

Some of the Whats, Whos, and Whens Related to Evolutionary Psychology

Lei Chang

Department of Educational Psychology, The Chinese University of Hong Kong, China

This article presents a brief account of the development of Darwinism and evolutionary biology and psychology in China and introduces some of the basic concepts and theories of evolution that are relevant to and provide theoretical foundations for evolutionary psychology. These include Darwin's evolution by natural selection, Hamilton's inclusive fitness theory, Trivers' parental investment theory, as well as game theory, life history analysis, and niche construction theory.

Keywords: Darwin, evolution, evolutionary Psychology, inclusive fitness, reciprocal altruism, parental investment, game theory, life history analysis, niche construction.

进化心理学的相关概念、理论与历史

该文概述了达尔文主义、进化生物学与心理学在中国的发展，同时也介绍了与进化心理学相关的概念与基本理论。该文内容包括，Darwin 的自然选择理论，Hamilton 的种系适宜理论与 Trivers 的父母投资理论，也包括博弈理论、生活史理论与生态位建构理论。

关键词：进化，进化心理学，种系适宜，相互利他，父母投资，游戏理论与生活史分析，生态建构。

分类号：B84-069

What are some of the basic concepts from which the emerging field of evolutionary psychology draws its theoretical foundations? Who are the contributors of these concepts and what are some of the time lines by which to define the development of these concepts and theories? The purpose of this article is to introduce some of the theories and concepts of evolution that are relevant to and provide the theoretical foundations for evolutionary psychology. A secondary objective also is to present some of the originators of these concepts and related historical circumstances to which references are often made in the writings by evolutionary psychological researchers. Clearly, the issues under discussion are diverse, with some closely related to one another and others standing independent. One such stand-alone topic is the scientific as well as ideological development of evolution and evolutionary psychology in China, to which the discussion turns first.

Darwinism, Sociobiology and Evolutionary Psychology in China

Twice in *The Origin of Species*, Darwin mentioned an ancient Chinese encyclopedia. "The principle of selection I find distinctly given in an ancient Chinese encyclopaedia" (Darwin, 1859/1979, Chapter 1, p.92). Darwin later mentioned the same encyclopedia in Chapter 5 on p.181 when talking about species and

animal acclimation (Darwin, 1859). Unfortunately, Darwin did not provide the source for this Chinese encyclopedia. Some Chinese writers believe that Darwin referred to the work by Jia Si Xie around 500 AD of Wei Dynasty that was entitled "Important Arts for People's Welfare" (贾思勰的《齐民要术》; 张润生, 1983). Over 110,000 words, the book contains mainly agriculture, husbandry, fishery and other livelihood and subsistence knowledge and techniques. The book also presents ancient biological theories and detailed accounts of livestock breeding and crop hybridization the content of which may well have interested Darwin. Additional and more ancient Chinese texts contain biological thinking that may even be considered evolutionary or Darwinian. One of the earliest examples is the Book of Changes 《易经》 which first emerged during the Western Zhou Dynasty about 1066 to 256 BC. Although in today's language, this book mainly recorded convoluted but systematic rules for fortune telling, it also dealt with nature, life, and changes of the universe. One of the book's themes that "all living things including men and women came from nature" (有天地，然后有万物。有万物，然后有男女) but not by creation is evolutionary or Darwinian. Another example is the Taoist text, Zhuangzi 《庄子》 which was written and came to circulation between 369 and 286 BC. The book contains essays written by Zhuang Zi and was titled after the author's name. One of the most famous essays, A Happy Excursion 《逍遥游》，started the text by describing how a fish of tremendous size from the vast northern ocean evolved into a huge bird with

Received 2006-06-30

Correspondence should be addressed to Lei Chang, Department of Educational Psychology, Chinese University of Hong Kong, Shatin, New Territories, Hong Kong; e-mail: leichang@cuhk.edu.hk.

wings obscuring the sky (北溟有鱼, 其名为鲲。鲲之大, 不知其几千里也。化而为鸟, 其名为鹏). Another essay stated that all living things came from nature and that elements were originally separated and, when combined, give rise to phenomenon (天地者, 万物之父母也, 合则成体, 散则成始) including life. Evolutionary thinking seems apparent in these ancient Chinese writings.

Two conclusions may be drawn from these quasi-historical notes. First, the long and rich Chinese civilization included much scientific knowledge and imagination that had in many historical periods enabled China to surpass many other civilizations and societies, including those that compose today's Western world. Second, despite these historical advantages, the 19th and most of the 20th centuries at least had witnessed the stifling of creativity in almost all aspects of life in China, including evolutionary studies. With respect to Darwinian evolution, this second conclusion can be corroborated by additional historical facts.

In 1859, while China was continuing with its active pursuit of opium import from Britain, the sensation of *The Origin of Species*, which was sold out the first day of its publication late that year, did not seem to have reached China's seaports or its opium numbed citizens. The Chinese translation of this most important text of the 19th century did not come until 1902 and even then only two chapters (Chapter 3, Struggle for Existence and Chapter 4, Natural Selection) were translated and published. It was not until 1920 when the translation of the full text was published, by the same translator, Ma Junwu (马君武), of the two earlier chapters. From its initial publication in 1859 to the Chinese translation of the full text in 1920, it had taken 60 years for *The Origin of Species* to reach China. However, China then lagged behind the West in science and technology and socioeconomic development by more than 60 years.

The interval of 18 years between the publication of Chapters 3 and 4 and that of the full text reflects the lack of public interest in evolution and biology at the time when China was occupied with its search for sociopolitical directions. Darwinian thinking was then also used by progressive politicians and social reformers to advocate "saving the country by means of science" (see 胡适作品集 2). This social emphasis of Darwinism (not social Darwinism) can also be seen from the fact that more than 10 years before the translation of *The Origin of Species*, a Britain-educated scholar and social reformer, Yan Fu (严复), had translated Thomas Huxley's *Evolution and Ethics* (only the first or the evolution part of the book) and Herbert Spencer's *The Study of Sociology*, as well as Adam Smith's *An Inquiry into Nature and Causes of the Wealth of Nations* and other important Western

social science and philosophy works. Dr. Sun Yat Sen, the founding president of China's first republic (that replaced the feudal dynasties) also was interested in and studied Darwinism. In the translation of *Evolution and Ethics*, Yan Fu translated "evolution" into "Tian Yan" (天演), the literal meaning of which is "nature's evolution." It was said that Dr. Sun Yat Sen did not like Yan Fu's translation and suggested "Jin Hua" (进化) as the Chinese translation of "evolution". This is because "Jin Hua" which means "progress and evolution" but not "Tian Yan" or "nature's evolution" can be used to refer both to nature's evolution and to society's evolution (孙中山选集第一卷 cited from 王 晓明, 2005). Apparently, Dr. Sun Yat Sen did not understand that evolution or nature's evolution does not imply progression or directionality, whereas his translation, "Jin Hua" (进化), suggests progress in a forward direction. Evolution was also translated into "Yan Hua" (演化), which simply means "evolution," and has since been used in Taiwan. Unfortunately, "Jin Hua" is currently and has been in the past used in China, and it is not difficult to imagine that, upon seeing the word, people may form the picture of apes progressing towards becoming humans. This special issue should in fact be called "Yan Hua Xin Li Xue" (Xin Li Xue means Psychology) instead of "Jin Hua Xin Li Xue" but readers may not accept or understand the term.

The slowness of the Chinese intellectual community in responding to *The Origin of Species* and its emphasis on the social interpretation and application of Darwinism may, as mentioned earlier, also reflect the fact that similar evolutionary and natural developmental concepts may be more historically and culturally rooted but not novel in China. As we know, the significance of Darwin's theory of evolution and the resulting social controversies surrounding Darwin, his contemporaries, as well as his predecessors (including his grandfather, Erasmus), are attributable in part to the success and valor in challenging the religious establishment, the associated class hierarchy, and the creationistic account of human existence (e.g., Desmond & Moore, 1994). Of course, interference from the Christian church had proven to be much more detrimental to scientific endeavors earlier in Western history. However, Chinese civilizations have been such that organized religion has never attained the kind of sociopolitical centrality and influence as in the West. Except for later imported Christianity and Islam, religious practices in China, including Buddhism, have remained relatively personal and idiosyncratic pursuits that have never been as organized and as systematically exercised as in the West.

Because of the lack of organized religious opposition (which, by the way, may also be

misinterpreted by some sectors of the West as a sign of government encroachment on religious freedom), Darwinian and neo-Darwinian evolutionary concepts have been part of the public school curriculum since the 1920s (王晓明, 2005) both in Taiwan and in the Mainland of China. Even during the Cultural Revolution when anything Western or traditionally Chinese (an odd combination indeed) was likely to be eradicated from public ideology including centralized curriculum, neo-Darwinian concepts remained untouched. Incidentally, this reality poses an interesting contrast to the fact that public school teaching of evolution remains an issue of debate in the United States where, based on a recent Gallop poll, 30% of the population believe that God guided the process of evolution (cited from Kanazawa, 2006, and Miller, 2006).

By the summer of 1975 when E.O. Wilson's significant but also controversial book, *Sociobiology: The New Synthesis*, was published, China was about to enter a new phase of its history that drew sharp contrast to the time when Darwin's *Origin of Species* was published over 100 years before; another sad fact is that in these 100 years, China had been wrung with one human mistake or tragedy after another which had stalled and at times completely halted academic development. Three years later, 1978 not only marked the beginning of a market economy, which, nearing its 30th year, has seen high single-digit to double digit annual GDP growth for over 25 consecutive years, but also heralded the beginning of serious catching up and development in science and scholarship, including evolutionary biology and psychology. Wilson's *Sociobiology* was first introduced to Chinese readers in 1978 when the journal, *Foreign Social Science Studies Digest* (国外社会科学文摘) published extracts of a *New York Times* article which introduced the theories of O.E. Wilson and Robert Trivers in the context of presenting the controversies surrounding sociobiology (Li & Hong, 2003). More articles soon appeared in various journals and newspapers that joined the sociobiology debate that was still sizzling in the West, but also brought in new arguments pitting the Marxist principle that human behavior is shaped by culture and economy-based social class against bourgeois biological determinism and social Darwinism (Li & Hong, 2003). The debate over Wilson's book resulted in two publications that had high impact in China. The first was *The New Synthesis*, an edited volume compiled by Li Kunfeng that contains Chinese translations of parts of Wilson's *Sociobiology* and *On Human Nature*, Richard Dawkins' *The Selfish Gene* and other Western authors' writings on evolution (Li, 1985 cited from Li & Hong, 2003). The first edition of *The New Synthesis* ran 62,400 copies (Li & Hong, 2003). The second was an article by Zhang Boshu published in

Biology and Philosophy that was entitled, "Marxism and human sociobiology: A comparative study from the perspective of modern socialist economic reforms (Zhang, 1987). Further work based on this article was later published as a book (Zhang, 1994). Full translations of *The Selfish Gene* and other evolution books soon followed.

Despite this initial success in finally keeping up with Western advances in evolutionary studies, evolutionary biology remains underdeveloped in China partly and ironically because the country does not want to repeat the same mistake of a century ago for not keeping up with important scientific development. However, the most active and highly visible scientific development today seems to take place in such fields as molecular biology and genetic but not evolutionary studies. These and other "trendy" and "revered" sciences have taken up much of the country's limited resources and talents. The same fate befalls evolutionary psychology. Even though Darwin's evolution by natural selection represents an overarching theory for all life sciences including psychology and it was derived based on the best humanly possible observations and defensible empirical methods, the common view toward evolutionary psychology in China has been that it is speculative and it is not as "scientific" as other fields of psychology. Similar views about evolutionary psychology are also common in the Western psychological community where the standard social science model (Tooby & Cosmides, 1992) represents the mainstream scientific framework. However, Chinese psychology seems to go even more extreme, again in keeping with the reverence for hard sciences. Cognitive psychology and, increasingly, neuroscience are given priority and more resources in discipline development than are other areas of psychology. In the last 10 years, the purchase of ERP and functional MRI machines has become a new parameter by which to show off departmental strength, and at this time almost all major psychology departments in China have acquired these technologies, with runaway expenses that have eclipsed the modest budgets of most psychology departments. For example, all four psychology departments in Beijing are ERP equipped. This cognitive and neuroscience bias is also seen in journal publications although the situation has been improving. In this context, evolutionary psychology remains a personal pursuit of a handful of researchers. Only one department in China offers a stand-alone course in evolutionary psychology, while the number of introductory psychology courses that also include evolutionary topics is equally low to non-existent. There is no journal that specializes in evolutionary psychology although this fact has to be considered within the context of the fact that China currently has

no more than a dozen psychology journals or journals that publish psychological research.

However, there has been encouraging development in the last few years, including the publication of the first, small volume introductory evolutionary psychology book (Xu, 2004). A second and bigger volume authored by Zhu Xinping (朱新秤) will be published by Shanghai Education Press (上海教育出版社). The 2005 Quadrennial Convention of the Chinese Psychological Association, which has since been changed into a biannual convention, included a symposium as well as one or two individual papers on evolutionary psychology. A small but steady number of evolutionary psychological papers have also been successful in competing for the much limited journal space (e.g., Chang, Lin, Zhang, Li, & Mo, in press; Chang, Zhang, Li, & Wong, 2006; Li & Chang, in press; Ye, 2005; Yue, Chen, & Zhang, 2005). Finally, the publication of this special issue comprised of Western leading researchers in this area should have a great impact in promoting evolutionary psychology in China. It is particularly courageous and perceptive of the editor and the editorial team of *Acta Psychologica Sinica* to publish this special issue. This effort will help to broaden Chinese psychology and will keep it abreast of the newest advances in the West. As Steven Pinker said on several occasions, evolutionary psychology has broadened our understanding of human behavior in at least two ways. "One is by documenting that beneath the undeniable fact of cross-cultural variation there is a bedrock of human universals: ways of thinking and feeling and behaving that can be seen in all of the cultures documented by ethnography." The other is "by showing that many human drives can't really be understood as ways people maximize their well-being in their own lifetimes, but can only be interpreted as adaptations to survival and reproduction in an ancestral environment, namely the foraging lifestyle that characterized our species through 99% of its evolutionary history, until the very recent invention of agriculture and then industrialization" (Pinker, 2006). To conclude this section of the paper, the publication of this special issue should help to broaden Chinese psychology in these two important ways. To understand how evolutionary psychology broadens the understanding of human behavior, the paper next turns to a discussion of some of the basic theories and concepts of evolution that provide the foundations for evolutionary psychology.

Darwin, Wallace, Natural Selection and the Modern Synthesis

Interestingly, Charles Darwin and Alfred Wallace both could have studied people instead of animals and plants and thus would have been known as psychologists. In 1797, a book by Thomas Malthus,

an economist, intellectual, and eugenicist, caused much sensation in England. (Possibly among the longest book titles, the full title of the book reads: *An Essay on the Principle of Population, as it Affects the Future Improvement of Society with Remarks on the Speculations of Mr. Godwin, M. Condorcet, and Other Writers.*) It warned people of the relentless pressure of population growth that could soon lead to famine and starvation. It was said that Darwin and Wallace, respectively and independently, were very inspired by this essay (Hodgson, 2004; Whitaker, 2005). Their goal was not to solve this potential human population problem, but rather to understand how species changed. Malthus' essay provided a core component of the mechanisms of change. The importance of this essay is revealed in the following quote in a letter written by Wallace to one of Darwin's sons and reprinted in Darwin's autobiography (edited by Darwin's nephew, Francis Darwin, 1887/2001, pp. 200-201):

This [Malthus' ideas about population expansions and contractions] had strongly impressed me, and it suddenly flashed upon me that all animals are necessarily thus kept down – "the struggle for existence" – while *variations*, on which I was always thinking, must necessarily often be *beneficial*, and would then cause those varieties to increase while the injurious variations diminished.

Darwin had the same insight and entitled a chapter of his *Origin of Species* as "Struggle for Existence" and wrote, "Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life" (Darwin, 1859/1979, p.117).

According to Darwin, struggle or competition sets the stage for natural selection. In the context of modern (versus Darwinian time) theory of evolution, natural selection refers to differential survival or reproduction of one genotype versus others in a population leading to changes in the gene frequencies of the population. However, in Darwin's time, natural selection was conceived on the level of individual organisms rather than genes. For natural selection to occur, there must be variations (either in terms of genotype or in terms of phenotype) with respect to a trait. Some proportion of the trait variation across individuals must be heritable. That is, different trait variants are passed on from one generation to the next mostly through sexual reproduction. Reproduction is also differential because competition and mate choice (i.e., sexual selection, described below), and trait variations enable some individuals to produce to their full potential and may prevent others from surviving past their reproductive age. This process comprises of

the Darwinian concept of natural selection through sexual reproduction. In other words, there is competition among individuals for survival and reproduction. Some of the heritable trait variants make their bearers more effective competitors who produce more offspring than others. As a result of the competition and differential reproduction, some trait variants are selected for or become more spread in the population, whereas other trait variants are selected against and become scarce or extinct in the population. "This preservation of favorable variations and the rejection of injurious variations, I call Natural Selection" (Darwin, 1859/1979, p.131).

At the time of the *Origin of Species* and for almost half a century afterwards, the mechanism for the inheritance of traits was not known at the level of the gene as it is today. This time lapse is rather surprising given the fact that Gregor Mendel's genetic discovery was made around the same time as Darwin's natural selection. Mendel first published his genetic work on garden peas in 1865 in the paper, *Experiments on Plant Hybridization*. As we know, Darwin's *Origin of Species* was published in 1859. However, researchers did not seem to connect these two important works until much later. R.A. Fisher was among the first to connect Mendel's genetic inheritance to the larger picture of natural selection. This connection can be seen from the publication in 1930 of Fisher's *The Genetic Theory of Natural Selection*.

Together with other work, Fisher's book heralded the beginning of natural selection at the genetic level and a new era of evolutionary biology known as the Modern Synthesis. The name, Modern Synthesis, suggests that prior to this integrated understanding of evolution by natural selection, researchers from biology, zoology and other fields and their work were not fully connected by an over-arching theory. The Modern Synthesis thus refers to a "connected" or unified interpretation of evolution. The Modern Synthesis also expands and modifies some of Darwin's original theory. One major modification came from the work on genetic mutation by Theodosius Dobzhansky, a Soviet-born geneticist who emigrated to the United States. He discovered that mutations which could be harmless could create variability far greater than anyone had previously imagined. He showed that, due to random mutation, fruit flies of the same species became quite distinct. This discovery changed the then commonly held misconception that individuals of the same species had practically identical genes. Armed with this and other advances in genetics and biology and paleontology, the Modern Synthesis recognizes several mechanisms of evolution in addition to Darwin's natural selection. These mechanisms include mutation, genetic drift, and gene flow all of which, unlike natural selection, may not be directly

adaptive. Thus, much of evolution is random or by chance, although nature selects those changes that are adaptive. The random and adaptive mechanisms both contribute to evolution or changes in gene frequency in populations. Underlying these ideas of the Modern Synthesis is the recognition of genes, rather than individuals, as the basic unit of evolution.

The name, Modern Synthesis, was made "official" in 1942 with the publication of Julian Huxley's book, *Evolution: The Modern Synthesis*. Julian Huxley was the grandson of Thomas Henry Huxley, Darwin's good friend and a staunch supporter and advocate of Darwin's theory. Naturally, these second and third generations of Darwinian scientists and those who subscribe to these new views about evolution are referred to as neo-Darwinists and, these new views, i.e., the Modern Synthesis, are referred to as Neo-Darwinian. The Modern Synthesis laid the foundation for evolutionary biology and other related fields for the next 60 years to the present day without paradigm changes. However, the genetic aspects of evolution have been increasingly emphasized, thanks to subsequent and ongoing DNA sequencing and many other genetic advances. Today, evolutionary scientists focus on DNA and specific DNA proteins as the unit of evolution changes. However, the theorizing about organismic, or whole organism, evolution originated by Darwin and Wallace remains the same.

The Level of Selection Debate

One key debate arising from the Modern Synthesis concerns whether individuals and genes or groups and species are the basic level or unit of selection. This debate, which is viewed by some evolutionary scientists today as an unfortunate distraction (Borrello, 2003), continued till the 1960s and, to a lesser degree, is ongoing today. The debate first started between David Lack (1910-1973) and V. C. Wynne-Edwards (1906-1997), both renowned British ornithologists and Oxford professors. Lack represented the mainstream view of the Modern Synthesis that individual organism is the level of selection. Wynne-Edwards spearheaded the much less popular campaign of group selection.

The major idea of group selection is that individuals may sacrifice their own reproductive interests for the benefit of the survival of the group to which they belong. Wynne-Edwards built this argument mainly on birth related behaviors of birds. He pointed out that many bird species have small clutches, have prolonged periods before reaching reproductive maturity, and have long breeding seasons sometimes in excess of one year. Other group selection supporters also argued that these behaviors must be social and altruistic in that, for example, when food supply is abundant, clutches are bigger than when food supply is more scarce. Birds thus can

regulate their population densities below starvation levels through social conventions. All of these characteristics run contrary to the idea that fitness is defined by individual organisms attempting to selfishly reproduce. These group selection ideas were later elaborated by Wynne-Edwards in his major book, *Animal Dispersion in Relation to Social Behavior* (1962).

However, it soon became clear that group selection was losing the battle. In 1966, George Williams published the influential *Adaptation and Natural Selection* which very much put the last nail on the coffin of group selection. By the end of 1960s, a neo-Darwinian interpretation of the modern synthesis has taken hold and it has become almost a gold standard that the unit of evolutionary analysis is at the individual's and the gene's level. The publication of the *Selfish Gene* by Richard Dawkins in 1976 has almost turned this biology's gold standard into laypersons' knowledge. To put it in the original group selection context, those altruistic birds who sacrifice their own interests by reproducing late or less during hard times would not have been able to pass their altruistic genes to the future generations, which will be dominated by the selfish genes from birds who take advantage of the situation by using up others' food supply to reproduce their own offspring (Dawkins, 1976).

Despite its losing battle from the beginning, variants of group selection still appear in theoretical and philosophical papers on evolution. For example, Sober and Wilson (Sober, 1981; Sober & Wilson, 1998; Wilson & Sober, 1994) argued both genes and groups should be considered as units of selection because of their part-and-whole relationship. Just as genes are parts of organisms, so are organisms parts of groups. When the parts of a whole, e.g., genes of an individual or individuals of a group, interact competitively, the fitness of the parts is enhanced at the expense of the whole in which they reside. When the parts of a whole interact cooperatively, the fitness of the whole is enhanced at the expense of the parts. In the former case, the parts, e.g., individuals, behave selfishly. In the latter, they behave altruistically. Like genes in an organism, individuals or organisms in a group have a "common fate" that explains why organisms do form into integrated wholes or groups. Pure group selection will lead to the evolution of altruism, whereas pure individual selection will lead to the evolution of selfishness. Selection happens on both levels resulting in within group competition as well as cooperation. Similar ideas have been discussed by Maynard Smith and Szathmari (1995) as conflicts between different levels of organization in their analysis of major transitions in evolution. They suggested that conflicts between the interests of individual cells and their multi-cellular organisms are

responsible for major transitions or drastic changes in the organization of biological units in the course of life's history on earth.

William Hamilton and Inclusive Fitness

In the obituary of William Hamilton published in *Nature*, Robert Trivers wrote that Hamilton's theory of inclusive fitness "is the only true advance since Darwin in our understanding of natural selection" (Trivers, 2000). Extending the Darwinian concept of fitness, which is defined by reproductive success (RS) or the number of surviving offspring produced, inclusive fitness refers to the fitness or RS of the individual plus the effects of a particular behavior or trait of the individual on RS of the individual's relatives. The extent of RS of a relative to be included in an individual's RS is appropriated by the degree of genetic relatedness between the individual and the relative. Inclusive fitness theory reveals a second channel by which behaviors or traits or the genes and alleles responsible for them are promulgated in a population, that of kin selection through reproductive success of kin, in addition to Darwin's natural selection through individual reproduction. Thus, Hamilton's inclusive fitness theory is also referred to as kin selection theory.

All this sounds simple in hind sight. In 1964, however, when Hamilton first published the theory from his dissertation, biologists and researchers of other related disciplines were puzzled by what is known as the "problem of altruism" (cited from Cosmides & Tooby, 1992). The problem refers to a century long question of how to explain the existence and spread of a behavior or trait of an altruistic nature that helps RS of others at the sacrifice of one's own RS. In other words, how can the same Darwinian framework that allows the spread of selfish genes also allow the spread of altruistic genes? Hamilton solved this puzzle.

Although previous researchers such as R.A. Fisher and J. B. S. Haldane (cited from Trivers, 2000) also tried to tackle the problem of altruism, Hamilton was the first to provide serious mathematical proofs. In fact, the story goes that Hamilton's dissertation was so mathematical that it was at first neglected by people including his own professor because they did not fully understand the complicated game theory formulas and proofs. Today most social scientists are familiar with Hamilton's rule that an altruistic allele can spread if $C_i < B_j r_{ij}$, where C is the cost to individual i conducting the altruistic act, B is the benefit conferred to relative j , and r is genetic relatedness between individual i and relative j or the probability that relative j carries the same allele that is responsible for the altruistic behavior of individual i . Here, benefit and cost are both defined in terms of reproductive success. In words, an altruistic behavior or trait will

be selected for if and only if the individual expressing the behavior suffers less reproductively than the reproductive benefit the relative receives, weighed by the probability that the relative carries the same allele responsible for the altruistic behavior. If the reproductive cost to the altruistic individual exceeds the reproductive benefit the relative receives from the altruistic behavior, the behavior and underlying genes will be selected against.

To put this in a more familiar human relations context, you can benefit by helping your biological sister if your cost is less than .50 times the benefit your sister receives; the value of .50 represents the average genetic coefficient among full siblings. Assume your loss is 9 points and your sister's gain is 10 points. Then, there is no gain in inclusive fitness because 9 is higher than $10 \times .50$. However, if you were to help two biological sisters with the same cost and benefit points, then there is a gain in inclusive fitness because your cost of 9 points will be smaller than genetic-relatedness-weighted benefit of your two sisters, or $20 \times .5 = 10$. For the same gain in inclusive fitness, you will need to help four cousins (or first cousins) whose genetic relatedness is averaged to be .25. Alternatively, either your cost needs to be reduced or your cousins' benefit needs to be increased so that you may achieve inclusive fitness gains by helping fewer than four cousins. For example, if your cost is reduced to 1, then you may gain by helping one cousin because $1 < 10 \times .25$. In life, these cost-benefit calculations may translate into the possible experience that, for example, you are more likely to give \$5000 to your sister than to a remotely related cousin, unless you are extremely rich and thus \$5000 is not a big amount for you (i.e., reduced cost) or the money has a kind of life-saving effect on your cousin (i.e., increased benefit).

As a biologist, Hamilton developed inclusive fitness theory initially to explain the existence of the sterile worker castes in bees and other social insects that, until Hamilton, had puzzled Darwin and other evolution researchers. However, little did Hamilton know at the time that inclusive fitness theory now provides one of the central theoretical foundations of evolutionary psychology, as well as evolutionary biology. Many psychological studies have applied the theory to explain family relations (Euler, Hoier, & Rohde, 2001; Geary & Flinn, 2001; Grych, 2001), sibling rivalry (Linnda, 2001; Sulloway, 1995) and other issues (Sear, Mace, & McGregor, 2003).

Reciprocal Altruism, Tit for Tat, and Game Theory

Whereas Hamilton's rule emphasizes the importance of r , or the coefficient of genetic relatedness, what about the common experience of helping a friend who is not genetically related to us?

Hamilton's rule does not explain the fact that humans and animals have been widely observed to help genetically unrelated conspecifics, and sometimes members of other species. Why do squirrels give out warning calls to fellow counterparts who share no genetic relatedness? Why does a lucky vampire bat with a bulging stomach of blood from a night hunt regurgitate it to feed an unlucky cave mate who comes back from the night empty-stomached? Why do we humans commit heroic acts to save the lives of our comrades or friends who are not necessarily our relatives? These are the types of questions that were raised by Robert Trivers, one of the most creative biologists and scientists of the 20th century. The answer Trivers provided is reflected in the title of his first master piece, *The evolution of reciprocal altruism* (1971), which is also among the most important biology papers of the 20th century.

The idea of reciprocal altruism is the same as kin selection except that the emphasis on reciprocation replaces the need for genetic relatedness. An altruistic trait or behavior may be selected for if, with sufficient probability, the recipient of altruism will return the benefit to the altruistic sender. If the reproductive benefit the altruistic sender receives in return is larger than the cost initially incurred by the altruistic act, individuals who engage in this kind of reciprocal altruism will out-reproduce those who do not. Therefore, a seemingly altruistic trait (which actually is reciprocally altruistic) can spread in a population. The reciprocation does not have to be immediate but can be delayed as long as the individuals involved in the trade, so to speak, have sufficient long term memory. Such explains many features of human social life, where we do a favor to someone with the expectation that the favor will be remembered and returned in the future.

However, what if the favor, although remembered, is not returned? Unlike Hamilton's inclusive fitness where the selection of an altruistic allele is "secured" by the extent of genetic relatedness between the altruistic helper and the beneficiary, reciprocation is no guarantee and, in fact, its opposite, cheating or not reciprocating, is evolutionarily stable because cheaters are doubly rewarded reproductively, that is, they receive a benefit from helpers and, at the same time, helpers bear a cost for the cheaters, albeit the cost being smaller than the benefit. With this unlevelled "breeding ground," it is only a matter of time before the population should contain only cheaters. Indeed, receiving but not reciprocating help is evolutionarily stable (Maynard Smith, 1982), i.e., the strategy always wins out over others and thus ensures reproductive success. However, as Trivers observed, altruistic behavior, i.e., doing good to genetically unrelated, is widely observed in humans and animals. Thus, the question becomes how

altruism spreads in a population when cheating is an all-win evolutionarily stable strategy (ESS) – a strategy that becomes fixed in the population.

Ten years after the publication of *The evolution of reciprocal altruism*, an answer to the question came in a *Science* paper co-authored by Axelrod and Hamilton (1981). In this paper, *The evolution of cooperation*, Axelrod and Hamilton showed that reciprocating the help received from another individual is evolutionarily stable as long as there are enough altruistically minded individuals in a population. They also showed that a population of such minded individuals could initially emerge through inclusive fitness, that is, helping among genetically related individuals. Subsequent simulation work shows that only a small number of altruism minded individuals is initially needed for the emergence of reciprocation in a heterogeneous population (Nowak & Sigmund, 1992).

Axelrod and Hamilton's paper is also significant for applying game theory to evolutionary issues. This paper and *Evolution and the theory of games*, written by John Maynard Smith and published the next year in 1982, illustrate that the process of natural selection can be mathematically modeled using game theory. In essence, natural selection entails differential replication of genes. That is, different traits and attributes are selected for or against because of the different effects they have on their “own” genetic reproduction or replication. The differential replication process, independent of its underlying nature being biological, physiological, or psychological, can be approximated by game theory. Different game-theoretical strategies have imbedded probabilistic functions that result in their winning or losing a game, similar to the selecting-for or selecting-against of genes.

The game-theoretical strategy discussed in Axelrod and Hamilton's paper is called Tit for Tat and the game theoretical problem they used is called the Prisoner's Dilemma. The latter is a classic game theory problem where the theme of reciprocating or cooperating versus defecting or cheating is played out between two players of imaginary prisoners who can either tell on the other person (Defect) or cover for the other person (Cooperate) about a committed crime. Tit for Tat represents such a strategy that, in a repeated game, the player starts by not telling on the other player or cooperates and subsequently reciprocates the same action undertaken by the other player. That is, the player cooperates if the other player cooperates and defects if the other player defects.

Prior to the collaboration and publication with Hamilton, the political scientist Axelrod had conducted several world-wide computer contests to figure out what strategy would provide the best

solution to a repeated prisoner's dilemma game. The results from almost all of these contests consistently pointed to Tit for Tat as the winning strategy. Axelrod and Hamilton's 1981 *Science* paper put this strategy in the context of natural selection and provided the mathematical proofs that Tit for Tat is evolutionarily stable as long as there is a high probability that the players get to meet each other, i.e., if the game is continued infinitely or for a long time, as in life. As a game theoretical strategy, Tit for Tat essentially entails the same concept as Trivers' reciprocal altruism. Unlike Trivers' original publication which provides conceptual explanations and examples, Axelrod and Hamilton's paper provides more rigorous mathematical proofs of the viability or ESS (evolutionarily stable strategy) of reciprocal altruism (Trivers, 2002). (Note: Although later work showed that pure altruistic strategies such as Tit for Tat are not evolutionarily stable (Boyd & Lorberbaum, 1987; Lorberbaum, 1994), reciprocal altruism is, as shown by the viability of hybrid altruistic strategies (e.g., Lorberbaum, Bohning, Shastri, & Sine, 2002; Nowak & Sigmund, 1992; 1993).

Reciprocal altruism has since become one of the major theoretical foundations of evolutionary psychology and game theory and the repeated prisoner's dilemma game have also become popular tools by which to derive and test evolutionary psychological concepts. Social interactions similar in form to Tit for Tat are prevalent in our daily lives. When someone does you a favor, you feel you owe that person. If you fail to return the favor, you are likely to feel guilty and may try to find ways to overcompensate for your friend. Generally, when you do favors for another person, you are also likely to expect something in return. When that person fails to reciprocate, you may feel cheated and may opt to seek revenge by not being generous to the person in the future. On the other hand, when someone gives you a large gift for which you did not do anything, you may feel uncomfortable and even resentful because you do not want to owe the person a debt. Observed across cultures, these behaviors and emotions that have clearly been selected for are consistent with the Tit for Tat game theoretical strategy and reciprocal altruism. Many psychological research studies have been conducted that are based on reciprocal altruism as an evolved behavior responsible for most human social exchanges (e.g., Crawford, 1998; Burnstein, Candall & Kitayama, 1994).

Robert Trivers and Parental Investment Theory

If Wilson's *Sociobiology* first published in 1975 is credited with being among the first biology books that have applied evolutionary theories in explaining human behavior in an explicitly organized section, i.e., the last chapter of the book, much of Robert Trivers'

work has cross-disciplinary value in laying the foundations for evolutionary psychology. Partly because of his undergraduate education in history and his beginning career as a biology textbook editor for middle school students, the biologist and animal researcher has always maintained a conscious human touch, so to speak, in his work. In *The evolution of reciprocal altruism* (1971), for example, Trivers devoted one third of the paper to the discussion of human reciprocal altruism. His second master piece, *Parental investment and sexual selection* (1972), provides general principles of parent-offspring conflict and illustrates these with humans. This work also provides a core part of the theoretical foundations for evolutionary psychology.

In addition to discovery of the principles of natural selection, Darwin (1871) discovered the basic mechanisms that drive within species competition for mates (intrasexual competition) and choice of mating partners (intersexual choice). These reproductive dynamics are called sexual selection. George Williams (1966) and especially Robert Trivers (1972) expanded the concept by integrating competition and choice with relative parental investment. In other words, sex differences in degree of parental investment are the engine driving sexual selection and the evolution of all related sex differences. Trivers' theory starts with the evolution of sex cells. Sex cells as eggs and sperm were evolved from an originally undifferentiated state where all sex cells or gametes were similar but not identical in terms of appearances, size, or mobility. This state is believed to unstable because selection pressure would soon set in to drive the slightly bigger gamete to become bigger and bigger because size confers survival advantages for the offspring. On the other hand, competition to combine with the slightly bigger gamete (rather than the smaller ones) puts pressure on slightly smaller cells to become more mobile and, consequently, to become even smaller in size but plentiful in quantity in order to combine with more of the larger gametes. This double-bladed natural selection has resulted in eggs which are scarce and larger and carry more parental investment (e.g., nutrients in yoke) and sperm that are plentiful and smaller and carry little parental investment (Trivers, 1972).

Because of the differential initial parental investment, selection pressure favoring continued parental investment beyond insemination or ovulation would act only on the egg carriers or females in most species including humans but not on the sperm carries or males. Clutton-Brock and Vincent (1991) later determined that the sex difference in the tendency to parent is linked to a sex difference in the potential rate of reproduction, which is the biological limit on how many offspring males and females can potentially produce in their lifetime. The upper limit is

determined by how fast the individual can potentially reproduce. For mammals, such as humans, the biological limit for females is determined by gestation time and length of postpartum suckling. The limit for males is determined by the number of females for which they gain sexual access. The result is that it is in the best interest of males to compete for access to mates and females to invest heavily in a small number of offspring. Female investment, in turn, makes them valuable to males and thus allows them choice of mating partner.

In humans, continued female parental investment beyond insemination include nine months of gestation and the associated physical handicap of various degrees, the subsequent labor and giving birth to the young, and lactation and breast feeding, all of which compromise the mother's ability to sustain her own survival. For males, the necessary continuing parental investment beyond spermatozoa is none. Nonetheless, in some species, including humans, males invest well beyond by procuring food resources and helping to raise the young or, in other words, being a good father (Geary, 2000). However, this selection pressure is limited in comparison to that acting on female parental investment. Similarly, selection pressure on females to favor post-copulation male parental attributes, such as provisioning, is weaker than that favoring pre-copulation genetic attributes, such as signals of health, simply because females can choose whom to mate with but cannot prevent desertion after mating (Trivers, 1972). Thus, female sexual selection and the resulting male-male competition has led to preferred male attributes that may be more closely related to sexual prowess or overall fitness than post-copulation parental investment.

This selection pressure also favors visible, dramatic and exaggerated male displays, such as those found in the plumage of many species of bird. This characteristic is known as sexual signaling which, first noted by Darwin (1859), refers to the fact that the exact nature of a male attribute matters less than whether the attribute is extreme. It was debated for decades, but it appears that the extreme form is often favored because it takes the largest amount of investment (e.g., time, calories) to develop and maintain and thus serves as a good indicator of genetic fitness and likely health of his offspring. As Trivers put it, "Natural selection will always favor female ability to discriminate male sexual competence, and the safest way to do this is to take the extreme of a sample, which would lead to runaway selection for male display" (Trivers, 1972, p.96 of the 2002 reprint).

Finally, differential parental investment theory suggests that in most species male parental investment is not only limited, but is also more variable than female parental investment. Because of female sexual selection, male reproductive success depends on the

ability to attract mates more than parenting offspring. Thus, male reproductive success varies much more than female reproductive success. Males can also be more flexible in adopting different parenting and mating strategies than females in part because the non-obligatory male post-copulation parental investment allows more latitude in the extent to which investment is made in the offspring.

By accounting for the different amount of investment males and females put into parenting versus mating, Trivers' parental investment theory becomes one of the theoretical foundations of evolutionary psychology. Many creative applications of this theory by evolutionary psychologists also point to new directions by which to conduct "mainstream" parenting research (e.g., Bjorklund & Kipp, 1996; Bjorklund & Shackelford, 1999; Buss & Schmidt, 1993; Geary, 1998, 2000; Geary & Flinn, 2001; MacDonald, 1992). For example, most of the existing work on parenting focuses on mothers. Whereas this emphasis is consistent with the evolutionary view that female parental investment is obligatory in mammals, as shown by Trivers (1972), the larger variability in male parental effort would allow more latitude for researchers to explore environmental factors that may contribute to male, as well as female and single parent, parental investment decisions, as proposed by Draper and Harpending (1988) and Geary (2000). This view may fruitfully expand existing parenting work by including theories and variables about human sexuality and sexual relationships to account for additional variations in parenting and child socialization. In short, parental investment theory and the related evolutionary psychological view may shed new light on mainstream research on parenting, family relations and other developmental issues.

Life History Analysis

Another foundational area of biology that has influenced evolutionary developmental psychology is life history theory and analysis. Life history analysis is a research field in biology that analyzes survival and reproductive strategies from the perspective of the specific features or events of the organisms' life cycle. Examples of life cycle features, which are called life history traits, include size at birth, size and age at maturity, pubertal timing, generation lengths, and growth patterns, including lengths and other characteristics of childhood, adolescence, adulthood and old age (Wake, 2003). Characteristics of each of these life history traits represent survival or reproductive strategies or designs that have been selected for to best fit the various habitat-based ecological conditions or social dynamics at different points in the life span. For example, the black eagle lays two eggs a few days apart to result in the first hatchling being bigger and stronger than its younger

sibling. The stronger of the two gets most or all of the food and, being well fed, will have the strength to commit what biologists call "obligate siblicide" by pecking and tearing at the hungry younger sibling until the latter's death within two to three days of its hatching (Mock, 2004). This life history trait seems to fit the scarce food supplies that may normally be enough to feed one but not two extra mouths. However, the unpredictable nature of a predator's life means, once in a while, windfalls of abundant prey supplies may feed two extra mouths. The eagle's life history trait of laying and hatching the second egg has evolved because during a good season both chicks can be raised. The otherwise loner's life of an eagle also seems to fit its habitat which consists of a narrow ledge hanging over mountain cliffs under the vast sky. This is in contrast to many species of ducks that hatch between a dozen and half a dozen chicks and synchronize their hatchings to be around the same time so that young ducks are raised together in a communal kindergarten by the lake side, so to speak. This life history trait and imprinting enable each youngster to easily find its mother while enjoying the company of many playmates, and enable orphan chicks to be easily adopted by other families (Mock, 2004).

As an example of a human life history trait, our premature birth accommodates the narrow birth channel through which a fully developed and hardened skull cannot pass. This life history trait, together with the accompanying trait of a prolonged childhood, also ensures that much of the brain development interacts with and adapts to the environment in which the person is raised.

One assumption of life history analysis is that, because of limited energy that is used to fuel different survival- and reproduction-enhancing activities, allocation of finite energy entails trade-offs between what life history traits or tasks are relatively more urgent or valuable at the time and what are less urgent or valuable within an organism's ecological niche. Life history theory focuses on how, in the face of trade-offs, an organism "decides" to allocate time and energy to different life history events in ways that maximize survival and reproduction throughout its life cycle (Kaplan & Gangstad, 2005). There are three trade-offs: The trade-off between present and future reproduction, the trade-off between quantity and quality of offspring, and the trade-off between mating effort and parenting effort (Kaplan & Gangstad, 2005).

One human example of present-future reproductive trade-off is pubertal timing. In comparison to other primates, humans have a much longer childhood and adolescence that allow learning and brain development to take place (Bogin, 2001). This life history trait may also respond to environmental cues by shortening or prolonging reproductive readiness.

As first proposed by Draper and Harpending (1982), the onset of menarche in girls may depend on expected parental investment effort. Further theorizing by Belsky, Draper and Steinberg (1991) argues that increased stress leads to decreased parental investment which, as part of the childhood experience, hastens young girls' reproductive readiness possibly at the expense of schooling and learning. Chisholm (1999) argues that female menarche may be sensitive to cues of mortality risk which, when experienced in the form of lacking parental investment or having poor subsistence conditions, may activate the "strategy" of reproducing earlier rather than later. These predictions have led to consider empirical studies of the relation between early parental investment, especially that of the father, and later maturational timing and reproductive strategies of daughters (see Ellis, 2004, for a review).

In comparison to that of other primates and animals, human child rearing and family life serves as a good example of choosing quality over quantity of offspring. This strategy seems to fit and may have resulted in the life history trait of a prolonged human growth and learning period whereby the reliance on non-adult food, the replacement of temporary teeth, the enlargement of the brain, the much later eruption of molars and premolars, and the learning of various technical and social skills are all indicators of us humans adopting quality-oriented mating and parenting strategies. The offspring quantity-quality trade-off is closely related to the mating-parenting trade-off because quantity of offspring relies on mating effort and parenting effort leads to quality of offspring. The result of a prolonged developmental period and intense parental investment is increased social competitiveness, that is, an enhanced ability to compete for mates and other valuable resources in adulthood (Geary & Flinn, 2001).

The mating-parenting trade-off mainly concerns sex differences in initial parental investment. The high investing sex tends to put more effort in parenting, whereas the low investing sex tends to emphasize mating (Trivers, 1972). Although humans are far less dimorphic than most other primates and mammals, men are still more likely to opt for mating than parenting effort. Applied in evolutionary psychology, life history analysis also studies evolutionary forces that tip such trade-offs as that between mating and parenting effort (Ellis, 2004; Geary, 2002). Relationship cues raising paternity doubt should certainly trigger mating rather than parenting effort in men, as it does in other species in which males can invest in mating or parenting. With decrease in future reproductive values due to old age, illness, or lack of resources, men should favor parenting rather than mating effort even with explicit paternity doubt.

Methodologically, life history analysis is inherently developmental or ontogenetic (Bogin, 2000); it is also comparative by comparing the life history traits across different species (Wake, 2003) as well as within populations; its variables are often dichotomous with most of the life history traits conceptualized and quantified as two opposing dichotomies (Wake, 2003). The three trade-offs mentioned earlier are good examples that cover the life span and are used to draw dichotomous comparisons within and across populations. Other examples of dichotomous life history traits include life span as long versus short, reproductive strategy as quantity- versus quality-oriented, and population growth pattern as K versus r. The last life history dichotomy, K versus r population growth strategy, which has become increasingly popular in psychological writings including its use by Philippe Rushton to draw racial comparisons (See Rushton, 2000), warrants special attention.

K and r Population Growth Patterns

In the glossary of *The Theory of Island Biogeography*, Mac Arthur and Wilson (1967) provided the following definitions:

K selection: Selection favoring a more efficient utilization of resources, such as a closer cropping of the food supply. This form of selection will be more pronounced when the species is at or near K.

r selection: Selection favoring a higher population growth rate and higher productivity. This form of selection will come to the fore during the colonizing episode, or in species which are frequently engaged in colonizing episodes and hence must frequently build back up to K.

These are concepts from population genetics, where, in its mathematical formulations, K represents the maximum population size limited by the carrying capacity of a habitat and r represents the "intrinsic rate of (population) increase" in a given unit of time. In expanding and colonizing species in an un-crowded environment such as islands, the fitness strategy (i.e., population growth pattern) turns out to be r. In these situations, the genotypes which make the largest use of the habitat resources, even though doing so wastefully, will bear most offspring and be most fit. In these circumstances, selection will favor quantity of offspring, rather than quality. In a crowded environment, where species have reached the habitat's maximum carrying capacity, large families can not be sustained because of the depletion of resources. In these situations, the fitness strategy is K by which genotypes that can replace themselves with a small number of offspring at the least resources utilization level will be selected for. In this case, selection favors

quality in offspring, that is, offspring that are able to compete for access to diminishing resources.

Climate may tip the balance in favor of one of the two strategies. In rigorously seasonal climate where winter survivors re-colonize each spring, *r* selection is favored by the sudden abundance of food supplies. *K* strategies such as planning and being efficient are favored by the consistency and predictability of a temperate and moderate climate. For new colonizing species on an island, for example, *r* selection is also accompanied by a shorter life expectancy, whereas, when the species survives and reaches a large size, it will persist for a long time by adopting *K* population growth pattern.

To put it more simply, species adopting *r* population growth strategy have high population growth rate. They reproduce early and have large numbers of young that mature rapidly with little or no parental care. They live in unpredictable and changing climates (Wake, 2003). In terms of the three trade-offs, *r* strategists favor early rather than later reproduction, quantity rather than quality of offspring, and mating rather than parenting effort. *K* strategists breed slowly with a population growth curve that is maintained at or below the carrying capacity (*K*) of their habitat. They live in a stable and predictable environment and provide parental care for the few, large offspring who mature slowly (Wake, 2003). They tend to favor later reproduction, quality of offspring, and parenting.

The human population growth pattern certainly follows *K* in comparison to other primates and animals. *K* and *r* are used to draw such a distinction between human population growth pattern and that of other animals. In evolutionary psychology, however, *K* and *r* are more often used to draw group comparisons within the human species. Philippe Ruston was among the first to make such use of the *K-r* dichotomy to compare three human races. He theorized that Asians and, to a lesser extent, Caucasians are *K* strategists who have relatively high intelligence, pay attention to family planning and education, and are relatively less promiscuous (Rushton, 2000). Africans on the other hand adopt an *r* strategy by maturing earlier and being relatively more promiscuous, having more children who often face starvation, and having relatively low intelligence and paying little attention to education (Rushton, 2000). (Note that I am merely highlighting the use of *K-r* dichotomy but am not making an issue of Ruston's racial views.) Ever since Ruston, the *K-r* dichotomy has been loosely used in evolutionary psychology to draw the dichotomous comparison between people or populations of people whose behavior indicate a bias in favor of early reproduction, quantity of offspring, and mating effort of the three trade-offs, on the one hand, and, on the other hand,

people or populations whose behavior is biased toward the other dichotomy of the three trade-offs. Evolutionary psychologists also tend to use interchangeably such terms as population growth pattern, population growth strategy, selection strategy, mating strategy, parental strategy, reproductive strategy loosely to draw the same *K-r* comparison. That is, for example, "*K-r* mating strategy" carries more or less the same meaning as "*K-r* population growth strategy," although the former may more narrowly focus on reproductive effort.

The Baldwin Effect and Niche Construction

Another evolutionary biological concept that has also found its way into evolutionary psychology is what is referred to as the Baldwin effect. It came from James Mark Baldwin who is best remembered today for his paper, "A new factor in evolution" (Baldwin, 1896). In this and other papers of his, Baldwin expressed the idea that, under some conditions, learned behaviors can affect the direction and rate of the evolutionary change by natural selection. There are three steps. First, learning or interaction with environment results in phenotypic changes that are adaptive. Second, mutations occur that lead to the same adaptive phenotypes initially produced only in response to environmental influences such that the expression of the phenotypes is in part heritable. Third, selection comes to favor the mutated genotype leading to genetic inheritance of environmentally induced phenotype or learned behavior (Hall, 2003). George Gaylord Simpson in a 1953 paper first named this evolutionarily unconventional idea the Baldwin effect which has since become an important topic of discussion in biology (Hall, 2003; West-Eberhard, 2003) and psychology (Bjorklund, 2006). In a way, the Baldwin effect refers to a learning effect. The learning effect takes place by changing the context of selection so as to speed up the otherwise random process in searching or hitting onto a hereditary or genotypic solution to an evolutionary challenge.

Because of its emphasis on learning, some of the ideas underlying the Baldwin effect are especially useful in psychology. Deacon (1997) made an unconventional use of the Baldwin effect in explaining cognitive and language evolution. Take reading and writing for example. Since reading ability should have an effect on reproductive success, reading and writing abilities which are initially acquired through learning can be selected for. Thus, the Baldwin effect can be used to explain culture as a facilitator of evolution (Deacon, 1997). When the result of learning spreads culturally and if it adds to reproductive success, it creates a new selection pressure by making certain genes visible to selection for the first time. If this selection pressure continues in successive generations, the originally learned

innovation or practice or culture can eventually come under genetic control and thus become a candidate for natural selection. Deacon (1997) argues that advanced thinking or symbolic representations and language use can in turn change the context of selection leading to rapid evolution of a large and complex brain. Dennett (1991) used the Baldwin effect to explain the evolution of consciousness, as shown by the title of his book, *Consciousness Explained*. In his later book, *Darwin's Dangerous Idea*, Dennett (1995) talked about how the random search for the correct genetic solution can be considerably speeded up by learning and how "the redesign at the genotype level" through natural selection may also "follow the lead of and confirm" the organism's learning and exploration or "redesign at the individual or phenotype level" (Dennett, 1995; p.78).

Similar to but also extending the Baldwin effect concept is the theory of niche construction. Niche construction emphasizes an even closer and more imbedded relation between the environment and organisms. The latter is not a passive receiver of environmental influences but is an active constructor of its environment (Lewontin, 1983). The organism-environment relationship is reciprocal and dialectical. Using Lewontin's famous analogy, evolution does not follow a "lock and key" model whereby environments present challenges, i.e., the locks, which would be solved by adaptations, i.e., the keys. Instead, environments are not static, objective, or separated but are constructed parts of the organism's solution to the problem. "Organisms do not adapt to their environments; they construct them out of the bits and pieces of the external world" (Lewontin, 1983, p.280).

The famous evolutionary biologist, Richard Lewontin, was among the first to develop the niche construction theory. Other authors have also contributed to the development and insemination of niche construction. Among them is the equally famous Richard Dawkins. In his first book, *The Selfish Gene*, Dawkins (1976) introduced the concept of a meme. Like genes which are genetic replicators, memes are cultural replicators. In his next book, *The Extended Phenotype* (1982), Dawkins extended the memetical idea by arguing that culture and technology are simply extended phenotypes which do not have to be bounded by physically produced genes. Like beavers' dams or groundhogs' underground tunnels, the human culture is the result of genes changing the environments of their hosts, i.e., organisms who are genes' vehicles. Such environmental modifications as beavers' dams and human culture in turn contribute to gene replications. Thus, the modified environments themselves such as culture and technology are phenotypes or extended phenotypes. Although not explicitly mentioning niche construction, Dawkins echoed but also extended Lewontin by emphasizing

human creative activities and behaviors as niche construction.

Lewontin's conception was formalized into more detailed models by Feldman, Laland, and Odling-Smee among others (e.g., Odling-Smee, Laland, & Feldman, 2003). In addition to elaborating and substantiating with much evidence the different niche construction concepts, these authors have also presented a reciprocal feedback process of evolution by which environmental modifications and natural selection interact with each other. More than the specific and detailed theorizing and delineating of niche construction, the flexibility and creativity by which these authors view evolution should provide an interesting direction for evolutionary psychology that is often caught between eschewing the standard social science model (Tooby & Cosmides, 1992) and being criticized as teleological, i.e., effects imply causes (Silverman in this issue). Use parenting research as an example. The standard social science model would predict child aggression, for example, from harsh parenting. The evolutionary psychological framework would use child aggression against parents and siblings, for example, as evidence to prove the evolutionary mechanism known as parent-offspring conflict (Trivers, 1974). By the principle of niche construction theory, one would consider parenting behaviors and parent-child relationships as gene-determined niche construction upon which socialization would its effect to result in a different extent and different kind of aggressive phenotype (see also Scarr & McCartney, 1983). Since aggression should have an impact on reproductive success, the feedback loop process would be complete when differentially exposed aggression phenotypes result in different parenting-related niche construction in succeeding generations. In short, the different and more flexible interpretation of evolution that is behind niche construction theory may open up new channels by which to extend and expand evolutionary psychology.

References

- Axelrod, R., & Hamilton, W. D. (1981). The evolution of cooperation, *Science*, *211*, 1390-1396.
- Baldwin, J. M. (1896). "A New Factor in Evolution." *American Naturalist*, *30*, 441-451, 536-553.
- Belsky, J., Steinberg, L., & Draper, P. (1991). Childhood experience, interpersonal development, and reproductive strategy. *Child Development*, *62*, 647 - 670.
- Bjorklund, D. F. (2006). Mother knows best: Epigenetic inheritance, maternal effects, and the evolution of human intelligence. *Developmental Review*, *26*, 213-242.
- Bjorklund, D. F., & Kipp, K. (1996). Parental investment theory and gender differences in the evolution of inhibition mechanisms. *Psychological Bulletin*, *120*, 163-188.
- Bjorklund, D. F., & Shackelford, T. K. (1999). Differences in parental investment contribute to important differences between men and women. *Current Directions in Psychological Science*, *8*, 86-89.
- Bogin, B. (2001). *The growth of humanity*. New York: John Wiley & Sons, Inc, Publication.

- Borrello, M. E. (2003). Synthesis and Selection: Wynne-Edwards' Challenge to David Lack. *Journal of the History of Biology*, 36, 531-566.
- Boyd, R., & Lorberbaum, J. P. (1987). No pure strategy is evolutionarily stable in the repeated prisoner's dilemma game. *Nature*, 327, 58-59.
- Burnstein, E., Candall, C., & Kitayama, S. (1994). Some neo-Darwinian decision rules for altruism: Weighing cues for inclusive fitness as a function of the biological importance of the decision. *Journal of Personality and Social Psychology*, 67, 773-789.
- Buss, D. M., & Schmidt, D. P. (1993). Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review*, 100, 204-232.
- Chang, L., Zhang, L., Li, H., Wong, L.H., & Mo, L. (2006). Folk physics and folk psychology: An evolutionary psychological perspective. *Psychological Exploration*, 26, 9-13.
- Chang, L., Lin, D., Li, H., Zhang, L., & Mo, L. (in press). The evolutionary modularity view about cognition. *Psychological Science*.
- Chisholm, J. S. (1999). *Death, hope and sex: Steps to an evolutionary ecology of mind and morality*. Cambridge: Cambridge University Press.
- Clutton-Brock, T. H., & Vincent, A. C. J. (1991, May 2). Sexual selection and the potential reproductive rates of males and females. *Nature*, 351, 58-60.
- Corballis, M. C. (1999). Phylogeny from apes to humans. In M. C. Corballis & S. E. G. Lea (Eds.), *The descent of mind* (pp.40-70). Oxford: Oxford University Press.
- Cosmides, L., & Tooby, J. (1992). Cognitive Adaptations for Social Exchange. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: evolutionary psychology and the generation of culture* (pp.163-228). New York: Oxford University Press.
- Crawford, C. (1998). The theory of evolution in the study of human behavior: An introduction and overview. In C. Crawford, & D. Krebs (Eds.), *Handbook of evolutionary psychology: Ideas, issues, and applications* (pp. 3-42). Mahwah, NJ: Lawrence Erlbaum Associates.
- Darwin, C. R. (1859). *The origin of species*. New York: Random House Value Publishing, Inc., 1979.
- Darwin, F. (1877). *The life and letters of Charles Darwin*. University Press of the Pacific, 2001.
- Dawkins, R. (1976). *The selfish gene*. New York: Oxford University Press.
- Dawkins, R. (1982). *The extended phenotype: The gene as the unit of selection*. San Francisco: Freeman.
- Deacon, T.W. (1997). *The symbolic species: The co-evolution of language and the brain*. New York: W.W. Norton & Company.
- Dennett, D. C. (1991). *Consciousness explained*. Boston: Little, Brown and Company.
- Dennett, D. C. (1995). *Darwin's dangerous idea: Evolution and the meanings of life*. New York: Allen Lane.
- Desmond, A., & Moore, J. (1994). *Darwin: Life of a tormented evolutionist*. New York: Norton.
- Draper, P., & Harpending, H. (1982). Father absence and reproductive strategy. *Journal of Anthropological Research*, 38, 255-272.
- Draper, P., & Harpending, H. (1988). A sociobiological perspective on the development of human reproductive strategies. In K. B. MacDonald (Ed.), *Sociobiological perspectives on human development* (pp. 340-372). New York: Springer-Verlag.
- Ellis, B. J. (2004). Timing of pubertal maturation in girls: An integrated life history approach. *Psychological Bulletin*, 130, 920-958.
- Euler, H., Hoier, S., & Rohde, P. (2001). Relationship-specific closeness of intergenerational family ties: Findings from evolutionary psychology and implications for models of cultural transmission. *Journal of Cross-Cultural Psychology*, 32, 147-158.
- Geary, D. C. (1998). *Male, female: The evolution of human sex differences*. Washington, DC: American Psychological Association.
- Geary, D. C. (2000). Evolution and proximate expression of human paternal investment. *Psychological Bulletin*, 126, 55-77.
- Geary, D. C. (2002). Sexual selection and human life history. In R. Kail (Ed.), *Advances in child development and behavior* (Vol. 30, pp. 41-101). San Diego, CA: Academic Press.
- Geary, D. C., & Flinn, M. V. (2001). Evolution of human parental behavior and the human family. *Parenting: Science and Practice*, 1, 5-61.
- Grych, J. H. (2001). On the origins of fathering: implications of an evolutionary perspective for understanding links among marriage, divorce, and men's parenting. *Parenting: Science and Practice*, 1, 67-70.
- Hall, B. K. (2003). Baldwin and Beyond: Organic Selection and Genetic Assimilation. In B. H. Weber & D. J. Depew (Eds.), *Evolution and Learning* (pp. 141-167), Cambridge, Mass.: MIT Press.
- Hill, K. (1993). Life history theory and evolutionary anthropology. *Evolutionary Anthropology*, 2, 78-88.
- Hodgson, G. M. (2004). Malthus, Thomas Robert (1766-1834). In R. Rutherford (Ed.), *Biographical dictionary of British economists*. Bristol: Thoemmes Continuum.
- Kanazawa, S. (2006). No, it ain't gonna be like that. *Evolutionary Psychology*, 4, 120-128.
- Kaplan, H.S., & Gangstad, S.W. (2005). Life history theory and evolutionary psychology. In D.M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 68-95). New Jersey: John Wiley and Sons, Inc.
- Lewontin, R.C. (1983). Gene, organism, and environment. In D. S. Bendall (Ed.), *Evolution: From Molecules to Man* (pp. 273-385). Cambridge: Cambridge University Press.
- Li, K., (1985). *The New Synthesis*. Chengdu: Sichuan People Press.
- Li, H., Chang, L., (in press). A life history analysis of puberty timing and adolescent development. *The Chinese Mental Health Journal*.
- Li, H., & Chang, L. (in press). The paternal certainty, child rearing and child development. *The Chinese Mental Health Journal*.
- Li, J., & Hong, F. (2003). Science as ideology: The rejection and reception of sociobiology in China. *Journal of the History of Biology*, 36, 567-578.
- Linnda, R. (2001). Evolutionary Psychology: Toward a unifying theory and a hybrid science. *Annual Review of Psychology*, 52, 607-628.
- Lorberbaum, J. P. (1994). No strategy is evolutionarily stable in the repeated prisoner's dilemma. *Journal of Theoretical Biology*, 168, 117-139.
- Lorberbaum, J. P., Bohning, D. E., Shastri, A., & Sine, L. E. (2002). Are there really no evolutionarily stable strategies in the iterated prisoner's dilemma? *Journal of Theoretical Biology*, 214, 155-169.
- MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
- MacDonald, K. (1992). Warmth as a developmental construct: An evolutionary analysis. *Child Development*, 63, 753-773.
- Malthus, T.R. (1797). *T.R. Malthus, An essay on the principle of population, Oxford world classic papers*. New York: Oxford University Press, 1993.
- Maynard Smith, J. (1982). *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.
- Maynard Smith, J., & Szathmary, E. (1995). *The major transitions in evolution*. New York: Oxford University Press.
- Miller, G. (2006). The Asian future of evolutionary psychology. *Evolutionary Psychology*, 4, 107-119.
- Mock, D.W. (2004). *More Than Kin and Less Than Kind: The Evolution of Family Conflict*. The Belknap Press of Harvard University Press.
- Nowak, M., & Sigmund, K. (1992). Tit for Tat in heterogeneous populations. *Nature*, 355, 250-253.
- Nowak, M., & Sigmund, K. (1993). A strategy of win-stay, lose-shift that outperforms tit-for-tat in the Prisoner's Dilemma game. *Nature*, 364, 56-58.
- Odling-Smee, F. J., Laland, K., & Feldman, M. W. (2003). *Niche construction: The neglected process in evolution*. Princeton: Princeton University Press.
- Pinker, S. (2006). The blank slate. *General Psychologist*, 41, 1-8.
- Rushton, J. P. (2000). *Race, evolution, and behavior: A life-history perspective* (3rd ed.). Port Huron, MI: Charles Darwin Research Institute.
- Scarr, S., & McCartney, K. (1983). How people make their own environments: A theory of genotype greater than environment effects. *Child Development*, 54, 424-435.
- Sear, R., Mace, R., & McGregor, I. (2003). The effects of kin on female fertility in rural Gambia. *Evolution and Human Behavior*, 24, 25-42.

- Sober, E. (1981). Holism, Individualism, and the Units of Selection. In R. Giere & P. Asquith, (eds.), *PSA 1980* (vol. 2, pp. 93-121). East Lansing, MI: Philosophy of Science Association.
- Sober, E., & Wilson, D. S. (1998). A Critical Review of Philosophical Work on Units of Selection Problem. *Philosophy of Science*, 61, 534-555.
- Sulloway, F. J. (1995). Birth order and evolutionary psychology: A meta-analytic overview. *Psychological Inquiry*, 1, 75-80
- Tooby, J. & Cosmides, L. (1992). The psychological foundations of culture. In J. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 19-136). New York: Oxford University Press.
- Trivers, R. L. (1971). The evolution of reciprocal altruism. *The Quarterly Review of Biology*, 46, 35-57.
- Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man 1871-1971*, (pp. 136-179). Chicago: Aldine Publishing Company.
- Trivers, R. L. (1974). Parent-offspring conflict. *American Zoologist*, 14, 249-264.
- Trivers, R. L. (2000). Obituary: William Donald Hamilton (1936-2000). *Nature*, 404, 828.
- Trivers, R. L. (2002). *Natural selection and social theory: Selected papers of Robert Trivers*. New York: Oxford University Press.
- Wake, M. H. (2003). Life History Evolution. In B. K. Hall, & W. M. Olson, (Eds.), *Keywords and concepts in evolutionary developmental biology* (pp. 234-242). Cambridge, Mass.: Harvard University Press.
- West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. New York: Oxford University Press.
- Whitaker, R. (2005). Malthus, Thomas Robert: Introduction. In R. Whitaker (Ed.), *Nineteenth-century literary criticism*, Vol. 145. Thomson Gale. eNotes.com, 2006. <http://www.enotes.com/nineteenth-century-criticism/malthus-thomas-robert>.
- Williams, G.C. (1966). *Adaptation and natural selection: A critique of some current evolutionary thought*. Princeton: Princeton University Press.
- Wilson, D. S., & Sober, E. (1994). Reintroducing Group Selection to the Human Behavioral Sciences. *Behavior and Brain Sciences*, 17, 585-654.
- Wynne-Edwards, V. C. (1962). *Animal Dispersion in Relation to Social Behavior*. Edinburgh: Oliver and Boyd.
- Xu, B. (2004). *Evolutionary psychology: A new approach of the development of psychology*. Beijing: Social Science Press.
- Ye, H. (2005). Evolutionary psychology's way of thinking and its implications. *Advances in Psychological Science*, 13, 847-855.
- Yue, G., Chen, H., & Zhang, Y. (2005). Verification of evolutionary hypothesis on human mate selection mechanism in cross-culture context. *Acta Psychologica Sinica*, 37, 561-568.
- Zhang, B. (1987). Marxism and human sociobiology: A comparative study from the perspective of modern socialist economic reforms. *Biology and Philosophy*, 2, 463-474.
- Zhang, B. (1994). *Marxism and human sociobiology: The perspective of economic reforms in China*. Albany: State University of New York Press.
- 胡适作品集 2. 台北远流出版公司, 1986 (Collection 2 of Essays of Hu Shi)
- 孙中山选集第一卷. 北京: 中华书局, 1981 (Volume 1 of Essays of Sun Yat Sen)
- 王小明 (2005). 西方进化论与近代中国社会 (Evolution and Contemporary Chinese Society and History). *教学与研究*, 10, 70-75.
- 张润生等 (1983). 中国古代科技名人传 (Important Scientists of Ancient China). 中国青年出版社.