If I were to give an award for the single best idea that anyone ever had, I would give it to Darwin, ahead of Newton and Einstein and everyone else. In a single stroke, the idea of evolution by natural selection unifies the realm of life, meaning, and purpose with the realm of space and time, cause and effect, mechanism and physical law*".

Darwin was much influenced by economists such as Thomas Malthus and Adam Smith. The former focused on resource scarcity and the resulting competition for scarce resources. Malthus recognized that for most of humanity's existence, it lived close to the survival income level – an era sometimes described as the "Malthusian trap". Adam Smith invoked an "invisible hand" to explain how beneficial market outcomes can arise spontaneously through self-interest and competition. Both of these ideas have important mirrors in evolution by natural selection. This is because, in nature, given that there is competition for scarce resources and that only those with access to resources survive and leave offspring, one can expect that if there is some trait or behaviour that a gives its possessor some advantage in gaining resources, this trait will dominate in subsequent generations.

Evolution by natural selection is thus a very simple and intuitive explanation. One only needs competition for scarce resources, replicating entities, traits that can be passed down generations, and a mechanism, such as mutation, for creating variation in traits[4]. This elegant and parsimonious mechanism – described by Dennett (1995) as an algorithm - is responsible for complexity. As humorously noted by Atkins (1981) "*Once molecules have learnt to compete and to create other molecules in their own image, elephants, and things resembling elephants, will in due course be found roaming through the countryside*".

While it was clear to Darwin and his contemporaries that offspring resemble their parents, i.e. there was inheritability; they were unclear as to its mechanism, being unfamiliar with genetics. In the early 20th century, Mendel's discovery of the genetic basis of inheritance provided this mechanism, and the discovery of the structure of DNA in 1953 by Crick and Watson provided a vindication of Darwin's theory. The synthesis of Mendelian genetics and Darwinian selection is known as the "Modern" or neo-Darwinian synthesis. It is the contention of the Modern Synthesis that slow, gradual, cumulative natural selection is the ultimate explanation for human existence (Dawkins, 1976:392).

Initially, the group as the unit of "selection" (upon which evolution acts) was not clearly excluded by early evolutionary writers. Only after it was made explicit by Wynne-Edwards did a number of scientists point out that it was fallacious. Thus, following contributions by Hamilton, Williams, Trivers, Maynard Smith, Dawkins and others, it is now widely accepted that the unit of selection is the gene. It is therefore not *per se* the survival of the particular individual organism (or its phenotype) that drives its behaviour, but the survival of its genotype[5]. This unit of selection

[3] In order to make the point that evolution (like, for example, gravity) applies universally, Dawkins (1976:1) remarked that "If superior creatures from space ever visit earth, the first question they will ask, in order to asses the level of our civilization is: Have they discovered evolution yet?"

[4] Although the biological details fall outside the scope of the present paper, it can be noted that genetic variation in any species can be due to mutation, genetic drift, recombination and gene flow (see Colby, 1996:5-6).

[5] Before the genetic basis of inheritance was understood, it was though by some that an organism could pass on its acquired characteristics to its offspring. This was known as Lamarckian evolution after Lamarck

is therefore reflected in the most widely accepted definition of evolution. This definition being a "change in the gene pool of a population over time". Natural selection is defined as the "differential reproductive success of pre-existing classes of genetic variants in the gene pool" (Colby, 1996:1,6). In the following sections on understanding co-operation and altruism in human behaviour, this will have important implications such as the concept of "inclusive fitness" that will be discussed in greater detail.

Evolution by natural selection cannot be seen as a purposeful process with any foresight. It is a principle of local adaptation, not of general advance or progress (Gould, 1994:92). There are two main arguments to support this notion. The first is that mutations are random which implies that it is not systematically directed towards any improvement (Dawkins, 1986:393). Secondly, evolution does not necessarily lead to optimal or "superior" outcomes. Biologically, the human body is characterized by numerous design errors and leftovers from evolutionary adaptations in the past (see Williams, 1996). From an economics point of view, it would be wrong to assume that an evolutionary approach to economics must necessarily favour a "laissez-faire" system or otherwise (Hodgson, 1999:75). It may also be wrong to assume that human life and society are the aims of evolution, or to depict humans as the pinnacle of evolution.

The principle of evolution by natural selection is not only useful in explaining biological diversity and change, it can be generalized to any setting where (a) units or entities can replicate, (b) the replication process is sometimes faulty, (c) there is competition for scarce resources (so that those with access to resources leave more offspring). Dawkins (1989) called this "Universal Darwinism" and its principles are today applied in as diverse fields as computer programming and cultural studies. In the latter regard, perhaps useful for economists to note, is the extension of the principles of evolution by natural selection from units such as DNA (genes) to bits of information transferred through human communication and interaction, known as "memes" – see e.g. Dennett (1995) and Blackmore (1999). Memes may have a large role in explaining most of human's unique behaviour such as our large brains and intellect. Research on memes is still in its infancy, but is seems to have promising applications in economics, marketing, and the social sciences in general (see e.g. Ball, 1984; Brodie, 1986; Lynch, 1991; Marsden, 1998; Henson, 2002). More recently Camerer, Loewenstein and Prelec (2004) and Zak (2004) amongst others, have been arguing the case for a "neuroeconomics", stating that "A key step is to think of human behaviour as resulting from the interaction of a small number of neural systems" (Camerer, Loewenstein & Prelec, 2004:575).

3.2 Sexual Selection

In 1871 Charles Darwin published the "Decent of Man" which contained the theory of sexual selection. This theory explains why certain traits evolve that do not, at first sight, seem to offer any advantages for survival – in fact some traits evolve and are passed on that seem to hinder survival. The well-known example is the peacock's tail, which is a huge and colourful display, but which can serve to attract predators, and does not even assist in flying, feeding, hiding or any other obvious act of survival (Barkow, 1989).

The solution to this apparent puzzle is that it is not sufficient for an organism or animal to merely survive: it must also reproduce for its genes to pass into the next generation. Sexual selection can therefore be defined as natural selection operating on factors that contribute to an organism's mating success (Colby, 1996:9). Gangestad and Simpson (2000:3) define sexual selection as "differential reproduction among individuals due to differential advantages in mating". Ridley (1993:19) argues that where survival and reproduction conflict, it may often be

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(1809). It is often posited that Lamarckian evolution may be relevant in economics where firms can pass on the benefits of R&D and technological advances over time.

reproduction that will dominate[6]. A trait that therefore increases reproductive success, like the peacock's tail that entices females to mate, may spread under certain circumstances even if it threatens survival (but as long as the reproductive benefits outweigh the survival costs).

This insight may be relevant for understanding much of human behaviour. In human societies, as in many other animal societies, males and females compete for access to mates. Mate choice, i.e. the preferences by males for females and by females for males, can therefore act as evolutionary driving force for the development of particular traits, behaviours and preferences. For instance, over evolutionary time males who were predisposed to actions that put their survival at risk but increased his chances of acquiring or retaining a mate, will have left more offspring, and those without this predisposition, would not. As a consequence we will find this predisposition in males today, all males alive today being descendants of males who where successful in mating. Although the implications of such risky behaviour will be dealt with later, it should be noted that sexual selection would drive competition for access to mating resources – i.e. a mate – in a similar fashion as natural selection. In many animal species, given the relative scarcity of female eggs versus male eggs, access to a female becomes the scarce resource for which males will compete. Because this competition by males for females is mediated by females (who choose amongst the competitors to mate), the female choice will drive male traits. An example of sexual selection in practice is that in polygynous species (where a few males monopolize all the females) sexual selection has led to significant sexual dimorphism[7] (Bakker & Pomiankowski, 1995).

Sexual selection means that the mate preferences of males and females may matter. For example peacock's colourful tails would eventually disappear if it were not attractive enough to entice a female of the species to mate. The question has been raised why females would prefer certain traits and behaviours to others? The so-called "Good Genes Model" states that females are partial to behaviours and traits that indicate or reflect some component of a male's genetic fitness. In humans, fluctuating asymmetry (FA) is seen by some scientists as the best marker for genetic fitness[8] (e.g. Gangestad & Simpson, 2000:12) although this may be a controversial issue, especially on how heritable FA is. This implies that men with greater symmetry would (a) have more sexual partners, (b) more extra-pair partners and (c) be preferred as women's extra-pair partners. Empirical evidence seems to support these predictions. For instance Thornhill and Gangestad (1994) and Thornhill and Gangestad (1997) find that more symmetrical men reported more lifetime partners than less symmetrical men and that they have a larger number of extra-pair sex partners. Waynforth (1998) finds that more symmetrical men have higher levels of fertility. This is corroborated by Moller and Thornhill (1998), who find from a meta-analysis of various similar studies that, on average, more symmetrical males have greater mating success.

Female preferences extend beyond good genes. Given the burden of giving birth and raising a child females have evolved preferences for males who are more likely to stay with them after insemination and help raise the offspring. This is known as male parental investment and will be discussed at greater length below. This implies that females will have preferences that focus not just on good genes, but also for attributes that signal qualities of a potential good provider, such as status and resources (they need not be all found in one mate). Another implication is that, given costly communication and possibilities for false signals (false

[6] It must be added here as a qualifier that current reproduction does not always trump survival, since organisms often benefit from delaying reproduction. The reproductive benefits of traits must outweigh the survival costs.

[7] Although it must be recognised that size dimorphism could persist through male-male competition even if female preferences are not involved.

[8] FA is measured by the symmetry on bilateral features such as foot width, ankle width, hand width, wrist width elbow width, and ear width and ear length. FA is seen as a good marker for genetic fitness, as it can be affected by mutations and diseases (Moller & Thornhill, 1998).

advertising) by males, females would have an evolved tendency to be more hesitant or careful than males before mating (Clark & Hatfield, 1989).

These female mating preferences give rise to both short-term and long-term mating strategies in females. Obviously, for more long-term mating, resources and the ability of her partner to provide for her offspring will be the important criteria. For short-term relationships, one can expect women to place greater emphasis on a man's physical attractiveness and physique. Empirical evidence to support these implications is reported by Baker and Bellis (1995) and Baker (1996) and Gangestad and Thornhill (1998). So when will females prefer a short-term to a long-term mating strategy and vice versa? A number of recent studies deal with this question (e.g. Gangestad, 1993; Low, 1990a; 1990b; Kirkpatrick and Ryan, 1991). The answer is that environmental circumstances have a determining impact. For example, in an environment where pathogens are more widespread (making good gene hunting important), and where women have more own resources, short-term strategies would tend to dominate and one would see a greater tendency towards polygynous forms of marriage (Low, 1990). Empirical evidence again supports this notion, with polygynous marriage more prevalent in regions with more health risks. In a more modern setting, the implication of females' evolved mating strategies would suggest that the more women participate in the economy and workplace and obtain more resources, that the more importance they will attach (without however, consciously thinking about it in this way) on good genes in their mate choice. In such an environment they will be more likely, on average, to engage in short-term and extra-pair mating (Gangestad and Simpson, 2000:20). Buss (1989) indeed reports empirical evidence that women's mean preference for physical attractiveness in a mate was positively correlated with the proportion of women who were involved in the economy.

Many human traits and economic behaviours and preferences can thus be explained by sexual selection. Sexual selection determines human mating strategies, which are often at the core of marital breakdowns, family dysfunctionality, and crime. It may also be vital to understand human culture, including art, music and language. Miller (1993) and Baum (1996) have proposed that the human intellect itself is a product of sexual, rather than natural, selection. In this view, the human brain is used to court and seduce members of the other sex (Ridley, 1993:33). Miller (2000) further argues that music, like language, is an adaptation due to sexual selection.

To conclude: from a consideration of sexual selection it is clear that different traits and predispositions in a species must have not just survival value, but also reproductive value in order for an organism or animal to pass on its genes successfully into the next generation. The term "fitness" is often used in reference to any trait to denote that such a trait's survival and/or reproductive advantages outweighs its biological and other costs (Miller, 2000:333). When such a trait promotes the genetic fitness of an organism (as against its specific phenotype) it is known as "inclusive fitness". Inclusive fitness can explain co-operation and altruism, as will be shown below.

3.3 Evolutionary Psychology

Evolutionary Psychology (EP) departs significantly from the still widely adopted "Standard Social Science Model" (SSSM) wherein human nature is seen to be unimportant, and where the human mind is seen as a "completely blank slate that is written on by culture and one's own experience" (see Tooby & Cosmides, 1992). The SSSM is often implicit in economic development theories, where differences in economic development outcomes between countries and regions are seen mainly the result of environmentally influenced "institutions". EP, by incorporating evolution by natural and sexual selection, is potentially much more useful as an approach to provide "ultimate' explanations in economics. This is against the "proximate" explanations more prevalent in the SSSM and current economic development thinking. For instance, in economics, Hausman and Rodrik (2003) and Rodrik and Subramanian (2003) argue

that "policies" are a proximate cause for economic development, and that "institutions" are the ultimate cause; in those institutions generate various policy decisions. Institutions may not however, be the ultimate cause, but rather human biology.

Ultimate explanations are also related to the quest for explaining the universality and persistence of social and economic phenomena (see Kenrick & Simpson, 1997). This is obviously very important for understanding why certain societies are economically more complex than others in certain respects, and is also important for illuminating the field of history, as by Diamond (1997) and Wright (2000).

Having defined EP, it is necessary to describe the main points of departure of EP. A key insight is that the human mind – and much else of human biology – is the result of evolution by natural and sexual selection. For the most part, given the slow speed of evolution, the evolution of human biology and the human mind took place during a period, which EP describes as the "Environment of Evolutionary Adaptation" (EEA)[9]. The EEA coincides with archaeological evidence of the Pleistocene era (Foley, 1996). In this EEA, humans faced a number of recurring problems that needed to be solved in order to ensure their survival. These included finding food (resources), finding a mate, procreating, raising children, co-ordinating and communicating activities with other humans. To solve these cognitive problems, the human brain evolved certain psychological adaptations, which result in what is known as human nature (Neuroeconomics emphasize that a notable feature of the human brain is its modularity, see e.g. Camerer, Lowenstein & Prelec, 2004:559). Consequently, EP posits that the human mind is a massively modular system comprising many domain-specific inference mechanisms (or subroutines) for solving the problems that confronted human ancestors during the Pleistocene (Buss, 1995). Potts (2000:196) points out that this suggests that humans may in fact have more instincts than other animals, and not fewer as is commonly thought.

Humans only ceased the hunter-gatherer way of life and started living in large-scale, permanent settlements very recently, generally following the invention of agriculture some 12 000 years ago. As a result, the information-processing algorithms that human minds possess today have been shaped by their ancestors between 200 000 and 12 000 years ago and may be mismatched with the current environment facing humans (Emlen, 1997:568). This mismatch is also termed that "adaptive lag" in EP. Given such an adaptive lag, EP casts a critical light on the standard assumption in economics of a rational economic agent maximizing some objective function, such as expected utility[10]. Evolutionary psychologists point out that human behaviour consists rather more of the execution of mental modules (i.e. people are adaptation executers)) shaped by natural selection in the EEA, than consisting of fitness maximizing behaviour (Cartwright, 2000). People may not therefore be rational optimizers as economic theory assumes, and according to Cosmides and Tooby (1994:330) even models of bounded rationality and heuristics "do not seem to capture adequately the distinctive organization of human reasoning". Camerer, Loewenstein and Prelec (2004:560) also cast doubt on the assumption of rationality pointing out that many brain processes are automatic parallel, rapid processes that occur without awareness, so that people may "genuinely not know the cause of their own behaviour".

Smith, Mulder and Hill (2000) indicate that fields such as Human Behavioural Ecology (HBE) compliments EP. HBE uses game theory to explain variation in human behaviour as a function of ecological and social context, with various adaptive trade-offs aimed at fitness

[9] EP is often criticized for its description of the EEA, of which our knowledge remains sketchy (Fleoy, 1996).

[10] In standard microeconomics the economic agent does not posses a mind. Rather it is rational and able to learn all actions and process all information. The economic agent either maximises utility (as in Bethamite utilitarianism) or he/she is a Bayesian agent with rational expectations. Experimental economics (and real life) are however filled with cases where people do not act in accordance with these assumptions (see also Campbell, 1986).

maximization. HBE has importantly drawn from animal biology, especially from biologists who have studied the foraging decisions of animals. Risk-Sensitive Foraging Theory (RSFT) is a contribution from HBE, which may hold important implications for both human behaviour and development economics. RSFT does not assume that animals are trying to maximize expected utility: rather animals are modelled as trying to maximize the probability of reaching a goal. With this, it is not just expected value that determines decision-making, but also the variability in returns from different options and the animal's aspiration level. Rode (1999) has applied these insights into human behaviour and proposed that the human mind has been designed by natural selection to take expected value, variability and aspiration level into account when deciding among choices. According to Rode (1999) this can then explain the apparent irrationality of human behaviour as, for instance, when in experimental economics people opt for gambles with a lower expected outcome in order to avoid ambiguity. EP can provide a bridge between economics and evolutionary theory, specifically in that EP recognizes that humans have evolved mental modules (adaptations) that make co-operation, altruism and trust possible.

Finally, a few warnings need to be sounded. In proposing and adopting greater consistency and multidisciplinary approaches for development economics, through making development economics more consistent with biological evolution, a number of possible obstacles or constraints can be envisaged. This is mainly because the ideas of evolution have, ever since Darwin's time, been received with a disdaining knee-jerk reaction in some quarters, and outright hostility in others. Consider the following. As recently as 2004, the Government of Italy considered the banning of the teaching of evolution in schools. Currently, in many countries, there seems to be an almost unofficial ban on the teaching of evolution in schools.

Resistance to neo-Darwinism not only takes the forms of outright banning of the teaching of evolution or of attempting to place notions of intelligent design on equal footing. There are also many misconceptions about neo-Darwinism. For instance neo-Darwinism should not be confused with the wrong and racist "Social Darwinism" of the earlier parts of the 20th Century. Proponents of this so-called "Social Darwinism", who advocated eugenics and the like, made a number of crucial mistakes in understanding evolution. Firstly, they were guilty of the "naturalistic fallacy", which means thinking that an "is" is an "ought". Evolution by natural and sexual selection describes how nature is, *not how it ought to be*. Secondly, they considered evolution to be a process resulting in "progress", which is factually wrong as was made clear in section 3. Evolution by natural selection is also inaccurately described as the "survival of the fittest" where fitness refers to the fastest or strongest or biggest[11]. As was shown in section 3, "fitness" really only refers to the average reproductive output of a class of genetic variants in a gene pool. It has been pointed out that "inclusive fitness" is the proper concept and also that survival is only one component of fitness, reproduction being the other (Colby, 1996:9).

Neo-Darwinism in general, and Evolutionary Psychology (EP) in particular, rejects racism and in fact provides a solid case against any form of racism as well as xenophobia, stressing that cultural and ethnic differences between humans are vastly overstated "*because beneath the existing surface variability all humans share the same set of preference-generating and decision-making devices*" (Cosmides & Tooby, 1994:329). Also, there is sometimes antagonism towards the clearly supported findings in evolutionary biology and EP that males and females differ, not only biologically, but also in their mating strategies, as was shown in this paper. Over evolutionary time, males and females developed different adaptations. It would, however, be a logical mistake to take this as grounds for discrimination, or to infer superiority from difference.

[11] The term "survival of the fittest" was not even coined by Darwin, but used before the publication of his Origin of the Species, by Herbert Spencer.

4. HOUSEHOLD BIOLOGICAL DYNAMICS: CO-OPERATION AND CONFLICT

In section 2, it was pointed out good institutions are at the heart of economic growth and development because institutions facilitate co-operation, trust and altruism. The household or family, a core unit of analysis in economics, provides the biological foundations, not only of trust and co-operation, but also of conflict and competition. Both of these forces, and the balance that society achieves between conflict and co-operation, are essential for long-run economic growth and development. In this section I will first deal with co-operation in section 4.1 and with conflict and competition in section 4.2.

4.1 Co-operation and Trust

In this process, despite competition and conflicts of interest, co-operation appears as a remarkable and ubiquitous feature of human society. Questions such as why humans co-operate, and whether or not human co-operation will spontaneously emerge (as opposed to having being enforced by, say, a Central Authority) are important questions with significant implications for economic development and the choice of economic development strategies. Specifically, institutions such as a system of voluntary exchange based on property rights can only be viable with morality as its basis. Kin-selection, reciprocal altruism and costly signalling theories have all been put forward to explain the biological basis of morality. In this sense, these concepts provide the biological foundations for economic institutions, and indicate how current institutional weaknesses and strengths are the results of natural and sexual evolution. The following sub-sections discuss kin selection, reciprocal altruism and costly signalling.

4.1.1 Kin Selection

Hamilton (1964) developed the concept of kin selection, which is a hypothetical evolutionary mechanism that is driven by particular conditions of inclusive fitness. Kin selection is important in explaining altruism, family relationships and other social behaviours that may seem at first glance to be inconsistent with implications of natural selection (fitness of the individual). Buss (1999) is of the opinion that Hamilton's kin selection theory is the single most important development in evolutionary theory since Darwin's (1859) Origin of Species.

Kin selection theory recognizes that family members have genes in common. For example, brothers share 50% of their genes. In economics, Becker (1976:818) illustrated that if an altruistic act by one brother towards another lowers his own genetic fitness by, say, B-units, but increases his brother's by C-units, then the altruism would increase the expected fitness of his own genes if C>2B. In this sense, altruism raises the fitness of his own genes.

The predictions of kin selection are supported by empirical evidence. Burnstein *et al* (1994) finds for instance that an individual's willingness to assist someone in a life-threatening situation could be predicted by the degree of relatedness to that person. Bossong (2001) finds that the likelihood that one will receive an inheritance from someone else can be predicted by the degree of genetic relatedness.

4.1.2 Reciprocal Altruism

Whilst kin selection is important in understanding family dynamics and altruism where genetic relationships hold, kin selection fails to explain the widely observed behaviour of kindness that humans quite often show towards unrelated persons and even towards strangers.

Trivers (1971) developed the concept of "reciprocal altruism" to explain kindness towards strangers. Reciprocal altruism can be defined as "co-operative behaviour among unrelated individuals that benefits everyone involved " (Cosmides & Tooby, 1992). Reciprocal altruism is an important requirement for economic growth and development as it leads to mutually beneficial co-operation, and escapes from prisoner-dilemma types of poverty traps. Understanding when and how reciprocal altruism may fail is thus important for economic development theorists and policy makers.

In understanding reciprocal altruism, game theory has played an important role. Axelrod (1984;1986) established that altruism, based on a social strategy of "tit for tat", dominates any other strategies. In the parlance of game theory, reciprocal altruism is an evolutionary stable strategy (ESS). Trivers (1971) argues that reciprocal altruism is dependent on a lack of a rigid dominance hierarchy in society, as this could prevent some individuals from having the power to help others. In a more stratified society reciprocity could therefore be more difficult to achieve. Less hierarchy and less stratification in human society may be better for family structures and family stability, perhaps benefitting more monogamous pair-bonding behaviour in humans (Boone, 1998).

4.1.3 Costly Signalling and Commitment

Whilst kin selection explains kindness and altruism towards family members, and reciprocal altruism explain kindness and co-operation with unrelated persons, there are certain aspects of human kindness with which these two concepts have difficulty. These are altruistic behaviours that appear to have no benefit to the giver, and cannot be reciprocated. A frequently used example is that of handouts and support to beggars, or donations to charity, the church, or even people who donate blood.

Zahavi and Zahavi (1997) have developed "Costly Signalling Theory"(CST) to explain such kinds of altruism. CST proposes that people will engage in behaviour that is costly as a way of signalling honest information about themselves. Apparently pure altruistic behaviour transmits social information about a trait or characteristic of the signaller that is desirable from the point of view of evolution – such as health, intelligence and access to resources.

To be effective, signalling needs to be credible. And for trust to hold there must be some indication of commitment. But how can a selfish being or organism make a commitment that is credible? Frank (1988) argues that emotions evolved partly to solve this problem of credible commitment. In this way emotions can generate genuinely altruist behaviour and makes trustworthiness possible. Trustworthiness is important in a myriad of terrains of economic development, but especially in the area of the division of labour and hierarchies within a firm. As Frank (1988:122) put it "*The honest individual in the commitment model is someone who values trustworthiness for its own sake…and it is precisely because he has this attitude that he can be trusted in situations where his behaviour cannot be monitored*". This remark suggests that the Prisoner's Dilemma can be escaped if we play it with people that we can trust.

Finally, even the mysterious phenomenon of love has a much more practical function. Love is often depicted as leading to irrational behaviour. Pinker (1994) states that this is precisely the reason that humans evolved love. It is a commitment device. As Buss (2000:11) explained,

"*if your partner chooses you for rational reasons, he or she might leave you for the same rational reasons: finding someone slightly more desirable*".

In the light of kin selection, reciprocal altruism and costly signalling, one may agree with Colby (1996:6), "*cooperating with or helping other organisms is often the most selfish strategy*". Natural selection has thus favoured altruism as described in the preceding sections because it increased a genotype's inclusive fitness.

4.2 Competition and Conflict

Analysis of the family can illuminate the biological bases of economic development by showing that many important institutional outcomes, such as the family, monogamous marriages, stratified societies, crime, and status seeking behaviour are all results of strategic interactions between humans who are attempting to maximize inclusive fitness and execute adaptations. In this strategic maximization process (which most often takes place subconsciously) conflict and competition can be identified as important determinants of economic growth and development. Humans tend to use their intelligence predominantly to outwit other humans, and not really to solve practical problems. Ridley (1993:33) states that "*Deceiving people, detecting deceit, understanding people's motives, manipulating people – these are what the intellect is used for*". In such circumstances, it is not necessary *per se* to be clever: it is necessary to be more clever than your competitors. The human intellect and brain can thus be the outcome of an arms-race where all progress is relative.

This section of the paper argues that human choice, competition for mates, and the resulting sexual selection, lead to different forms of pair-bonding such as monogamy or polygyny, each with different institutional repercussions, since the family / kinship environment in which children grow up may have important implications for technology adaptation, innovation and learning.

4.2.1 Mate Choice

How do humans choose their mates? In the popular literature there has been much reporting of increasing numbers of empirical studies across cultures, that find that human males are generally most attracted to females that are youthful looking and attractive (specifically, men seem to prefer women with large eyes, symmetrical features, a clear complexion, large breasts, long legs and a waist:hip ratio of about 0.7 (Singh, 1993; Gribben & Cherfas, 2001). Why would males have a preference for these traits? The explanation is that in the EEA, these traits would have been associated with higher disease immunity and a longer period of reproductive fitness. Put differently, males who had other preferences failed to leave offspring, so that genes/adaptations for such other preferences would not have made it into the present generation. It must again be stressed than males do not consciously think about these features in such a calculating manner – rather, the preference had been selected over many generations and operates subconsciously: males who in the past had a preference for more fertile women left more offspring than others, and since we are the offspring of those successful males, we have inherited their preferences.

Through a game theoretic lens, males' sexual or mating strategies are determined by the mating strategies of females. Females have preferences for good genes and resources and, depending on environmental circumstances, females will engage in either short-term or long-term mating strategies. This choice, in turn, affects males' sexual strategies, in particular their intrasexual competition.

Empirical evidence suggests that the reason why men tend to be intensely competitive and strive for high status is that this is exactly what attracts women more. When following a long-term mating strategy, women may find a man's social status more attractive than his physique or

age (Bereczkei & Csanaky, 1996:18). Again, the evolutionary logic is clear: there is no age-limit on male fertility and higher status males may tend to have more access to resources to provide better for his offspring and, of course, to engage in parental investment. This sexual selection will have lead over the ages to men who are extremely status conscious, and who strive and compete to raise their own economic status. One way of competing is through innovation that will raise a male's status, implying that an important foundation for technological progress (as well as art) in society may in fact be male intrasexual competition! Another implication is that since self-interest and competition may be driving status seeking and innovation, truly communistic societies will be less successful (see e.g. Wright, 2000).

The importance of male economic status has often been confirmed through cross-cultural studies. For instance, the International Mate Selection Project (IMSP) studied mate preferences in 37 cultures spread over six continents and five islands. Subjects rated 18 mate characteristics on desirability. In 36 out of 37 samples, women placed significantly more value on good financial prospects that did men, and overall the females valued "good financial prospects" more highly than "good looks". This study also confirmed other predictions of differential mate choices such as twomen tending to marry older males, who would tend to have more resources, and that physically attractive females were more often than not married to males of high occupational status – this was true even for financially independent and occupationally successful women (Buss, 1989; 1990; Ellis, 1992:270; Thornhill & Thornhill, 1983). Bereczkei and Csanaky (1996:20-21) also find that males who choose younger and attractive females and females who choose males with greater resources do, in fact, have more surviving children than those who follow alternative strategies.

The value that women places on a mate's status or financial prospects would only have evolved if males stayed around to care for their children, i.e. invested resources in their offspring. If they did not stay around to invest in offspring, female mate choice would be solely determined by the quality of genetic material to be gained from a mate. However, in human society this is not the case, and human males do care for and invest significantly in their offspring. In other words, "Parental Investment" (PI) by human males is high when females follow a long-term mating strategy (see e.g. Williams, 1975). When however, a situation exists where women engage in more short-term mating (e.g. with high pathogens, higher own resources and polygyny) men would apply (sub-consciously) cost-benefit analysis that would lead them to reduce their parental investment and put more effort into competing for short-term mating success (Tooby, 1982; Clutton-Brock & Vincent, 1991).

There is a reason for this difference in mate preferences between males and females. An economic perspective makes clear that these differences are, in fact, sensible, given the biological differences between males and females (Becker & Landes, 1977). These biological differences need no elaboration here; suffice it to note that females have a limited number of eggs, can have a limited number of children, and given internal fertilization spend a disproportionate time raising children. Females should thus be much more selective in choosing who they mate with (Clark & Hatfield, 1989). In contrast, males have the potential for unlimited offspring, limited in theory only to the number of females they can mate with. From these biological differences in the mechanics of reproduction between males and females follow a number of predictions, all of which have been confirmed by cross-cultural empirical evidence:

Firstly, males will tend to be more promiscuous than females, and less discriminatory in their choices of mating partners. This means that men will be more likely to adopt short-term mating strategies. The Sexual Strategies Theory (SST) proposed by Buss and Schmitt (1993) builds on the work of Trivers (1972) and attempts to explain why men tend to adopt short-term mating strategies more than women. They propose that both men and women have developed mixed strategies involving both long-term and short-term mating. The actual type of strategy will depend on environmental circumstances so that men and women will shift between these strategies and one will observe some variation within each sex (Gangestad & Simpson, 2000:3).

What this implies is that males' choice between short or long-term strategies will depend on females' choice between short and long-term strategies and vice versa, a truly game theoretic scenario. Because females are careful in their choice of mate, not all males will necessarily find a mate all of the time. This leads to the fact, commonly observed, that the reproductive success of men has a greater variance than that of women.

Secondly, males will compete intensely among one another for access to females to mate with, given that the female's reproductive potential is the limiting factor. Male fitness is limited only by access to fertile females, whereas female fitness is limited by physiological and energetic constraints (Wilson & Daly, 1985:60). The resulting competition amongst males is known as intrasexual competition. One form of this competition, given female preferences for social status in a male, is for males to strive (mostly subconsciously) for status. Competition amongst males for access to, or choice among, potential mates has to be recognized as a major source of conflict and aggression in most societies (Emlen, 1997:572).

Thirdly, males would have a tendency to want to monopolize as many females as possible. In other words one should expect a tendency towards polygyny in human society (Buss, 1994).

Fourthly, males would tend to be much more sexually jealous, and exhibit behaviour such as mate guarding, since males were, until fairly recently at least, uncertain about their paternity. Male sexual jealousy would probably be much less, were it not for the fact that, in humans, one observes a high level of male parental investment coupled with what Hrdy (1981) termed paternity uncertainty inducements by females[12]. As stated the concept of "parental investment" (PI) was contributed by influential social scientist Trivers (1972:139) who defined PI as "*any investment by the parent in an individual offspring that increases the offspring's chance of surviving at the cost of the parent's ability to invest in other, including future, offspring*". PI has been influential in biology to explain, amongst other things, male-female pair-bonding patterns, female menopause, parent-offspring conflict as well as personality differences between siblings. As Ellis (1992:275) stresses, "*evolutionary considerations lead one to expect that women will be sexually attracted to men who display traits that are reliably correlated with social dominance*." This is because mates tend to engage fairly significantly in parental investment. In the language of EP, PI is an adaptation. Through the lenses of economics and game theory, PI is a clear example of an adaptation with trade-offs. It has costs and benefits for both males and females, and as such, males and females will have different mate selection and reproductive (or sexual) strategies. Consider for example the question of why human males engage in parental investment, which is a long-term mating strategy, as against opting for only short-term mating strategies with no investment? The answer is that relatively few men may have the attributes most women desire in short-term mates, so that it would generate relatively low pay-offs for men to pursue short-term mating strategies. As stated by Gangestad and Simpson (2000:8) "*the most profitable mating strategy for the typical man may be to devote most of his reproductive effort to enhancing the phenotypic quality of his offspring by investing heavily in a single mate's offspring*". Males' sexual strategy, seen in this context through a game theoretic lens, is aiming at the best reproductive payoff given females' preferences, is thus an important causal factor in parental investment and monogamy.

To understand the factors that determine preferences for mates, it is necessary to realize that despite co-operation between male and female, man and wife, this relationship is also characterized by conflict. This conflict is clearly seen in the different mating strategies and mating choices of males and females. Fundamentally, the difference between male and female

[12] According to Hrdy (1981) females may follow a strategy of inducing parental uncertainty in males through concealed ovulation and/or having multiple mates which could, depending on environmental circumstances lead to either greater male protection or greater tolerance of offspring by different men.

mating strategies and mating choices is due to the asymmetry in investment made in offspring, and the resulting different trade-offs for males and females (Perusse, 1994).

From the above discussion the question is, why is monogamy found in human society (especially the high-growth Western societies) given that males would tend towards polygyny[13]? Put another way, the question can be asked whether monogamy is better for males, or for females.

The answer to this question seems to be: it seems monogamy is better for males than for females! It would give more males access to females (i.e. a few high status males cannot monopolize the females) and females would find it perhaps more difficult to mate "upwards" with preferred high status males. It has also been established that monogamy is more prevalent in more egalitarian societies than it is in socially and economically stratified societies (Emlen, 1997:573). Given that democratic societies tend to produce more egalitarian outcomes, it can be conjectured that the emergence of key institutions in economic development, such as the monogamous marriage / nuclear family unit, supported by democracy, is an evolutionary stable strategy (ESS) resulting from intense intrasexual competition by males for females.

4.2.2 Sexual Strategies, Inequality and Crime

A further perspective on the influence of various mating strategies and types of pair-bonding systems on social and economic phenomena can be obtained by considering the relationship between crime, inequality and the institution of marriage (Bloom & Dess, 2003). Throughout the world, family dissolution, family violence and conflict, and marriage breakdown are more frequent and impose a rising direct cost on societies. Emlen (1997:564) notes that the extended family that typified many societies in the past is becoming rare, and that even the so-called "nuclear" family is being replaced by increasing numbers of single parent and reconstituted (stepparent) families. He also argues that the break-up of the relational extended family is a recent evolutionary phenomenon – but one that imposes huge costs on society and is detrimental to its development – socially, politically and economically. This is because the family as an institution facilitates co-operation through kin-selection, and reduces aggression and conflict. In intact family groups most potential extra-pair sexual partners are also close genetic relatives. The development of inbreeding avoidance mechanisms therefore has, as a by-product, reduced sexual competition. The breakdown of the intact (genetically related) family or household disrupts both "social harmony and stability of the new family unit" (Emlen, 1997:573). A huge and accumulating amount of empirical evidence from evolutionary biology and evolutionary psychology bears out these observations and predictions. For instance, empirical evidence finds that:

- Children in stepfamilies have a higher probability of behavioural, emotional and health problems than children in biologically intact families (Kiernan, 1992; Dawson, 1991).
- Stepchildren suffer much higher rates of physical abuse and even death than children in intact families – and stepparents are often the primary abusers (Daly & Wilson, 1985; 1988;1994).
- Stepdaughters are at far greater risk of sexual abuse than genetic daughters, and stepfathers are overwhelmingly in such cases the abusers (Young, 1982; Gordon, 1989; Russell, 1984).
- Children in stepfamilies leave home significantly earlier than children in intact families (White & Booth, 1985; Flinn, 1988; Kiernan, 1992).

[13] Another reason for monogamy, which favours both males and females, is that it limits the dangers of sexually transmitted diseases (STDs), which were perhaps prevalent in the EEA.

The breakdown of monogamous marriages would tend to result in more males not gaining access to females, given females' mate preferences discussed above. This would, in particular, be the case in a highly stratified society, where a relatively few men would tend to monopolize resources and females would not be allowed to accumulate much own resources. In such a combination of environments (low rates of marriage / high divorce rate and income inequality between males and females) we would tend observe greater polygyny (or serial monogamy). It would be an optimal strategy for women to attempt to "marry up" as this would raise their reproductive success. This phenomenon is also described as hypergamy. We would also observe much more risk-taking behaviour by males in order to raise their status in order to compete for females. Wilson and Daly (1985:59) note that we would see higher incidence of risky and violently competitive behaviour in young male age groups whose present circumstances "are predictive of reproductive failure" such as single, unemployed men who have the least to lose in escalated conflict over status. Indeed, there is substantial evidence that the more polygynous a society, and the more that women engage in short-term mating strategies, the more intense the male competition. For instance, amongst animals, the more polygynous, and the larger and better-armed males are relative to females, and where male mortality exceeds female mortality (Wilson and Daly, 1985; 1997). Also, high economic inequality will exacerbate criminal behaviour as this increases male intrasexual competition. Evidence to support this link between inequality and crime is provided in, amongst others, Kaplan et al (1996), Kennedy et al (1996), Krahn *et al* (1986) and Hsieh and Pugh (1993).

Various aspects of human anatomy and life histories suggest that the human species has an evolutionary history of polygyny. Indeed, Bergstrom (1994:1) declares that polygyny is a common mode of family organization around the world. Of about 1170 societies recognized by ethographers, polygyny is prevalent in 850. Betzig (1982) specifically finds that in most human societies successful and high status men attempt the monopolization of multiple women with great regularity. Also, even modern "Western" societies are "far from completely monogamous. About 25% of all children born in the United States in 1990 were born to unmarried mothers who were not cohabitating with the fathers" (Bergstrom, 1994:1). In Africa, the percentage of women living in polygynous households range from 10% in Southern Africa to over 55% in the Sahel region. In a polygynous society, one can also predict that parents will leave their inheritances rather to their sons than their daughters, since this endowment of resources can increase their son's reproductive success significantly, and empirical evidence across cultures tend to suggest that this is indeed the case (Kuper, 1982). Other suggestive evidence for humans' history of polygyny is that human males are larger in size than females, females become sexually mature earlier than males, and that males tend to have lower life expectancy than females (Barash, 2002:3-4).

In contrast, in a more egalitarian society, where access to resources is allowed for females as well, we would tend to find more monogamous relationships and more homogamy. This is because fewer high-status males are available from which females can choose. However, in societies with fewer high-status males, serial monogamy would tend to increase (Bereczkei & Csanaky, 1996:21). Evidence has been found for this in that marital dissatisfaction, wife abuse, and divorce are more frequent when the wife is more highly educated that the husband (Hornung, 1981).

The differences in types of pair bonding can therefore have important implications for stability and development. Importantly, young, single and unemployed males can be expected to engage in risky competitive and violent behaviour (Kanazawa, 2003:262-263). Bacon, Child and Barry (1963) found that crime rates were indeed higher in more polygynous societies, with males being everywhere more likely to engage in crime. Barash (2002:1) states that if we could eliminate or even significantly reduce male violence, we would "*pretty much get rid of violence altogether*". Daly and Wilson (1988) established that a male is about 20 times more likely to be

murdered by another male than is a woman of being murdered by another woman. In more modern, but stratified societies, the relatively young males are predominantly the perpetrators of crime[14]. In a USA crime study, Wilson and Daly (1985) found that 41% of adult male offenders were unemployed, 73% of male offenders over the age 14 were unmarried, and that males committed 93% of robberies, 94% of burglaries and 91% of motor thefts. Other indicators of young males' predilection for risky behaviour come from studies on gambling and motor vehicle accidents. Experiments have established that the larger the stakes, the more male-dominated gambling becomes. Young males are also responsible for a disproportionate number of motor vehicle accidents, and it is well known that motor vehicle insurance premiums reflect this. Daly and Wilson (1985:69) noted that this reflects the unconscious pressures of intrasexual competition stating that, "*dangerous driving by young men appears to be a social display*". Kazanawa and Still (2000) extends Daly and Wilson's (1988, 1990) theory of homicide and explains all types of violent and property crimes as consequences of young men's competition for access to women's reproductive resources.

The EP approach to criminal and violent behaviour also implies that criminal violence will be higher if local life expectancy is drops[15]. This is because lower life expectancy leads to people discounting the future relatively highly. With high discounting of the future, reckless or risky behaviour can indeed be optimal when the expected returns from safer courses of action are negligible (Wilson & Daly, 1997:271). Lower life expectancy, and a situation such as when many people die from HIV/AIDS, has been found to raise people's awareness of mortality. Solomon *et al* (2003) found that greater awareness of the inevitability of death leads to lower self-esteem and may also raise violence. In an experiment, they introduced "mortality salience" by asking subjects what they think will happen as they physically die. Their results found that this increased participants' bigotry and anger.

Naudé (2005), using panel data from South Africa to identify the determinants of crime found that the EP on crime explained a greater variation of crime in South Africa than traditional explanations of inequality and education. For instance, he found that once the proportion of the population that falls within the prime reproductive age has been controlled, poverty, income and inequality do not turn out to be robustly significant determinants of crime in South Africa, as they do in some other studies. The variable with the most significant effects on crime was found to be the proportion of young people in a province's population. Amongst the more traditional variables, only educational status and police per unit of population (deterrence) remained significant in determining (lowering) crime levels.

It must be emphasized that people are not consciously aware of these deep ingrained motivations. Men do not consciously engage in risky behaviour or crime with the explicit goal of furthering their reproductive success. They are however, executing mind modules that evolved during a period when such behaviour was successful in solving the problems of reproduction that they frequently encountered in the EEA. In the same vein, it must be added that the fact that the ties between mating and reproduction can be disrupted by the technology of contraception, does not imply that evolved psychological mechanisms no longer influence human mating decisions (Gangestad & Simpson, 2000:2).

5. IMPLICATIONS FOR EVOLUTIONARY DEVELOPMENT ECONOMICS

Although economics has still a long way to proceed to be more fully consistent with evolutionary social and natural sciences, there has been a start. This is most apparent in the rapidly growing field known as evolutionary economics which started from the work of Nelson and Winter (1982)

[14] The same pattern of violence being dominant amongst males is found in other animals.

[15] Another prediction is that, when life expectancy starts to decline, reproduction will occur earlier in life (Geronimus, 1996).

The field of evolutionary economics has made progress in understanding the macro-economic complexities of technological change and dynamics, but is still relatively isolated from other evolutionary sciences, most notably EP. As Potts (2000:214) describes, evolutionary economics can be seen as a branch of economics that deals with technological and institutional change, industrial dynamics and the statistical side of economic dynamics – in other words it focuses more on economic issues that evolve, instead of the economic actors and their institutions as the results of biological evolution. Also, where psychology has been incorporated, as in Kahneman (2003) the explicit assumption is still that humans are rational, albeit "bounded rationality".

Having provided an overview of EP and the roles of co-operation and conflict, it remains to be shown in this section how this can illuminate and add to our understanding of long-run economic growth and development.

One of the first features to be explained by any theory of long-run economic growth and development is the sudden increase in per capita incomes that began roughly around 1750. A particular feature of economic growth and development is that it is a relatively recent phenomenon in human history. As Galor and Moav (2002:1133) point out, most of human history has been a continuing struggle for existence. For most of human history (the so-called Malthusian trap) per capita incomes fluctuated around the subsistence level, held in check on the one hand by diminishing returns to labour and on the other by a positive effect of the standard of living on population growth. During most of human history, mortality rates were high. Williams (1996:215) points out that in an evolutionary perspective, "*our experience of human life histories today, with the great majority of our babies surviving to adulthood, is grossly abnormal*". It is really only since about the 18th century that growth in per capita income took off. Figure 1 plots the world per capita income from about 1 million BC to the present (taken from Maddison, 2001).

Figure 1 : World per capita income : 1 million BC to 2000 AD

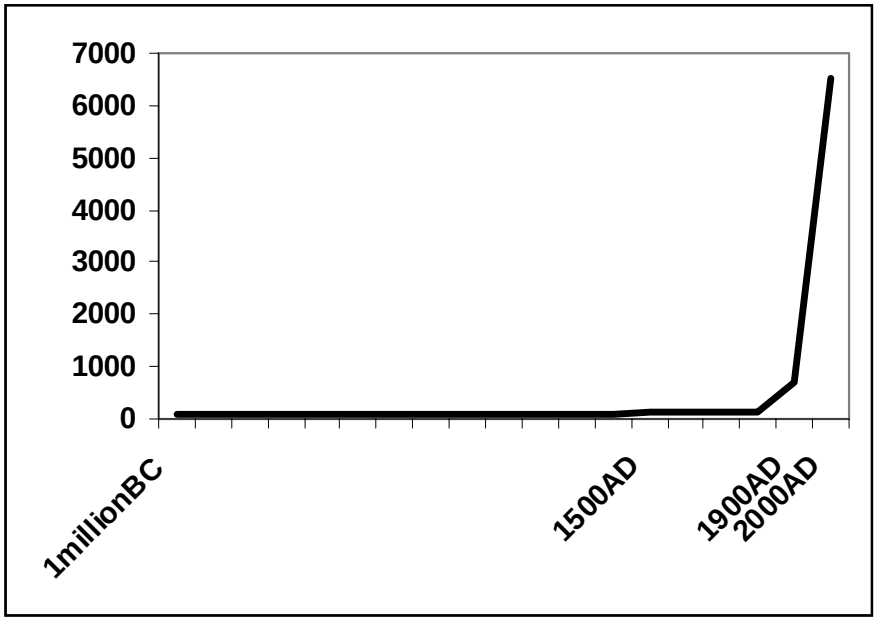

Figure 1 shows that for the major part of human history, from 1 million BC to 1500 AD, per capita income hovered around an estimate of US$90 (in 1990 $-equivalents) increased to about $140 in 1500 AD, to $680 in 1900 AD and to its current level of about $6500.

What caused the escape from the Malthusian trap depicted in Figure 1 above? According to Galov and Moav (2002) this escape or take-off from the Malthusian trap was made possible by conditions which allowed parents to switch from focusing on the quantity of offspring to their quality. One of the conditions they identified is the development of technology that assists survival and reproduction beyond a certain critical mass. In such an environment, producing offspring that can learn to use technology will have increased chances of survival – especially if it takes place in an arms-race type of environment where pressures exist for continual technological upgrading to remain competitive. A second condition that was identified by Wright (2000) for the shift in preferences from quantity to quality is population density. This allowed specialization, division of labour and agglomeration economies to be reaped in dynamic fashion. However, population density only served as a catalyst because humans had evolved adaptations to allow them to co-operate and minimize harmful conflict. Without kin-selection and reciprocal altruism (see section 4.2.1), much of the gains from population density might not have obtained, since then division of labour and specialization would not be possible.

To endow children with greater learning would require more investment in offspring – i.e. it calls for greater parental investment. Such a switch from quantity of offspring to quality of offspring would be more likely to be a successful strategy with high and positive ***male*** parental investment. This in itself would require changes in sexual selection strategies – i.e. changes in preferences on the level of the family unit. This required change in preferences emphasizes the importance of not taking preferences as exogenous in economics, as has been the assumption over much of this past century. Once this process has started, it can lead through a positive feedback effect to ever-higher technology and learning. Children with greater predilection or genetic predisposition for learning will be more successful in adopting technology and in improving technology.

The selection pressures will therefore drive learning abilities to greater heights, which, through innovation, lead to better technology and higher productivity (output per person). In this fashion rapid technological progress, growth in investment in human capital, growth in per capita output, as well as the demographic transition can be explained (see Moav & Galor, 2002; Acemoglu & Zilibotti, 1997; Zak, 2002).

The conditions that allowed the take-off from the Malthusian trap were therefore broad environmental conditions (population growth, density) interacting with the mental modules that human hunter-gatherer societies had developed over millions of years. Adverse external conditions may limit the take-off from the Malthusian trap and may suggest that such a take-off is not necessarily automatic or inevitable. As pointed out in section 4.2.1, the degree of stratification in society will determine sexual strategies. Given that democratic societies tend to produce more egalitarian outcomes, it can be conjectured that the emergence of key institutions in economic development, such as the monogamous marriage / nuclear family unit, supported by democracy, is an evolutionary stable strategy (ESS) resulting from intense intrasexual competition by males for females.

Adverse external conditions may also interact with humans' propensity to co-operate and specifically to engage in reciprocal altruism. Reciprocal altruism has been ingrained in humans given the environments they faced in the EEA. In this regard Cosmides and Tooby (1994) point out that hunting, which dominated in the EEA (before the invention of agriculture) is an effort-independent high-variance activity. Because of the high variance of returns for individual hunters, food sharing amongst the members of a society becomes is an optimal strategy. It is a form of risk pooling that smoothes individual consumption and offers to make everyone better off. But this optimal strategy of food sharing is subject to a Prisoner's Dilemma type of effect wherein some members of society may attempt to free ride. This danger, Cosmides and Tooby (1994) note, has led to humans developing the high sensitivity mind mechanisms to detect reciprocal altruism and trustworthiness. We are constantly on the lookout for people in our social circles who do not reciprocate or who we cannot trust. Whilst hunting was a key economic activity in humans' past,

there may be many instances in latter day economies where there exists effort-independent variance in economic outcomes, for instance due to geographical or institutional factors such as climate and political unrest. In such cases, Cosmides and Tooby (1994) suggest, human nature (again see kin selection etc) would tend towards greater community-wide sharing (as in the days of hunter-gatherers) and depressed investment and savings. In this way, one can link the institutional explanations for economic development with both geographical factors as well as with EP.

6. CONCLUSIONS

Evolutionary Psychology (EP) can greatly enrich development economics, specifically in adding to our understanding of the micro-foundations of the family unit and the explanations of long-run economic growth and development. In this paper, emphasis was placed on the evolutionary foundations of the family unit, on the understanding of human co-operation, and how these result in institutions, such as monogamous family units with positive male parental investment, where a switch from preference for quantity of children towards the quality of children leads to improved technology and learning. Given that monogamy is more prevalent in a more egalitarian society, institutions such as democracy and an equality sensitive state have biological roots. Contemporary development economics have provided much empirical evidence to suggest that democracy and other institutions that promote equity are good for growth and development. By making explicit the biological foundations of this, the potential ability of development economics to contribute to further improvements in institutional design and sustainability may be further enhanced.

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