

# Ilkka Hanski

\* 14/2/1953 † 10/5/2016



**ILKKA AULIS HANSKI**, academician, academy professor and professor of animal ecology at the University of Helsinki, died of intestinal cancer on 10th May 2016 at the age of 63 years. He was born in Lempäälä on 14th February 1953.

Even though his career came to an end in the midst of an active and highly creative period, Ilkka Hanski achieved in the course of his life practically everything that a biologist can hope to achieve. This can be appreciated from the fact that he produced some 350 papers and 10 books, almost all of which were aimed at an international scientific readership, and from his attainment of the title of academician in Finland in 2015, membership of the Royal Society in Great Britain in 2005, membership of the National Academy of Science in the USA and many other prizes and honours over the last 15 years or so. These latter included the Italian-Swiss Balzan Prize in 2000, the Royal Swedish Academy of Sciences' Crafoord Prize in the Biosciences in 2011 and the Banco Bilbao Foundation's Frontiers of Knowledge Award in 2015, all of which are equivalent in prestige to a Nobel Prize. In international circles he ranks alongside celebrated scholars who gained a similar range of

prizes such as the Odum brothers, Edward O. Wilson, Paul Ehrlich and Robert May. He was elected a member of the Finnish Academy of Science and Letters in 2001.

Ilkka Hanski became a biologist while still attending the Sampo Lyceum in Tampere, where his biology teacher was the small mammal specialist Dr. Johan Tast. Meanwhile his interest in butterflies, moths and birds began at his parents' summer residence in the village of Hanski in Virolahti. In fact he published his first observations of Lepidoptera while still at the upper secondary school. He also claimed that the renowned lepidopterist and geneticist, academician Esko Suomalainen had done much to encourage him during his schooldays to think of a career in science. He began his studies at the University of Helsinki in 1972.

Prof. Hanski himself wrote about the university situation in his *Viestejä saarilta* (Messages from the Islands, 2007), "The older generation of zoologists in Helsinki were absorbed in their own research or had drifted away from research entirely and the field was open for young scientists. The new generation took advantage of this and the latest trends in ecology, evolutionary biology and nature conserva-

tion biology quickly found their way into Finland.” His models in the field of ecology were Robert MacArthur, the father of the theory of island biogeography, who died in 1972 at the age of only 42 years, Edward O. Wilson and the developer of the notion of metapopulation, Richard Levins. The most immediate model for the young, radical generation of researchers in animal ecology, however, was the future professor of that subject, Olli Järvinen, and the future professor of environmental policy, Yrjö Haila.

In 1970, just prior to Hanski’s arrival, the university’s Biological Research Station at Lammi had been completed and new buildings had been provided for the Tvärminne Zoological Station, which meant that there were then excellent facilities for ecological research and for developing teaching in this subject. It was the Lammi Biological Station that became Hanski’s number one university, starting out from the 1973 summer field course in ecology. At that time the Pääjärvi Project financed by the Academy of Finland was in progress at the station all the year round. This was a quantitative investigation into the dystrophic lake ecosystem that is typical of Finland, performed in the spirit of the International Biological Programme (IBP). Hanski eagerly joined this youthful group of scientists, even though the subject of his degree dissertation was in quite a different field, the population dynamics of blow-flies, modelled on the work of Pekka Nuorteva and the research of Hannu Koskela, who was also working at Lammi, on dung beetles. Collaboration with Hannu began on the pasture lands of the farms near to the biological station, and their joint publications dealt with interspecies competition, expansion of the

habitats of certain species and the structure of their communities. The central idea that emerged in their later work, that of the ecology of metapopulations of species, i.e. the exchange of individuals and genes among scattered local populations, first arose during those summers at Lammi when studying the rich organic communities to be found in animal carrions and dung. It was this that gradually steered Hanski’s attention away from species biology to ecological theories.

Ilkka Hanski also took part in other people’s research while a student at Lammi, assisting them in collecting or handling material. One of his strengths lay in his ability to conceive of whole theories and discover the essential features of large bodies of data. He was also happy to cross the boundaries between branches of science, as was the case when he published Finland’s first investigation into the effects of temperature on gas exchange in bogs together with Jouko Silvola. This is a field that has developed enormously with time, and is still doing so nowadays in connection with climate change. At the same time Hanski learned laboratory methods for studying energy ecology, which he would later apply to blow-flies and shrews.

Having graduated with a master’s degree in 1976, Ilkka Hanski applied for a scholarship to study at The Queen’s College, Oxford. His choice was partly determined by its long tradition of research into animal populations, and in particular by the work of Charles Elton (1900–1991). The subject chosen for Hanski’s doctoral thesis was the dung beetle community, a classic area of study in the Elton tradition, and he spend the summer of 1977 collecting a material of over 30 000 dung beetles

from pasturelands in order to study their mutual competition for cow dung, as it was this that was held to determine the structure of the community in each case. All basic research contains an element of surprise, something that could not have been foreseen, and in this case, when visiting a library, Hanski stumbled upon a doctoral thesis in archaeology that discussed insect remains dating from Roman times that had been found in London. To his surprise, the same species were involved. In addition, still older fossils were found that pointed to the existence of these species during the interglacial period, so that the whole perspective was broadened to include the biogeography of Eurasia and the history of the spread of dung beetles. His thesis, *The Community of Coprophagous Beetles*, was approved in Oxford in 1979.

While the research for his thesis was still in progress, Hanski had the opportunity to travel to Borneo with a Royal Geographical Society expedition, giving him an opportunity to collect tropical dung beetles. The journey through the Gunug Mulun National Park in Sarawak was highly successful and he came back with almost 6000 beetles representing 66 species, about a third of which were new to science. Two flightless beetles have been named after him, and besides the value of the material itself, the work on it revealed Hanski's unique ability for networking among other researchers in the same field.

Ilkka Hanski returned to Finland in 1979 and initially took up a position of research assistant with the Academy of Finland, this was then upgraded in 1981 to a junior fellowship and eventually to a senior fellowship. He arranged to carry out most of his work at the Lammi Biological

Station, where he had two or three research assistants or postgraduate students most of the time. The issues that he set out to resolve were becoming increasingly theoretical and involved complicated ecological experiments, frequently with insects living in unsavoury environments, dung, carrions or fungi. They generally concerned both common and rare species and the differences in their population ecology in the case of blow-flies, pine sawflies and shrews. In the end he evolved what he called the "nucleus – satellite theory", which he tested on various sets of material. Particularly surprising – and suitable for his purpose – was the material used by Kaarlo Linkola in his doctoral thesis of 1916 on the cultural indicator plants of the villages of the Ladoga region of Karelia, which Hanski used to test by means of his new methods the distributions of common and rare species among villages of different types.

From his student days onwards Hanski had been interested in small mammals, particularly shrews, six species of which occur in Finland. All of these were bred at Lammi for his use in experiments to determine their energy ecology, behavioural traits, population fluctuations and predator-prey relations in experiments that were ahead of their time in sophistication. In connection with his small mammal research he devised the idea of raising large numbers of pygmy weasels in cages, fitting them with radio transmitters and releasing them on islands in the larger lakes in order to determine their predator-prey relations with the voles. Hanski and his students generated a great deal of other information about the population biology of pygmy weasels and voles, and equally significant was the part that he played in

research into the Arctic collared lemming in Greenland, where the modelling of predator-prey relations revealed an influence from climate change. It was typical of Hanski that when testing his models he would not commit himself to them entirely but was ready to adapt his opinions where new results warranted this. This happened in the case of certain highly problematic studies of fluctuations in the populations of small mammals, where the fluctuations appeared to have ceased for a couple of decades.

Ilkka Hanski's career in university teaching began when he was appointed docent in zoology in 1981 and was expected to give lectures in that capacity. Then, when Olli Järvinen became an academy professor in 1988 Hanski deputized for him as professor of animal ecology, and when Järvinen died at the age of only 40 years in 1990 Hanski was appointed to succeed him in 1993. The teaching of zoology as a whole was reformed during his term of office, the teaching of biology was transferred from the city centre to the Viikki campus in the mid-1990s and the administration was reorganized. Hanski should also be thanked for improving the students' ability to use computers, for redesigning the field courses in ecology, for developing the more advanced stages in the degree course and for initiating study modules in English. After his appointment to an Academy of Finland professorship in 1996 and his gaining of a centre of excellence of his own in 2000 he concentrated almost entirely on postgraduate teaching. In the end he led the university's Doctoral Programme in Wildlife Biology Research for 20 years and gained a prize for the best programme of its kind. There is no doubt at all that he acquitted himself ex-

remely well of the principal duty of a university teacher, that of training young people to carry out research.

Dung beetles persisted in Hanski's working portfolio up to the end of his life. The University of Helsinki was involved in the activities of the research station in the Ranomafana National Park in Madagascar, and Hanski set out in 2002 to examine its dung beetles, since Madagascar is one of the areas with a high concentration of endemic and seriously threatened plant and animal species and has large numbers of dung beetles. As a result of his visit some new findings in the field of evolutionary biology were published and a research group was gathered together to continue with that work. The last time Hanski visited Madagascar was in 2007, but a Madagascan postgraduate student of his gained a doctorate in conservation biology in Finland in 2015.

Hanski's dream of returning to the rain forests of Borneo came true when he went there with nine students in 2013, 35 years after his first expedition. The national park was still untouched, but its surroundings had been turned into oil palm plantations. His search for dung beetles was successful, however, yielding 12 000 individuals which have now been studied preliminarily, so that the first results have been published. The world-wide warming of the climate had nevertheless raised the upper and lower altitude limits for the species studied so far by an average of 110 metres over the interval of 35 years, implying a warming of over half a degree. The research is still going on.

At the beginning of the new decade in 1990 Hanski had considered testing the metapopulation theory on a new experimental animal, as it were, and by a happy

coincidence the choice fell upon the Glanville fritillary, *Melitaea cinxia*, and its populations and habitats on the Åland Islands. Now, a quarter of a century later, we have an internationally acclaimed model metapopulation experiment on our hands. The species lives in the meadows of a traditional agricultural landscape and its larvae feed on only two plant species: the ribwort plantain (*Plantago lanceolata*) and the spiked speedwell (*Veronica spicata*) It is easy to find, to rear in a greenhouse and to label for research purposes. The species has died out on the mainland of Finland, but there are more than 4000 patches of meadow on the Åland Islands which are suitable for populations of its larvae. Hanski was never put off by the amount of work involved in what he was doing; everything was possible. In this case the butterfly populations of the meadows were assessed by dozens of students every year, which enabled them to monitor the disappearance of the butterflies from certain sites and the establishment of populations in new meadows, resulting in new models for the reaction of species affected by human-induced fragmentation of their habitats. Hanski worked with his colleagues on developing theories and models to fit this situation, but it must be admitted that the combining of the theory with the vast amount of measurement data that they had would never have succeeded without a large research group that included mathematicians. The findings have been applied in the designing of conservation areas in Finland and elsewhere in the world and have been used to estimate the threshold for the disappearance of the species from a fragmented habitat and its extinction debt, i.e. the time lag in the extinction of the species.

Experiments have also been carried out in connection with this work, mostly involving the building at biological stations of glasshouses for rearing the butterflies and greenhouses for raising the plants on which they feed.

Hanski's ecological studies of the Glanville fritillary butterfly soon led to determinations of their evolutionary properties and genetic differences, so that this became only the third butterfly species in the world to have its genome described. Meanwhile, its most important property as far as its metapopulation biology was concerned was its flight ability, which meant that it could easily settle in new surroundings. In genetic terms this property is concentrated in certain genes that affect its metabolism while in flight. Natural selection has improved its ability to migrate in a fragmented living environment, but this is not the only feature that selects between butterfly species. Hanski and many other researchers have shown that ecological and evolutionary dynamics can act quickly to improve the vitality of a population, but Hanski would also emphasize in his writings that man is capable of altering environments so quickly that their diversity will suffer and the sixth wave of extinction will be a reality before long.

The Metapopulation Research Group rapidly developed into a centre of excellence headed by an academy professor, the Metapopulation Research Centre (MRC), the annual report of which for 2015 listed 16 research groups led by five academy professors and about ten academy research fellows. The groups themselves included about 30 persons with a doctorate, approximately the same number of people working for a doctorate and large numbers of auxiliary personnel. Almost a half

of the research staff are from other countries. More than 30 people trained by Ilkka Hanski have gained a doctorate to date. There are naturally many other things being studied within the MRC as well as Granville fritillery metapopulations, e.g. biodiversity in general, evolutionary genetics, phytopathology, parasitology and conservation biology.

A typical demonstration of Hanski's ability to throw himself into new endeavours was his collaboration with the allergologist Tari Haahtela and his team to study the dependence of allergies and other non-infectious inflammatory diseases on the natural environment in which people live. The aim was to determine whether the human skin, mucous membranes and diversity in the intestinal microbial biome can provide protection against certain non-infectious diseases such as allergies and what is the significance of living habits and the environment as far as natural immunity is concerned. The health advantages to be gained from nature and the associated savings in terms of cost can be great and could have a considerable influence on the planning of communities and their health services. This looks like a promising new opening, one which the researchers themselves refer to as the "natural step".

Hanski published a great deal jointly with members of his own group and with colleagues from abroad, and generally in journals that had a wide readership and were frequently cited. A number of these publications were papers in *Nature* and *Science*. He also wrote or edited about ten books, mainly for an international readership and mostly published by university presses. On his appointment to the chair of animal ecology he wrote together with

various teaching colleagues an extensive work in Finnish entitled *Ekologia*. His reputation was also greatly enhanced by the prize that he received in 1999 from the International Ecological Institute and the book *The Shrinking World* which appeared in that organization's *Excellence in Ecology* series in 2005 and was also translated into Chinese, Finnish and Russian. One book that Hanski wrote specifically for Finnish readers was his *Viestejä saarilta* ("Messages from the Islands", 2007), a cry for help in the face of the general decline in biodiversity and at the same time an account of the work of a research scientist. He then continued on the same theme in his *Tutkimusmatkoja saarille* ("Expeditions to the Islands"), completed just before his death, although he did not live to see any further works published in either Finnish or English.

Ilkka Hanski always believed that a researcher should take part in public debates and exercise influence in society. Similarly, the advancement of science was important to him and he was prepared to speak on its behalf, write about it and act as an expert advisor as required. Examples of this would be the Science Forum events arranged in Helsinki and the long period for which he served on the governing board and board of trustees of the Finnish Cultural Fund. Also connected with the promotion of science and learning were his membership of the governing board of the University of Helsinki, advisory boards for various universities at home and overseas, and various scientific bodies attached to the European Union or the United Nations. He also gave lectures, and even whole lecture courses, at universities in other countries, most notably China, Great Britain and the United States. In the

last article that he wrote, for the Finnish journal *Kanava* (2/2016), he expressed concern at the state of basic research in Finland and the situation of young researchers in this country: "With research and high education policy being administered in an executive fashion there is a danger that we will lose our enthusiasm and passion for pursuing science, and with it the trust and respect that has existed between researchers and decision-makers. And worst of all, we will lose our results and moments of success."

Another thing that was close to Ilkka's heart was nature conservation, particularly with regard to forests. His expertise was in fact much needed for the protection of forests, to which he contributed his "impact theory", an extension of metapopulation theory. The book *Uusi metsäkirja* ("The New Book of Forests", 2006) arose

out of a series of seminars entitled *Argumenta*, conceived of by Ilkka and financed by the Finnish Cultural Fund, in which a large group of people engaged in forest research pointed the way to a new direction in forest management policy that would make better provision for the preservation of biodiversity and the creation of conservation areas. Given the recent increase in the exploitation of forest reserves, the situation in Finland is more worrying than ever. Ilkka himself wanted to contribute to forest conservation in the Virolahti area by donating the last international prize that he received, a sum of 0.5 million euros, to create a network of protected forests that would carry his name. It now remains for his family – his wife Eeva Furman and their children Katri, Matti and Eveliina Hanski – to carry the project through.

*Obituary by  
Rauno Ruuhijärvi*