Profile of Ilkka A. Hanski

Watching birds and collecting butterflies in the field behind his boyhood home, young Ilkka Hanski marveled at the isolated habitats in which many insects live. Decades later, the Director of the Metapopulation Research Group at the University of Helsinki in Finland admits that many of his most successful research projects on the study of metapopulations, or isolated yet interconnected populations of the same species, were inspired by childhood adventures in his own backyard. Hanski, elected to the National Academy of Sciences (NAS) in 2010, has helped predict how plant and animal populations respond when their habitats are broken into fragments, whether by urbanization, deforestation, climate change, or entirely natural processes. His studies have earned him the 2011 Crafoord Prize in Biosciences from the Royal Swedish Academy of Sciences, as well as election to the Royal Society, the Finnish Academy of Science and Letters, and most recently, the NAS.

Before the 1970s, ecologists paid little attention to the spatial structure of populations, whether they were continuously distributed in space, assemblages of local populations, or a mix of both. In 1969, American population biologist Richard Levins first introduced the concept of a metapopulation. However, it was Hanski—who has since led the field of metapopulation biology through the development of basic concepts, models, and informative empirical examples—who helped gauge the prospects of long-term survival for species living in fragmented landscapes.

Hanski’s mathematical models have revealed how a collection of many small local populations survive in a network of habitat fragments. For the past 2 decades, Hanski has used the Glanville fritillary butterfly as a study system to fuel his models and to probe the ecological, genetic, and evolutionary consequences of habitat fragmentation. To date, Hanski’s models have been used to predict the dynamics of animal and plant populations and to guide habitat conservation in the United States, Canada, Australia, Brazil, United Kingdom, Sweden, Finland, and many other European countries.

Chasing Butterflies and Beetles

Hanski says he cannot remember the moment he first became interested in the spatial structure of populations; it was simply a part of life growing up in Tampere in southern Finland and especially, during the summers, at his grandmother’s countryside home. So it was no surprise that, as a graduate student at the University of Oxford, his doctoral thesis focused on the community ecology of dung beetles, small resourceful insects that inhabit very isolated habitats: cattle dung pats. He was intrigued by the observation that most species of beetle clumped together, with particular species common in some dung pats but scarce or absent in others.

During graduate school, Hanski became intrigued by mathematical metapopulation models and now has an interesting question to study: Could the spatial distribution of beetle species in the dung pats on a pasture explain the coexistence of ecologically similar species within a community? His models indicated that coexistence was bolstered when individuals of the same species formed small clusters throughout a landscape. Moreover, Hanski realized that if individuals are not extremely mobile and good at dispersing, geographically separate populations may lose the ability to interact. A physically fragmented landscape at larger scale will further amplify the spatial structure of populations and lead to genuine metapopulations, or networks of local populations, he mused.

Glanville Fritillary

After receiving his Ph.D. from the University of Oxford in 1979, Hanski continued to develop simple mathematical models to predict the conditions for metapopulation survival. By the late 1980s he was ready to test his predictions in the field. Hanski struggled with the details—which insect to study, and where—until a fortuitous visit by renowned conservation and population biologist Paul Ehrlich from Stanford University. During the visit, Ehrlich described his research on Edith’s checkerspot butterfly (Euphydryas editha). Moved by Ehrlich’s experience and Hanski’s own teenage exploits, he selected the Glanville fritillary (Melitaea cinxia), a black, brown, and orange checkered relative of the Californian checkerspot (Euphydryas editha bayensis).

Although the Glanville fritillary lives in meadows across Europe, Hanski’s metapopulation occupies a specific niche in the largest of the Åland Islands in the northern Baltic Sea just off the southeastern corner of Finland. The 1,500-km² landscape is a mosaic of surface bedrock, forest, small villages, and a network of approximately 4,000 dry meadows that represent the butterfly’s naturally fragmented habitat—ideal for Hanski’s studies.

The butterfly itself is a research-friendly organism, says Hanski; it is easy to breed, keep in the laboratory, and study in the field. In the case of the Glanville fritillary, the female lays eggs in large clutches. The caterpillars remain as a group and spin a silken web around the host plant. The rather conspicuous webs enable Hanski and his team to conduct an accurate census of the large metapopulation, which consists of tens of thousands of butterflies in a network of 4,000 meadows. To perform the census, Hanski employs an “army” of 70 undergraduates every autumn. “It is a very big operation,” he says.

Hanski’s studies remain a blend of laboratory experiments, modeling, and large-scale observational fieldwork, powered in large part by the students tasked with counting and sampling the larval families. Some of the experiments on laboratory-reared butterflies are performed in large outdoor cages measuring up to 900 square meters—about the same area as a single meadow.

Predicting Extinctions

The combination of fieldwork and modeling led Hanski to craft some of his most influential papers, including one published in Nature in 2000 that described how species respond to fragmentation (1). That pivotal study explained how a metapopulation can persist when a balance is struck between local extinctions and re-colonization of vacant habitat. “The question, then, is how the structure of the habitat—the network of habitat patches, or fragments if you like—influences the processes of local extinction and colonization,” he says. Hanski’s model demonstrated that landscape properties such as the number and spatial distribution of habitat patches influence extinction and colonization, ultimately determining a species’ viability. The model provides a recipe for calculating the metapopulation capacity, essentially the carrying capacity of a fragmented landscape for a particular species.

However, what makes Hanski’s work so important is that it goes beyond...
butterflies. Although his mathematical models were developed through fieldwork and experiments with the Glanville fritillary, the results can be tentatively applied to other species and landscapes. “What if human land use causes further fragmentation of a habitat? What if some fragments of the habitat are completely lost?” he asks. “What are the likely consequences for the species?” Hanski’s models attempt to answer these questions, and more.

**Predator and Prey**

While working on the Glanville fritillary in the 1990s, Hanski became interested in a question that had stumped ecologists for decades. Every 4 or 5 years, the population densities of Arctic lemmings and boreal voles peak, then plummet. “The cyclical change in population numbers is striking,” Hanski says. “The question is, why?” Over the past 100 years, ecologists in North America, Europe, and Russia have proposed numerous mechanisms to explain the cyclic nature of small mammal populations, yet the phenomenon’s true nature remains elusive.

Hanski proposes that the oscillating populations reflect the interaction between lemmings and voles and their natural predators. Much work has been done on voles in Finland and Scandinavia, as well as in the high-Arctic tundra of eastern Greenland, where there is just one species of small mammal—the collared lemming—and four species of predators. Hanski developed a model to mirror what he maintains is the simplest vertebrate predator-prey community in existence. His model revealed how the predator-prey interaction could trigger a waxing and waning of the populations every 4 years, even when food is plentiful. Ecology (2).

To prove his point, Hanski continues to refine his models and track beetles. That’s why his annual trip to the island where, for 2 or 3 weeks, he camps in a rain forest to sample beetles and perform experiments. He admits it is the most enjoyable part of his job. “No e-mail, no one telephoning; you are alone in the forest, eating rice and tracking beetles. That’s a very good time.”

**Ecology Meets Evolution**

These days Hanski is determined to unravel the underlying genetic aspects of butterfly populations by sequencing the genome of the Glanville fritillary. Over the past 6 years, Hanski has been searching for the genetic roots of the life history characteristics of individual butterflies, including their reproductive potential, their lifespan, and their abilities to disperse and establish new populations. Specifically, he has searched for a genetic explanation for why one butterfly might be a better colonizer than another (4). “We have discovered a couple of genes that have a big influence on many aspects of the biology of butterflies. Although these genes are highly conserved, they can be a genetic explanation for why one butterfly might be a better colonizer than another.”

Hanski and his students are currently attempting to reconstruct the evolution of these species on an island where only 10% of the natural forest cover remains. Because the beetles are largely forest dwellers, knowledge of their ecology and population distribution is vital to establishing effective conservation measures.

Although the project differs dramatically from his studies of metapopulations, Hanski enjoys the opportunity to focus on the spatial aspects of evolution, including how the species’ geographical ranges have changed over time. His team uses molecular techniques to construct a family tree of the 300 or so species of beetles on the island (5). By searching for patterns in the evolution of these species, the researchers also hope to learn whether—and how—evolution can be predicted.

Whereas his Finnish and Malagasy graduate students perform year-round fieldwork, Hanski cherishes his annual trip to the island where, for 2 or 3 weeks, he camps in a rain forest to sample butterflies and perform experiments. He admits it is the most enjoyable part of his job. “No e-mail, no one telephoning; you are alone in the forest, eating rice and tracking beetles. That’s a very good time.”

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As his team sequences the Glanville fritillary genome, they remain on the lookout for genes like phosphoglucose isomerase that impact the demographics of populations and the metapopulation. Hanski’s team analyzes large numbers of butterflies collected from the field to create a comprehensive genetic framework for traits that influence mating success, fertility and fecundity, lifespan, and other aspects of a species’ fitness. Each butterfly is genotyped for thousands of genes, as the researchers search for associations between the genotype and the phenotype.

Although Hanski considers himself an ecologist, the phosphoglucose isomerase revelation whet his appetite for population genetics and evolution. “Researchers used to think that evolutionary changes occur on a very slow time scale and demographic changes occur on a fast time scale. That may not always be the case. They might occur on the same time scale and influence each other,” he says. “To prove his point, Hanski continues to develop models that integrate the genetic and demographic changes in the Glanville fritillary (6), a topic that he elaborates on in his Inaugural Article (5).”

“These are very exciting days for population biologists, with so many lines of research coming together. The Glanville fritillary in the Åland Islands used to be a great system to study metapopulation ecology; now it is helping us integrate ecology and genomics in the spatial context. I can hardly wait to see what we will have learned in a few years’ time!”

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