

AMOTZ ZAHAVI 1928–2017

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Last May (2017) Professor Amotz Zahavi passed away. He was known to many as a founder of the Society for the Protection of Nature in Israel and as a scientist who introduced to the world the Handicap Principle. Amotz had indeed a personality that is hard to sum up in words. He combined levels of determination, vision, leadership, outstanding originality, clarity of observation and intuition with which few are favoured. Within the scientific community outside of Israel, not many knew of his lifetime dedication to the conservation of nature; and few among the nature lovers in Israel were aware of the depth of his contributions to the world of science. Those who did know him personally knew that this combination constituted one more aspect that made Amotz such a unique and special individual.

First steps

Amotz Zahavi was born on August 14, 1928, in Petach Tikva, a town founded in 1878 as one of the first two settlements established by Jews in the Land of Israel in the early years of the Zionist Movement. According to his mother, he would watch the birds in the garden even before he learned to talk, and throughout his childhood he wandered around the settlement and its environment following the birds. When he was 12 years old, he discovered the small teaching Zoo in Tel Aviv, where he encountered Dr Heinrich Mendelssohn, who had arrived from Berlin in 1933 and was at the time the only scientist in Palestine under the British Mandate who studied birds and had a deep knowledge of them. Due to the lack of suitable books in the Hebrew language, Mendelssohn became the focus of everyone interested in nature. Amotz's encounter with Mendelssohn was to influence him throughout his life, and he took every opportunity to visit Mendelssohn. Already at this stage of his life Amotz was known as one of the best bird-watchers in Israel. He studied at the Pardess Hanna agricultural high school, which allowed him to spend time in the wild and to engage in nature studies. He also served as an instructor in the Boys-Scouts, and turned a great part of the Scouting activities into trips into nature. In Autumn 1947, following his high-school studies, he began to study biology at the Hebrew University, Jerusalem, but this was cut short in 1948 with the outbreak of Israel's War of Independence and his conscription into the military.



Photo: Oded Keynan

At the end of the war, in 1949 he took up his studies once more, and went on many nature trips, in the framework of both his studies and on his own. Among others, he joined a geological survey carried out by geologists from the Hebrew University. The survey dealt with rocks and fossils in the Negev and initiated Amotz's interest in the desert, an area that he studied for most of his adult life. Amotz and Azaria Alon (who had also joined the survey) spent the long nights in the desert discussing the idea of establishing a public society that would bring together the many nature lovers and experts living at the time in the country - rangers, scientists, nature teachers and amateur nature enthusiasts, and that would function to protect nature wherever it was necessary to do so. Back at the Hebrew university, Amotz engaged, together with his friend (later professor) Yaakov Wahrman, in a study of gerbils in Israel. Their work on the evolution, ecology and cytogenetics of these gerbils was published in a series of articles at the end of the 1950s, and one of the articles was even accepted for publication by the prestigious journal *Nature*.

In 1954 Amotz received his M.Sc. in Zoology. His thesis, supervised by Mendelssohn, focused on the birds of the Hula lake and swamp, an area known as the richest in the country for waterfowl and other birds. The Hula Valley was a particularly impressive place because of its mix of African and European flora and fauna.

During the same year he married Avishag Kadman, who was also a biology student and serious amateur bird-watcher. Avishag later became a botanist and served as a professor of botany at the Vulcani Institute, while also contributing immensely to Amotz's scientific work and of course bring up their two daughters, Naama and Tirza.

Amotz received a grant from the British Council in 1955 for a one-year study period in England, which he spent in Oxford at the laboratory of Prof. Niko Tinbergen, who later received the Nobel Prize. During this period he also met Dr. David Lack, the senior ornithologist in England, as well as the students of these two eminent scientists. They greatly influenced his scientific work.

Despite his research achievements and experiences with eminent scientists, Amotz chose to delay further work in academia. He instead devoted the next 15 years, which were some of the best years of his life, to the conservation of nature in Israel having the foresight to realize that the country's development would threaten its biodiversity.

Nature conservation and the establishment of the Society for the Protection of Nature

In parallel with Amotz's scientific development, dramatic changes were taking place in Israel: at the country's establishment there were 0.6 million Jewish citizens, and between 1948 and 1958 an additional one million new immigrants arrived. The economic situation was poor and the State's authorities promoted development plans, aimed among others at establishing an economic basis for the State. One of these plans was to drain the Hula lake and the swamp to its north to convert the area into agricultural land. This plan was a cornerstone of the government's development plans and was swiftly advanced in 1952, as were development plans for other vast areas. A dramatic change in Israel's landscape was about to happen, and there was a need for someone to represent the side of nature.

A small group of scientists, nature teachers and students, under the direction of Mendelssohn, attempted to minimize the environmental damage rapid development plans would cause and founded "The Committee for the Preservation of Nature," This committee, acted mainly through meetings in which they attempted to persuade the developers, who in the main did not understand why they should not go ahead with their intensive development plans. Amotz, who studied the area for his master degree, was sent by Mendelssohn to persuade the committee discussing the Hula swamp project of the need to preserve part of the natural area. He guided a group of the committee members on a trip to the Hula, but in the discussion that followed it became clear

that nothing had changed among those who advocated the development plan. Amotz then tried another approach, describing to the committee the nesting of a pair of white-tailed sea eagles in the mountains overlooking the valley, one of the only two pairs of this species nesting in Israel. When asked about the home range size that sea eagles need, he explained that this pair required 4,000 dunam (ca. 1,000 acres) in order to raise their young. This "explanation" that Amotz improvised during the discussion, and which had no clear scientific basis, convinced the committee to allot an area of this size for a nature reserve in the Hula valley. And so they did.

That was not the only "scientific" achievement of Amotz during this period, and another example is that of the coral reef in Eilat. Israeli citizens discovered this amazing reef located in the northern part of the Gulf of Eilat, at the northernmost tip of the Red Sea, and they flocked to visit it. Upon returning to their homes in the north they would often bring with them a 'souvenir' from the reef in the form of uprooted coral fragments, cleaned and displayed on a shelf. Amotz sought to prevent the destruction of the reef and explained to the responsible bureaucrat in the Ministry of Agriculture that corals are living organisms and thus should be protected, but the fellow stubbornly insisted that they are just 'stones', and rejected the student's opinion. There seemed no legal way to deal with the issue until Amotz came up with a solution: he found among the Mandate fishing laws a clause noting that every living creature in the sea can be called a fish, and that any fish can be declared a protected species. Amotz went to his teacher, Prof. Heinz Steinitz, a marine biologist, and despite the latter's doubts he convinced him to sign a letter defining corals as fish! Steinitz agreed, and the corals were declared to be fish and thus protected by law.

In 1953, Amotz together with Azaria Alon and others, and with the help of Prof. Mendelssohn, founded the "Society for the Protection of Nature," which became the largest such association in Israel. In the early days of its establishment, its members amounted to only a few dozen individuals and their influence was small. Despite this, they sought to ensure that the development plans would



Amotz Zahavi (on the right) in the Hula

take into account the need to protect the flora and fauna within the borders of Israel.

When Amotz returned from England in autumn 1955 he found the Society for the Protection of Nature barely functioning and decided to postpone his plans to continue on to a PhD and instead to dedicate two or three years - which eventually turned into 15 - in organising the Society. It is no exaggeration to say that this decision changed the face of the State of Israel. Prof. Mendelssohn supported it, and arranged for Amotz to receive a salary as a teaching assistant at the university, thereby enabling him to carry out his plan. Amotz served as director of the Society for the Protection of Nature from 1955 to 1970, doing so with originality, creativity, vision and stubbornness; all characteristics that would later become prominent in his scientific work. During those years Amotz coalesced the unique character of the Society, collected and instructed a dedicated team of workers, guided the course and struggles of the Society and recruited many new members. He had an original style of leadership: upon hiring new personnel, he explained the required tasks to the workers and his expectations, but then gave them the independence to perform and promote those tasks. Resourceful and energetic individuals found in him a loyal supporter when needed and succeeded in promoting the important objectives of the Society, while those who were expecting to be functionaries carrying out precise instructions given daily, found themselves quickly outside the Society. It should be noted that many did not find this approach to management to their taste.

Under Amotz's management the Society for the Protection of Nature founded a network of field schools, initiated establishment of the Nature Reserves Authority, and acted to establish and then supervise nature reserves (the first of which was the Hula nature reserve). Amotz's work in nature conservation in general, and in establishing the Society in particular, won broad public recognition: in 1980 the Society was awarded the Israel Prize, and Amotz, together with Azaria Alon and Yoav Sagi, the then secretary of the Society, accepted the award on behalf of the Society. In 2016 Amotz was also awarded a prize by the Israeli Ecology Society for lifetime achievement.

Amotz's work for nature conservation did not cease with the end of his work with the Society for the Protection of Nature. In 1965 Amotz established and headed The Institute for Nature Conservation Research at the Tel-Aviv University. He also contributed to many new struggles that arose, and offered new ideas for the advancement of nature conservation. One such far-reaching idea was to found an international nature reserve that would extend from the Dana reserve in southern Jordan, through the central Negev (the crater region), to the western Sinai Peninsular in Egypt.

After Amotz completed his term as director of the Society for the Protection of Nature, he served for many more years as a member of its board of directors, although in more recent years he became highly disappointed with some of the Society's policies. Initially, he tried to change the polices by means of talks and discussions, and when these did not help the relationship between him and the management became extremely tense. The Society even

went to the extent of preventing young instructors from meeting with him. What mainly angered Amotz was the closure of many of the field schools, which had been one of the high points of the Society, and he refused to accept the rationale that lack of funding was the main cause. When the Society wanted also to close his beloved Hatzeva field school, which served as the location for his long term research on babblers, he strongly objected and he took the management of the school upon himself in order to prevent its closure. He raised resources for this, and when these were lacking he mortgaged his apartment in Tel Aviv in order to finance the field school's existence. In his recent years, however, much of the dispute has been resolved and Amotz's relationships with the new leadership of the SPNI were good.

In summary of Amotz's work in nature conservation, it can be said that without it the face of nature conservation in Israel would have looked very different. His unswerving dedication, imagination and execution ability (of course together with others, first and foremost Prof. Mendelssohn, and with his friend and collaborator Azaria Alon), led to the State of Israel being the only country between Morocco to the west and India to the east, in which a vibrant nature protection program exists, and nature conservation in Israel is today one of the most advanced in the world. To non-Israelis, it is a source of wonderment that a country that has improved the lives of its growing numbers of citizens to such a great extent has also been able to do such a remarkable job at preserving its natural heritage while even at times having to fight for its very survival in a part of the world hostile to its existence. It is likely that demonstrating Israel's conservation achievements was one of the reasons Amotz was such a gracious host to scientists who visited Israel. Besides showing his babblers and the local study area to visitors, it was evident that Amotz delighted in generously taking visitors around the country to show them its many natural riches.

Back to Science

Towards the end of his term as secretary of the Society for the Protection of Nature, Amotz began his PhD studies at Tel Aviv University. His doctoral work dealt with the social behaviour of the white wagtail and the resulting dissertation submitted to Tel Aviv University in 1969, was short and concise (a slim booklet of 50 pages), but it summarised a highly impressive field study. Amotz discovered that some of the wagtails overwintering in Israel establish a territory and live in pairs (male and female), while others gather in large flocks. He posited that the determining factor of this social structure was that of food distribution, and in order to examine this hypothesis, he performed the first ever such field experiment in which he demonstrated that a change in food distribution in the field can make wagtails become territorial. These findings, published in 1971 in the journal *Ibis*, provided one of the first pieces of experimental evidence that the pattern of food distribution can determine social behaviour in animals in nature. Upon completing his doctorate Amotz set out for postdoc studies in Oxford, England, where he continued his research on the wagtails while focusing on the subject of communal roosting (sleeping) and its function as a centre of information for locating food. These studies, and in particular his article in collaboration with the British researcher Peter Ward (Ward & Zahavi 1973), attracted much attention among the scientific community and paved the way to the permanent position in the academic world that awaited him in the Department of Zoology at Tel Aviv University. His academic standing during those years is attested to by the fact that his recommendation letters for his university position were provided by two Nobel Prize winners - Niko Tinbergen and Konrad Lorenz - as well as by David Lack who had hosted him during his post-doc period in Oxford. Over time, Amotz recounted that this recognition, as well as his lifetime experience acquired in the Society for the Protection of Nature, had established his confidence and helped him to fight for his ideas in the years to come.

Babblers, Peacocks and the Handicap Principle

In the early 1970s, Amotz began to study the babblers in the Arava and to investigate their special life style, which includes group nesting, communal roosting, mutual feeding and preening and even a morning dance. Amotz and Avishag Zahavi continued to study the babblers in the Hatzeva area for 47 years, and it would seem that there was no zoologist in Israel who did not visit the place and spend at least one morning with Amotz and the babblers. The visit always included "gossip" about the babblers, each of which had its own name, based on the arrangement of four coloured rings on its legs, and a fascinating history, as well as many exciting observations of the babblers' battles with neighbours, in courtship or dance, or in mobbing a snake or an owl or caracal. This magical experience, which also included the privilege of observing wild birds awakening in the desert and feeding them from the hand, also provided the opportunity to understand Amotz through his observations of the birds. The babbler research served him not only as a research tool and for teaching, but also as an unceasing source of inspiration for his many ideas that were to develop over the course of those years.

Amotz had already begun to develop the Handicap Principle in 1973, but the first scientific paper in which he described the principle was only published in 1975. This was soon followed in 1976 by a paper in which John Maynard Smith, among the greatest theoretical biologists of the time, explained why Amotz Zahavi's interesting idea could not work. Amotz and Maynard Smith had already had discussions prior to the publication, but neither had been able to convince the other. Finally, Maynard Smith explained to Amotz that he was ready, as editor of the Journal of Theoretical Biology, to publish the article, but would also publish his own article explaining why the Handicap Principle could not work – and so he did. In the following years a number of theoretical articles were published that modelled the idea and also found it could not in fact work. In parallel, Amotz, against the entire scientific community of the field, continued to lecture on his idea and to publish

articles that explained and expanded upon its application in a variety of areas of biology. He would sometimes start his lectures with the admonition that almost no one else believed what he was going to say, a tactic that certainly got people's attention and his forceful presentation kept that attention.

The main lack of understanding of the handicap principle arose from the way in which the theoretical biologists interpreted the principle in their mathematical models. Amotz, who spoke about the peacock's tail or a deer's antlers, compared them to an expensive motor car that only a wealthy man could afford to buy, and through the purchase and maintenance of which he advertised his wealth. By using examples of this kind, it was clear to Amotz that the cost of such advertising for the wealthy man was relatively small in comparison to that for a man with only an average income. It was this differential cost that converted the expensive signal into a reliable measurement of wealth, quality or ability - only a wealthy, strong or very able individual could allow himself to fully express the handicap of an expensive signal. In contrast, a weak, unhealthy or physically inferior individual, would either be unable to produce such an expensive handicap or would be unlikely to survive for long if it succeeded in doing so. However, theoreticians like Maynard Smith did not manage to demonstrate through their mathematical models how this intuitive principle could in fact work and produce the evolution of costly handicaps. It is interesting to note that while the community of biologists contended that the Handicap Principle was mistaken, in the field of economics during the same period Michael Spence posited a somewhat similar and more specific theory in connection with acquiring education as an expensive and reliable signal of the quality of candidates applying for jobs. This principle eventually led to Spence being awarded the Nobel Prize for Economics in 2001 (jointly with two other economists). Today the similarity of the two ideas is well recognised but at the time there was little connection between the two areas.

The change in the academic community in regard to the Handicap Principle began in 1989 when Amotz proposed that his friends in England invite him to give a series of lectures that would enable a longer and more detailed discussion of his theories. The visit was arranged by Bill Hamilton, among the greatest of the evolutionary biologists at Oxford. He had previously visited the babbler research in Israel and held Amotz in great esteem, despite their differences of opinion. The British listened politely to Amotz's lectures, but what truly made the change was that after the second lecture Alan Grafen, a young theoretical biologist considered a rising star at Oxford at the time, approached Amotz and told him that he was indeed right. Grafen said that he had found a way to build a mathematical model that proved that the Handicap Principle can indeed work. Richard Dawkins, with whom Grafen had been a former student, and who was also present, told Amotz in response that if Alan Grafen said he was right, then, it seems he was indeed right. A year later Grafen completed his work and published two articles demonstrating through Evolutionary Game Theoretical models, how the Handicap Principle can work, both in connection with mate choice and as a general model for the evolution of communication. Furthermore, in his articles Alan Grafen dedicated several paragraphs to explaining and emphasizing that his model was a direct translation of Zahavi's Handicap Principle and that the idea itself was simple and brilliant.

In a 1991 revised edition of his famous book The Selfish Gene, Richard Dawkins wrote that the handicap principle was indeed correct, and Maynard Smith himself dedicated a special plenary lecture at the International Conference on Behavioural Ecology, in order to retract his criticism of the idea and to explain how in fact the Handicap Principle can work. Amotz was sitting in the audience and rose at the end of the lecture to thank Maynard Smith for recognising the Handicap Principle. But he added in his characteristic and direct way, in front of the entire large audience, that Maynard Smith's lecture indicated he still did not completely understand the Handicap Principle. And Amotz went on to explain why! In the early 1990s the Handicap Principle won broad recognition and a wave of studies by researchers supporting the principle flooded the field. All of this did not appease Amotz but only heightened his determination to continue to advance those additional aspects of the idea that had still not won broad recognition.

Altruism

One of the aspects of the Handicap Principle that was particularly important to Amotz was the idea that it could also provide a general explanation for altruism in nature. Based on his observations of the babblers, Amotz contended that the help that the babblers give to other members of the group, expressed in guarding, fighting, caring for the young of other members, and feeding other individuals, are all not really purely altruistic acts but a reliable signal that expresses their quality which then leads to net fitness gains in some other context. Just as a heavy tail attests to the quality of a peacock, so too do feeding or help attest to the quality of the help-giver. In other words, not every babbler can allow itself to give up on a food item or spend an hour guarding when all of them are hungry, but if it does so, then it signals that it is a strong, healthy individual that is better at finding food than the others. The use of the Handicap Principle as an explanation for altruism is familiar world-wide today and even supported by a number of theoretical models, but limited in acceptance nonetheless. Many agree that the phenomenon exists among humans but the explanations for altruism in other animals are still controversial. In contrast to the evolution of communication in nature, for which the Handicap Principle provides a currently accepted model, the evolution of altruism in nature has alternative theories, such as that of kin selection or models of group level selection and reciprocity, which Amotz consistently rejected but which most in the academic community perceive as wholly sufficient or at least partial explanations for the numerous examples of behaviour that seems to be altruistic. In regard to this issue Amotz persisted with his struggle but to no great avail. Only time will tell if he was correct in this case too.

Testing the bond, mafia cuckoos, and communication at the molecular level

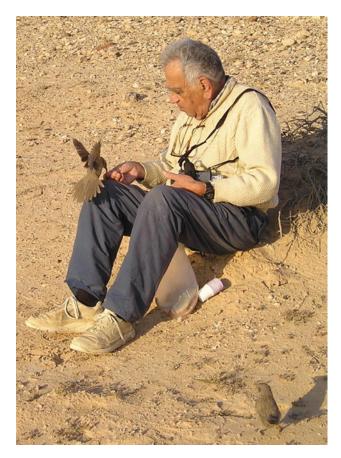
The variety of original notions posited by Amotz Zahavi went far beyond the basic idea of the Handicap Principle. Amotz contended more than once that, in his personal opinion, one of his most important articles was the short paper he published in 1977, titled "The Testing of a Bond." He was in the habit of saying that because noone in Maynard Smith's league had contended that the article was incorrect, many had not bothered to relate to it; but that it constituted the most important completion to the Handicap Principle. In that article, Amotz suggested that when an individual wanted to receive information from another individual, but the second individual did not transmit that information, the way to receive it was to impose a burden on the first individual and to observe the extent to which it was prepared to suffer the imposition forced upon it. Amotz used the idea in order to explain gestures between partners or loving couples and between children and parents. He contended that every physical gesture, from preening feathers to holding hands or sex unconnected to procreation, as well as children's attempts to gain their parents' attention at precisely the moment when the parents were busy or tired – all these constitute a tool to test the bond due precisely to the fact that they exert a cost from the other party.

Another area in which Amotz came into conflict with the approach of leading researchers in the field was that of the relationship between parasitic cuckoos and their hosts. In an original article published in 1978 he suggested that it is incorrect to perceive the behaviour of a surrogate (host) bird that fails to reject parasitism and instead raises the intruder at the expense of its own reproductive output as non-adaptive and stemming from an evolutionary lag in the development of defence mechanisms during an evolutionary arms race between the cuckoo and its host. Similar to his approach to animal communication, Amotz did not believe that cheating is a stable strategy. He considered evolution as constantly working also on the side that is being cheated, so the explanation of an evolutionary lag that leaves the cheated individual behind seemed, to Amotz, to be merely a lazy excuse. According to his perception, if the researcher cannot explain the adaptive logic of animal's behaviour, then he should try harder and not hurry to conclude that the animal is stupid. In the case of the cuckoo, Amotz suggested that the tendency of female cuckoos to rob nests of other birds creates a situation in which it would be preferable for a host to accept and care for the cuckoo's nestling rather than risk losing the entire contents of the nest if the cuckoo will destroy it if its egg or nestling are missing. This would be like a businessman who pays 'protection money' to the mafia rather than risk experiencing greater harm that the latter could inflict upon him. Like his other ideas, here too Amotz's idea received a cool reception, leading to debate and a variety of interesting studies. The mafia model itself has not been supported in most cases and there is general agreement that it can't explain the many situations in which a parasitic nestling kills off all of a host's young. But experimental support for the mafia model has been found in studies of two parasite-host systems. While controversy over this issue continues, there is no doubt that Amotz introduced a counter approach that stimulated new research.

Perhaps the most ambitous of Amotz's research attempts was his desire to fit the Handicap Principle to the entire biological world, far beyond that of animal behaviour - i.e., to every means of biological communication from the cellular and molecular levels to communication between brain cells. Moreover, Amotz suggested that Darwin's famous distinction between natural and sexual selection should be better viewed as a distinction between natural and signal selection. Amotz claimed that natural selection, as proposed by Darwin, is indeed selection for efficiency, but sexual selection is merely a sub-set of the more general mechanism of "Signal Selection," a mechanism that reduces efficiency through handicaps in order to ensure the reliability of signals. With this view in mind it was clear to Amotz that everyone who studies communication in nature should understand and use the handicap principle. In the last decades of his life Amotz energetically engaged in reading the broad literature on intracellular communication and in countless meetings with experts in the field. Together with collaborators he also published a series of articles implementing his approach on cooperative amoebas and on communication between brain neurons and other cells. In this case too not everyone was convinced, but many admitted that the direction was a fascinating and inspiring one. Amotz of course believed that it was only a matter of time before everybody would understand that even when referring to communication inside the body or within cells, it is always necessary to consider how reliability is preserved, and the solution is always in the form of signals that are given at a cost. It is still too early to tell whether Amotz's ideas on cellular communication have penetrated the scientific world and will be revealed as correct; but the very attempt teaches us that when it comes to Amotz – almost anything is possible.

The brain that never ceases to think and stimulates others to think too

Among all the things that made Amotz so unique, was of course his ability for deep and original thought while stimulating others into thinking too. It could be mentally exhausting to argue scientific points with Amotz in person because it forced one to marshal all of one's intellectual resources. Nevertheless, even when his colleagues came away from an interaction and still didn't believe a particular idea Amotz advanced, they often realized that he had identified weak points or flaws in their logic that required them to rethink or at least reformulate their ideas. So even when Amotz's own explanations were not necessarily the most correct, he often perceived a problem no one else had identified and stimulated new lines of inquiries and arguments. When Amotz arrived to lecture at an international conference the auditorium was always full and the aisles



Amotz Zahavi with his babblers (photo: Avishag Kadman-Zahavi)

packed with people sitting on the floor. People knew that his lectures constituted the best show in town. This was where things happened. Whether one agreed with him or not, Amotz was dynamic and challenging, and forced his colleagues out of their comfort zone.

Amotz's direct and very Israeli style of arguing was on occasion problematic for his European or North American colleagues, and some might say that that was what stood in his way. But Amotz also had many good friends who loved him exactly as he was, who knew him as a zoologist and lover of nature, and who formed deep friendships with him for those reasons. Amotz, for his part, knew how to appreciate also those researchers with whom he had deep scientific disagreements. In the early years of teaching the Handicap Principle at the university Amotz refused to give a grade for the course. "How can I blame students who don't understand me," he said, "when many of my best friends abroad who are eminent scientists and whom I greatly esteem, also don't understand me?" Someone once said about Amotz that when standing next to him while he is observing birds, one can hear his brain working. There is something very genuine about that description -Amotz's brain was always working, always thinking ahead and always a little different. Those who visited him during his last days know that Amotz's brain continued to think and to advance up to the very end. Amotz was scheduled to give a lecture at the University on May 24th. He hoped that he would be able to do so as he still wanted to tell the members of the department about new things he had discovered. He passed away on May 12th.

Amotz Zahavi was a highly unique individual, a man of original, deep and penetrating thought. A stubborn man,

a man of nature and of ideas that he fought to realise in both nature conservation and in his scientific work. Over the course of his life his contribution was enormous, both to the preservation of nature in Israel and to his scientific field. May He Be of Blessed Memory.