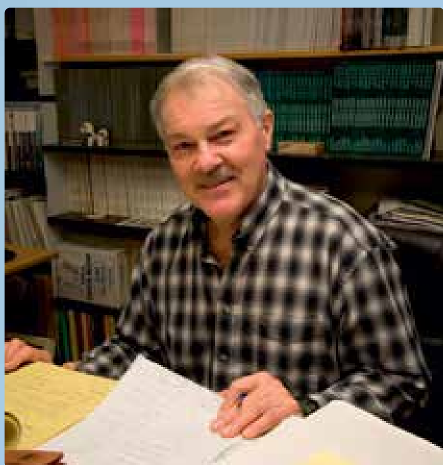
Habitual learning

According to **Professor Douglas Morris**, innovative ideas are paramount to the study of biology. Here, he describes some aspects of his work into density, adaptation and isodars, and other key concepts in his field

PROFESSOR DOUGLAS MORRIS



Traditional behavioural studies rely heavily on theory and observation. How does your research draw on new innovations?

The best science has always been centred on linking theory with observation: the questions we ask, and the theories we invent and refine to answer them, change through time. What does not change are the basic processes of science – curious minds, risky ideas, valid logic, creative tests, objective observation, critical assessment, pause for reflection, and honest reporting. Great science is less about drawing on new innovations and more concerned with inventing them.

Does population density relate to the overall carrying capacity of animal populations? Do you address the needs of animals that do not exhibit group behaviour?

Most population models assume that carrying capacity is constant and corresponds to that density where births equal deaths. Problems arise in determining what exactly the population of interest might be, whether that population can actually maintain a stable equilibrium and whether the population is closed or open to dispersal. Dispersal can produce intriguing outcomes whereby so-called 'source' populations or habitats (which produce a surplus of recruits) export individuals to 'sink' populations that would otherwise become extinct. The resulting source-sink dynamics are intriguing because they are often associated with human impact and our attempts to conserve biodiversity. The fitness consequences, the way in which one measures fitness, and effects of density vary with group behaviour, but the basic theory of why animals might choose one habitat over another does not.

What are isodars and can you explain their significance to biologists?

Isodars (or 'equal fitness' from the Greek 'iso', meaning 'equal' and 'Darwin', a unit of evolutionary change) represent the relationship where two or more alternative 'strategies' yield the same fitness. I invented them in order to test and explore theories of density-dependent habitat selection where strategies correspond to the relative abundance of individuals living in two or more habitats. In the case of two habitats, the isodar is a graph of the density in one habitat versus that in another such that an individual's expected fitness is equal in both. A set of strategies corresponding to the isodar is a so-called dynamic equilibrium that cannot be displaced by any other strategy of habitat use. Thus, if we 'draw' the isodar and learn how it is changing through time, then we can forecast future patterns of habitat use. The same is true of any other strategy where fitness changes with population density and the frequency of alternative strategies.

Evolutionary fitness is a balance between cost and benefit. Do opportunities emerge in light of changing environmental factors? Will animals have enough time to make these evolutionary changes?

The fitness of a strategy depends on the net benefit of that strategy (eg. stay in habitat A) relative to the net benefit of other strategies (eg. move to habitat B). Frequently, however, those benefits will depend on the size of the population and the number of individuals with alternative characteristics or behaviours. Also, for virtually all of the traits that interest ecologists, fitness depends on environmental factors; if the environment changes, so too will the fitness of alternative strategies. As long as a novel beneficial strategy can increase, then the population should often be able to adapt to changes in the environment. If the environmental change is too severe, or too rapid, then even the best strategy that the population can currently achieve may be incapable of allowing the population to increase. Such a population will most likely become extinct despite adapting to the changing conditions as rapidly as possible.

Can you offer examples of adaptive behaviours that might emerge to cope with apparent predation risk?

Apparent predation risk refers to the situation where the effects of a competing species – such as aggressive encounters towards a subordinate species – mimic those caused by and frequently ascribed to predators. So adaptation to apparent predation risk involves adaptation to the effects of competition. Avoidance, for example, can be a particularly effective way to cope with a dominant competitor. This strategy might, however, create the most common pattern associated with apparent predation risk: preferential use of one type of patch over others. If the effects of dominant species' aggression are concentrated in patches that appear risky, then avoidance of those patches by subordinates will increase their use of safe patches; an observation usually attributed to predation rather than to competition.

The evolving nature of **ecological research**

A research group from **Lakehead University**, Canada has made substantial contributions to the combined understanding of evolutionary and ecological domains; providing a new dimension to knowledge of complex changes in the biosphere and how these impact upon biodiversity

THE NATURAL WORLD is a dynamic and heterogeneous system in a perpetual state of change. From seasonal variation through to anthropogenic manipulation, the global environment provides both challenge and choice for the organisms living in it. One of the most central and important choices an individual can make is where to inhabit, a choice referred to as habitat selection. Understanding habitat selection is fundamental to our understanding of how populations change in time and space and helps determine appropriate measures to conserve biodiversity. But habitat selection is not an isolated concept. Influenced by the complexities of changing temporal patterns and environmental pressures, the choices individuals make depend not only on their relationship with the environment, but also on the population's ability to adapt when change occurs. Worryingly, environmental change may often occur more quickly than a population's ability to evolve to those changes. Research conducted by Professor Douglas Morris and colleagues from Lakehead University in Canada is directed towards understanding this complex interplay among environment, ecology, evolution and the future of Earth's biological heritage.

OBSERVING CHANGE

Morris and his team have identified the value in connecting the behavioural choices and life histories of organisms with population dynamics and interactions among species, describing their research philosophy as a merger between theories and perspectives in ecology with those in evolutionary biology. The Lakehead group, which includes both undergraduate and graduate students, is working on understanding changes in habitat selection and future evolution in a number of ecosystems and most notably, their work focuses on the changing polar environment, with field work conducted in Canada's Arctic.

One of the key studies tracks lemming populations to assess how they are likely to adapt their use of space to global warming and its associated climatic changes. Morris elaborates: "In our work on lemmings, we asked whether the indirect effects of climate change are more important in determining patterns of habitat use than is its direct influence". It may not come as a surprise that the investigation found fewer lemmings in warmer years, but the ecological pathway that elicits this effect is more intriguing. By comparing their current work with data they collected in the 1990s, Morris and his group were able to confidently identify global warming as the main factor causing changes in lemming habitat selection and population density. Subsequent research, which measured annual growth rates of deciduous shrubs over an 80-year period, also identified climatic variation as a significant factor influencing terrestrial Arctic ecosystems, providing both floral and faunal evidence of the change.

> The work of Morris and his colleagues is improving understanding of the changing ecology of the Arctic and other ecosystems

THEORY AT WORK

Morris and his colleague's theories are primarily generated through first principles augmented by observation of natural systems. Theory and fieldwork demonstrate that habitat selection can appear counter-intuitive. Work in western India by recent graduate Sundararaj Vijayan led to the novel insight that Spotted Deer prefer habitat overgrazed by domestic cattle as the presence of livestock reduces their predation risk from Asiatic Lions. However, as in all areas of science, experimental manipulation is required to test ideas. To this end, the team built an extensive experimental field facility in northwestern Ontario known as the 'Habitron'. This investment allows them to test their ideas in a naturally controlled system. Research conducted in the Habitron on voles has, for example, confirmed the hypothesis that mammals actively select some habitats over others in a way that corresponds with our understanding of adaptive evolution.

One of the novel features of the Habitron is that it can serve as a template for computer simulations of habitat selection and the spatial distribution of populations. Data on habitat quality and the movement of animals among the Habitron's interconnected rodent enclosures can inform

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computer models with the capability to explore new scenarios of habitat selection that can then be tested experimentally in the Habitron. Although it would be best if ecologists possessed the necessary field and computational skills for both tasks, Morris notes that the skills are not necessarily complementary: "Whether simulations are best carried out by individuals or teams depends on the importance and complexity of the problem and the degree to which it can be reliably simplified".

Reliable simplification is a serious challenge for ecologists and evolutionary biologists who must invent tractable models in order to summarize the often-times complicated interactions between ecology and evolution. It would be a mistake, however, to assume that ecological processes such as population growth necessarily occur more rapidly than does evolutionary change. Morris elaborates: "We are becoming increasingly aware that time scales for evolutionary change are similar to those we normally attribute to ecological events". This critical perspective is exemplified by Morris and co-author Per Lundberg's treatment of evolution as six pillars: mechanics, function, structure, scale, dynamics, and adaptation merge genetics and environment into a single eco-evolutionary process called 'Evology'. The result is an: "Evo-ecological feedback loop where evolutionary change can occur rapidly enough to influence the demography and dynamics of populations," explains Morris. This can blur the boundaries between population dynamics and evolution and once again highlights the importance of considering the two together.

POLITICAL ECOLOGY

The work of Morris and his colleagues is improving our understanding of the changing ecology of the Arctic and other ecosystems. Improved theory, intelligent observation, and carefully conducted experiments are vital to understand how climate and other changes will impact biodiversity and human welfare. Unfortunately, knowledge without political action or awareness will precipitate little progress towards solutions. A core problem in environmental policy formation is the focus on solving short-term social, economic and political exigencies rather than using informed scientific advice to solve overarching problems such as climate change. Similar concerns exist regarding the general absence of properly educated science graduates involved in the relevant politics. When complex ecological research is presented as evidence of the need for action, politicians need to be able to understand the work and its implications. Subsequently, Morris suggests that: "Universities must do more to properly educate their graduates in the basics of ecology and evolutionary biology".

Despite global warming, Morris states that global extinction is the biggest issue requiring immediate attention: "We are living in the midst of a deepening global crisis that portends the massive extinction of much of Earth's biodiversity," he explains. Human livelihood and welfare depend on biodiversity. The loss of a few species of insects, for instance, can have profound effects on crop productivity. Many species are recently extinct and many more threaten to follow, yet the impact of these events is poorly appreciated. Clearly in this context Morris's work is vitally important. Although the challenges within his work and the surrounding societal inertias are significant, Morris believes that not all is doom and gloom, pointing out that: "If we work hard to instigate policies protecting Earth's species and habitats, we will also live in a world where climate will take care of itself".

Clockwise: Arctic wolf, Woolly lousewort, Arctic ground squirrel, Antler on tundra

INTELLIGENCE

THE EVOLUTIONARY AND POPULATION ECOLOGY OF HABITAT SELECTION

OBJECTIVES

- To merge theory, computer simulations, controlled experiments and detailed field observations in order to assess habitat selection, by designing and building the world's first Habitron; a field facility designed explicitly to study habitat and habitat selection by mammals
- To learn whether animals choose habitats that maximize their evolutionary fitness, how patch use by animals can measure the quality of their habitat, how environmental change modifies habitat choice, how habitat selection helps to regulate population density, and how adaptation can be used to predict future evolutionary strategies

KEY COLLABORATORS

Canada's Polar Continental Shelf Program (PCSP) • Northern Scientific Training Program (NSTP) which provide logistic support for the Arctic research • **Per Lundberg**, Lund University • **Angélique Dupuch**, Université Laval

FUNDING

Natural Sciences and Engineering Research Council of Canada • Canada Foundation for Innovation • International Polar Year, Canada • Ontario Innovation Trust • Lakehead University

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DOUGLAS MORRIS is Professor of Biology and Research Chair in Northern Studies at Lakehead University. Much of his research uses habitat selection and foraging experiments on small mammals to probe interactions between the adaptive behaviours of individuals with the dynamics of populations and the structure of ecological communities.

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