

Amotz Zahavi (1928–2017)

Evolutionary biologist who proposed the handicap principle.

Why animals produce costly and extravagant displays and ornaments has preoccupied evolutionary biologists since Charles Darwin first outlined the process of sexual selection. In 1975, Amotz Zahavi supplied an ingenious and, at the time, controversial explanation for the evolution of these seemingly maladaptive traits. In the handicap principle, Zahavi reasoned that the flashy ornaments, such as the proverbial peacock's tail, evolved precisely because they are costly — to signal the genetic and phenotypic quality of the bearer. The handicap principle maintains that the costly signal will be honest because a weaker individual would pay a higher cost to carry the same handicap than a stronger animal.

Zahavi, who died on 12 May 2017 in Tel Aviv, Israel, first described this principle in relation to mate choice. Ornaments that are costly to produce or to display show the individual's ability to survive and maintain its physical condition despite being burdened by such a handicap. He later developed this idea to encompass a wide range of evolutionary conundrums, from prey–predator communication to altruism.

The unifying feature of these hypotheses was honest signalling, in which honesty is maintained by the costs associated with producing the signal and there is a direct link between the signal and the trait that is being advertised. For example, gazelles that are chased by a predator occasionally spring into the air while holding their legs still. This seemingly reckless behaviour, called stotting, slows the gazelle down. But the animal may be signalling its running ability to the predators — only a gazelle in good physical condition can afford such a stunt while running for its life. Similarly, altruistic behaviours, such as food sharing or charity funding, can reliably signal that the donor possesses both the resources and the willingness to share them.

Zahavi was born on 14 August 1928 in Petah Tiqva, Israel, which was then under the British Mandate for Palestine. From an early age he was fascinated by the surrounding nature and, in particular, by birds. Because there were no guidebooks available to him at the time, he made up



Credit: Arabian Babblers Research Project

his own names for them. Meeting Heinrich Mendelssohn, the then director of a zoo that belonged to the Biological Institute in Tel Aviv, at the age of 12 changed that — Zahavi could use the scientific collection of stuffed birds at the zoo to identify the species he saw in the fields and orchards around his home.

It was Mendelssohn who persuaded the budding naturalist to study biology. Zahavi's initial plan was to study agriculture and become a member of the communal settlement (a kibbutz) while bird-watching in his free time. Mendelssohn argued that there were few professional ornithologists in Israel at the time and that adding one would be a greater service than adding another farmer, of which there were plenty.

Much of Zahavi's thinking about the natural world was influenced by his life-long work with a population of Arabian babblers, a thrush-like group-living bird. This research was conducted at the Hatzeva research station in the Arava Valley of southern Israel, in the heart of prime desert habitat. Zahavi's keen naturalist's eye, as well as his intimate knowledge of the birds' behaviour and biology, allowed

him to develop the handicap principle theory and apply it to the evolution of altruistic behaviours.

Alongside his contributions to science, Zahavi was a most ardent nature conservationist. In the 1950s, the government of the young Israeli state was mostly concerned with things other than nature conservation. When Zahavi learned of their plan to reclaim the Hula Swamp in northern Israel for agriculture, he rushed to study the diverse waterfowl of the area before they disappeared. One day, he found himself accompanying Mendelssohn to the final meeting of the planning committee that would decide on the size of the nature reserve that would remain after the swamp was drained. Zahavi made an emotional appeal for the natural beauty of the area, focusing the committee's attention on the majestic white-tailed eagles that nested there. He asserted that only a large reserved area would ensure their survival — and it worked.

This event showed Zahavi that naturalists can influence government decisions on conservation. In 1952, he, together with his friend Azaria Alon, a biology teacher,

proposed to form a non-governmental organization that would solely deal with nature conservation. The Society for the Protection of Nature in Israel (SPNI) was born. The society remains one of the key guardians of nature in the country, and it coordinates a large system of 'field schools' focused on the natural history of the local areas. Zahavi served as the head of the SPNI for over a decade and in 1980 he received the Israel Prize for this work.

Amotz Zahavi was one of the true giants of evolutionary biology, whose

contribution to the development of the field can be matched but not surpassed. In his own words, he did not always use conventional terminology when presenting his theory to the peers. Despite this, the handicap principle — the concept that costly signalling underlies the evolution of exuberant ornaments and displays — flourished and revolutionized our understanding of the natural world. Zahavi's ideas, which at a time were as unconventional as the terms he used to express them, will continue to inspire

the future generations of evolutionary biologists and ecologists. □

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