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A Concise Introduction

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David McFarland
Emeritus Fellow, Balliol College, University of Oxford, UK

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Preface

This book is firmly aimed at students of economics. It offers an opportunity to think about microeconomics from a biological viewpoint. Biologists may well be dissatisfied by the level of explanation, but we have in mind that economics students, on the whole, have relatively little biological background. Economists may well be dissatisfied with the level of economic detail, but we are assuming that economics students will be getting that anyway.

Economics students do not have to defend any particular viewpoint. Given time, they can choose their own particular viewpoint. All we hope to do in this book is to stimulate some thought along biological lines.

The first Nobel Prize for Economics was awarded to Ragnar Frisch and Jan Tinbergen in 1969. Jan Tinbergen's brother, Niko Tinbergen, was awarded the Nobel Prize for Medicine, together with Karl von Frisch and Konrad Lorenz in 1973.

Niko Tinbergen believed that the behaviour of any animal could only be properly understood in terms of four questions (causation, development, function, and evolution). Humans are animals, and it seems to be an irony of history that Tinbergen's four questions are not asked, or addressed by economists, in relation to the economic behaviour of humans. One would hope that behavioural economists, at least, would have some grasp of these essentials, but it seems to us that there has been little progress since John Maynard Keynes, in 1936, conjured up "animal spirits" to account for the apparently aberrant behaviour of economic man. I thank my friend Tom Bosser for encouraging me to start this book, and I thank my wife, Penelope, for putting up with the consequences.

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The Evolution of Economic Behaviour

The biological bases of economics include all those biological factors that influence the economic behaviour of individual animals. Humans are animals, and another way of addressing the subject is to ask – what are the fundamental biological factors that influence microeconomic behaviour? We need to start with some fundamental biological concepts, because human behaviour, including economic behaviour, is the product of evolutionary pressures that are the result of **natural selection**, whether they be cultural or genetic. Any student of economic behaviour should consider whether, and to what extent, such influences are important, because it is possible that the homunculus within current economic theory may be too simple, and not truly representative of the behaviour of ordinary people. In this book we will be exploring an array of biological phenomena, and inviting the student of economics to consider to what extent they are relevant to the modern economic situation.

Evolution by natural selection

Biological evolution is the development of species' characteristics from earlier forms, now acknowledged to be due to the process of natural selection. Animal behaviour can only be fully understood in terms of its evolutionary history, and in terms of the role that it plays in survival and reproduction (more precisely, the **inclusive fitness** of the animal).

Evolutionary biologists are interested in explaining how a state of affairs observed today (such as the behaviour typical of a certain species) is likely to have come about as a result of evolution by natural selection. To account for the establishment of a particular genetic trait, they imagine a time before the trait existed. Then they postulate that a rare gene arises in an individual, or arises with an immigrant, and that individuals carrying the gene exhibit the trait. They then ask what circumstances will favour the spread of the gene through the population. If a gene is favoured by natural selection, then individuals with genotypes incorporating the gene will have increased fitness. The gene may be said to have invaded the population. To become established a gene must not only compete with the existing members of the gene pool, but must also resist invasion by other mutant genes. It is as if genes develop a strategy to increase their numbers at the expense of other genes. Thus an **evolutionary strategy** is a passive result of natural selection that gives the appearance of a ploy employed by genes to increase their numbers at the expense of other genes. So an evolutionary strategy is not a strategy in the cognitive sense, but a theoretical tool employed by evolutionary biologists.

Life history strategy

Individual animals are born, enjoy a particular lifestyle, and then die. The characteristic lifestyle of a given species is the subject of life-history theory. This body of theory asserts that natural selection shapes the timing and duration of key events of an organism's life to produce the greatest possible number of surviving offspring.

The most important events include juvenile development, the age of sexual maturity, the timing of reproductive events, the number and size of offspring, the level of parental investment, and the lifespan that is typical of the species. For a given individual, the resources that can be allocated to these events are finite. The time and energy devoted to one event diminishes the time and energy available for the others.

Of prime importance is the notion of **reproductive value**, the expected contribution to the population by current and future reproduction. Animal species that live in unpredictable or unstable environments usually reproduce quickly (i.e. have a short generation period). There is little advantage in adaptations that permit competition with other animals, since the environment is likely to change. They tend to invest in numerous, inexpensive offspring that disperse widely. For species that inhabit stable and predictable environments competition with other animals is an important factor. Such species tend to have a long generation period and few well-cared-for offspring. Examples include elephants, whales, and humans. The majority of animals fall between these two extremes. Indeed we can look at the situation as a life-history spectrum. The implication of this line of thinking is that it is in the nature of individual humans (i.e. their characteristic **life-history strategy**) to care not only for their personal lifestyle, but also for that of their offspring and relatives. You may think this a bit far-fetched, but consider the following.

The experimental physiologist Michel Cabanac (a name to remember) asked his subjects (students) to adopt a certain posture and to hold this posture for as long as they could. It was a sitting posture, back against a wall but with nothing to sit on. After a short while holding this posture becomes painful. In a series of experiments Cabanac paid the subjects differing amounts (per session) per second for holding the posture for as long as they could. He found that, within limits, the greater the rate of pay, the longer the subjects would hold the painful posture. This experiment was repeated in Oxford, but with a difference. In some sessions, the money went, not to the subject, but to a named relative of the subject. In other words, the subject was told before the session that today the money would be sent to their aunt, or cousin, and so on. The subjects had previously been asked for details of their relatives. The amounts of money sent out were rather small, usually about £1. The experiment was then repeated in London, and in South Africa where the subjects were Zulus from both urban and rural backgrounds (in the latter case the payment was made in food).[1] In all cases it was found that the subjects would hold the posture for longer the more closely related (in terms of their **coefficient of relatedness**) they were to the recipients of the money/food. In other words, the subjects were putting up with pain, not for their own benefit, but for that of a relative. Apart from the biological implications of these results (see below) there are economic implications. They suggest that a person's economic aspirations are likely to include benefits to relatives, albeit implicitly.

Kith and kin

It is a biological imperative for parents to be able to identify their offspring. For example, amongst a flock of sheep, when the young lambs gather together in play, there is a danger that a mother may have her milk taken by a lamb that is not hers. She identifies her offspring by smell, turning around to check whoever is suckling. To permit another's lamb to suckle would be a form of **altruism.**

Altruistic behaviour benefits other animals at some cost to the donor. In evolutionary biology, altruism is defined by reference to its effects on survival prospects without reference to any motivation or intention that may be involved. The possibility that animals may have altruistic or selfish intentions is, of course, of interest, but it is not relevant to consideration of altruism from an evolutionary point of view. This distinction is sometimes forgotten.

As we have seen, the age at which an animal should ideally become sexually mature and capable of reproduction is a matter of evolutionary life-history strategy. In unpredictable environments natural selection usually favours early maturity and large numbers of offspring which are left to fend for themselves. In more stable environments it is a better strategy to mature late and have few offspring which are well cared for. In general, the more time and energy a parent expends upon a particular offspring, the fitter that offspring will be. There is often an inverse relationship between the total number of offspring produced and their average fitness. An animal's individual fitness is a measure of its ability to leave viable offspring. The process of natural selection determines which characteristics of the animal confer greater fitness. However, the effectiveness of natural selection depends upon the mixture of genotypes in the population. Thus, the relative fitness of a genotype depends upon the other genotypes present in the population, as well as upon other environmental conditions.

The concept of fitness can be applied to individual genes by considering the survival of particular genes in the gene pool from one generation to another. A gene that can enhance the reproductive success of the animal carrying it will thereby increase its representation in the gene pool. It could do this by influencing the animal's morphology or physiology, making it more likely to survive climatic and other hazards, or by influencing its behaviour, making the animal more successful in courtship or raising young. A gene that influences parental behaviour will probably be represented in the offspring so that by facilitating parental care, the gene itself is likely to appear in other individuals. Indeed, a situation could arise in which the gene could have a deleterious effect upon the animal carrying it but increase its probability of survival in the offspring. An obvious example is a gene that leads the parent to endanger its own life in attempts to preserve the lives of its progeny. This is a form of altruism.

By the mid 20th century, biologists had realized that the fitness of an individual gene could be increased as a result of altruistic behaviour on the part of animals carrying the gene. However, William Hamilton (1964) was the first to enunciate the general principle that natural selection tends to maximize not individual fitness but inclusive fitness; that is, an animal's fitness depends upon not only its own reproductive success but also that of its kin. The inclusive fitness of an individual depends upon the survival of its descendants and of its collateral relatives. Thus even if an animal has no offspring its inclusive fitness may not be zero, because its genes will be passed on by nieces, nephews, and cousins.[2]

Reciprocal altruism

Altruism towards kin can be regarded as selfishness on the part of the genes responsible, because copies of these genes are likely to be present in relatives. Altruism could also be regarded as a form of gene selfishness if by being altruistic an individual could ensure that it was a recipient of altruism at a later date. The problem with the evolution of this reciprocal kind of altruism is that individuals that cheated, by receiving but never giving, would be at an advantage.

It is possible that cheating could be countered if individuals were altruistic only toward other individuals that were likely to reciprocate. For example, when a female olive baboon (*Papio anubis*) comes into oestrus, a male forms a consort relationship with her. He follows her around, waiting for an opportunity to mate, and guards the female from the attentions of other males. However, a rival male may sometimes solicit the help of a third male in an attempt to gain access to the female. While the solicited male challenges the consort male to a fight, the rival male gains access to the female. The altruism shown by the solicited male is often reciprocated. Those males that most often gave aid were those that most frequently received such aid.[3]

This type of **reciprocal altruism** obviously provides scope for cheating. An individual that receives aid may refuse to reciprocate at a later date. However, if opportunities for reciprocal altruism arise sufficiently often, and if the individuals involved are known to each