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I wish to express my thanks to the Board of the Fyssen foundation and to its scientific committee for their decision to give me the Fyssen prize and for the invitation and the honour to come to Paris and present this talk. The theory I shall present in this talk, with its wide implications for signaling and the evolution of altruism, was developed with my wife Avishag Zahavi and with the help of many students. Thanks to all.

I am especially indebted to my late teachers: my mentor in Israel Heinrich Mendelssohn who coached my childhood enthusiasm of watching birds into meticulous observations and raised my interest in conservation; to Niko Tinbergen who showed me that observing birds can be a scientific task, and to David Lack who convinced me that all adaptations evolved from the direct contribution of traits to the fitness of the individual.

I have been watching birds from early childhood. In 1971 I returned to science after investing 15 years in establishing conservation in Israel, creating and acting as the general secretary of the NGO, "The Society for the protection of Nature in Israel."

In the early seventies I developed the hypothesis of the handicap principle to explain why peahens prefer peacocks with a long and heavy tail that handicap their ability to move and avoid predators. The prevailing argument at that time was that since all females prefer long tailed males, a female that mates with such a male would bear male offspring that will be attractive to the females.

I suggested an alternative. I suggested that the burden, the handicap that the tail imposes, is a test for the ability of the male to move in spite of the handicap. My model also explains why the long tail deter male rivals, since it is a reliable evidence of quality.

Once I realized that the tail is a handicap that tests the information about the phenotypic quality of the peacock, I started to examine whether other signals also test the reliability of the information encoded in them. I was able to discover handicaps (tests) in signals given by voice, colour patterns, movements, body form and also in chemical signals and even in signals within the body.

If signals are tests of the reliability of the information encoded in them, then there must be a logical relationship between the properties of a signal and the information it provides. For example, a rich man advertises his wealth by waste, something a poor man cannot do. Courage can be signaled by taking risks that cowards do not dare to take. This relationship can help one understand the messages encoded in signals, and can explain why a particular signal is selected to transfer a particular message. The handicap is an investment that increases the fitness of an honest individual that takes a handicap which fits its quality, but it decreases the fitness of individuals that try to invest in the handicap more than their quality permits. In other words, the handicap guards against cheating.

The handicap principle shaped also the human body. For example, in close combat a beard is a real handicap, because the rival can grab it and pull his opponent out of balance. For this reason Alexander the great ordered his soldiers to shave before battle. Women's breasts advertise their fat reserves, an important asset for reproduction when food is not readily available.

Another interesting use of handicaps is in imposing handicaps on a partner, a mate or a friend. It is possible to test the motivation of a partner to invest in the partnership by imposing a handicap. When a man holds the hand of his girlfriend he turns both himself and her into one handed persons with somewhat limited ability to move. When he embraces her he deprives her of the freedom to move. When partners accept the burden of a handicap imposed by their partners, they display in a reliable way their motivation to keep the social bond.

As a parent I did not realize that when I was reading for my children their favorite book at bed time, I was tested by my children about my willingness to invest time in them. By listening to a story the child knows well, the child is able to assess the time and patience the parent is willing to invest in the child. Reading a story is a handicap that displays in a reliable way the social bond of the parent to the child at that particular evening as compared to former evenings. That is why children have their favorite books; a new story will not give them a base for comparison.

Signalers compete with each other on the attention of observers. They invest in handicaps in order to convince observers that they are better than their competitors. But what happens when changing circumstances make it easy for all to signal alike? Signals then lose their value as a mean to display differences among individuals and are consequently selected out. This process is similar to the inflation of currency when money is easily acquired. In contrast, traits which are not signals persist even if all can use them alike. For example, peacocks most probably have evolved in India, a country with many predators. The handicap of the heavy cumbersome tail, serves to display the ability of the peacock to escape predators in spite of its tail. In Japan peacocks were introduced to parks with few predators. After many generations peahens no longer appreciate the size of the peacock's tail but rather are attracted to peacocks

according to their ability to quiver the tail, which probably tests another quality. The inflation-like process of signals suggests that signals are selected by a different selection mechanism from that of all other traits.

Darwin already suggested that natural selection cannot fully explain the evolution of all traits. Therefore he proposed the theory of Sexual Selection as a second selection mechanism to explain the evolution of traits such as the peacock's tail. Unfortunately Darwin did not demarcate clearly the difference between the two selection mechanisms, and the term sexual selection persists at present only to describe a set of traits that are involved with sex. I follow Darwin's suggestion that two selection mechanisms function in evolution. But I suggest that they are the selection of signals for reliability, and the selection of all other traits for efficiency. The evolution of signals decreases efficiency, while selection for all other traits increases efficiency.

The existence of two opposing selection processes that benefit the individual, one which increases efficiency and the other that decreases it, provides the way to evolve new body parts such as horns and feathers, which selection by efficiency alone could not create.

With the help of Avishag (my wife who is also a biologist) we wrote a book: "The Handicap Principle" in which we describe the evolution of signals in many modalities and their function in several social systems, including that of man. Unfortunately the book is not available in the French language.

Perhaps the most important result of the handicap principle is its potential to explain the evolution of altruism as a handicap that advertises a claim for social prestige (or "Image scoring" as some prefer to call it now). We have learned it from the babblers. Over the last 40 years we have been working in the desert of the rift valley with a population of some 20 groups of hand-habituated colour-ringed individuals.

Babblers live in groups which are usually composed of several males and several females, often with several adult offspring. Babblers perform a great variety of altruistic acts: perching as sentinels when other individuals feed, sharing food with other adult group members even when they are still hungry, risking themselves by mobbing predators or defending the common territory and tending to offspring which are not their own.

We found that babblers compete with one another to act as altruists, and that dominants often interfere aggressively with the subordinates that try to act as altruists. These observations could only be explained by the assumption that the individual babbler gains directly from its altruistic activities. We propose that their altruism is the handicap they take in order to establish their social prestige within their group.

Social prestige functions like an invisible peacock's tail. It attracts collaborators and deters rivals. Among social animals, altruism can replace threats and aggression in the competition for dominance.

The competition over altruism is not compatible with any of the current theories which interpret the evolution of altruism by models of indirect selection, such as group selection, kin selection or reciprocity.

All models of indirect selection are vulnerable to social parasitism, and thus are not stable. My theory on altruism is based on the direct benefit to the altruist, although the altruism benefits also its group. Hence it is a stable evolutionary theory.

It is satisfying to realize that doing good to others may also be good for the altruist.

Not all altruists benefit from their altruism, but selfish individuals may also lose. It is possible to succeed by being selfish and also possible to succeed by being an altruist. It is so much nicer to succeed as an altruist.

I shall end with my own personal history. As a young student I left my position as an instructor at the university and started working for conservation. I was ready to "sacrifice" my academic career for the sake of conservation. I spent 15 years as an administrator, establishing a new NGO for conservation. I was sure that I was sacrificing my academic career in order to conserve the animals I loved. However, I succeeded in my altruistic efforts, and my success paved my way back into the Tel-Aviv University. I was accepted as a lecturer although at that time I had published only one scientific paper.

Now I know that it is also possible to succeed in life by altruistic acts. However not every one has such an opportunity.

Perhaps human society will improve from giving more social prestige to altruists.

In closing I would like to thank once more the Fyssen foundation, and Nadia who took care of our stay in Paris.