Heritage Lecture / Allocution du patrimoine By Richard Ring

Insect Adaptations: A personal perspective

ood Morning Ladies and Gentlemen, Mesdames et Monsieurs! It is my privilege as well as a great honour to have been invited by the Organizing Committee to present this lecture on the 20th anniversary of the Heritage Lecture Series. I remember well the introduction to the Heritage Lectures given by George Ball followed by the inaugural lecture delivered by Paul Riegert at the 1983 meetings hosted by the Entomological Society of Alberta. Indeed, Paul went on to deliver three more lectures in the series, including one in 1985 entitled Northern Insect Studies, which had an important influence on my work and thinking on Arctic insects. This has lead me directly to the title of today's lecture, Insect Adaptations: A personal perspective. In thinking about the topic from a historical, but yet personal point of view, I decided to divide the topic into the following sub-headings: People, Places, Projects and Passion (I was in alliterative mood!).

People

I have long been interested in insect adaptations since my days as a student at Glasgow University, where I went on to complete a PhD degree in insect diapause. As a result of these studies (overwintering diapause in the sheep blowfly, *Lucilia caesar*), I became familiar with the re-

Richard Ring has spent the bulk of his scientific career at the University of Vicotria studying insect seasonal adaptations such as cold hardiness and diapause. He recently retired from teaching and has taken on the role as Editor-in-Chief of The Canadian Entomologist. For contact information see the inside of the front cover. Presented at the Joint Annual Meeting of the Entomological Society of Canada and the Entomological Society of B.C. in Kelowna B.C., 5 November 2003.



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markable work of R.W. Salt, Agriculture Canada, Lethbridge, who, in 1961, published the paper The Principles of Insect Cold-Hardiness in the Annual Review of Entomology (Salt 1961). This paper established the working principles in studies of insect cold tolerance for the next forty years, and became the paradigm within which we still operate today. I met Reg Salt only once in my career, and that was in Quebec City in 1972 when he was awarded the Gold Medal of the ESC and delivered the address Cold Comfort at the Joint Annual Meeting of the Entomological Societies of Quebec, America and Canada. However, I did get the opportunity to learn much more about him later, both personally and professionally, when Paul Riegert and myself co-authored a chapter entitled A Tribute to R.W. Salt in the book Insects at Low Temperature (Ring and Riegert 1991). This book has since become the modern standard text in the subject. On reflection, I realize that by the time I came to Canada as a raw PhD graduate in 1964, I was already well aware of the rich heritage of entomology in this great country.

As most teachers and researchers will agree, one's career is often a long tortuous path, along which doors open for you - often at the most unexpected times and places! Well, for me one of the first of these doors was opened by Geoff Scudder (ESC Gold Medalist, 1975), Zoology Department, UBC, who invited me to apply for the position as his sabbatical replacement for the academic year 1964-

65. This turned out to be one of the most influential events in my life. It was the same year that Salt's first PhD student, Lauritz Somme, Zoology Institute, University of Oslo, published his influential papers on insect cold tolerance (Somme 1964). He later became my mentor, and in 1972-73 I spent my first sabbatical leave at his laboratory in Oslo. Since then, we have shared many symposia, conferences and visits together, culminating in 1988 with our field trip to South Georgia with the British Antarctic Survey and our expedition leader, Bill Block (Fig. 1). In three months we produced five joint papers on the adaptations of insects on this small sub-antarctic island.

The second main door to be opened for me was by Antony Downes (Gold Medal 1977), head of the Entomology Research Institute, Agriculture Canada, which was later incorporated into the Biosystematics Research Institute, Ottawa. In 1965-66, he secured a Post-Doctoral Fellowship for me that introduced me to the Northern Insect Survey. The Northern Insect Survey in its 18-year history from 1948 until 1966 sent over 80 field parties all over the Canadian Arctic, ultimately yielding the baseline data for all future studies (see Danks,

1981). Although I was still working on the phenomenon of overwintering diapause in insects at the time, it quickly became apparent that diapause and cold-hardiness were concurrent events in northern insects, and that both were important ecophysiological adaptations to arctic habitats with long cold winters and short growing seasons. The ecophysiological relationships between diapause and cold-hardiness in insects are still unresolved today. The most important experience for me that year was to be introduced to the members of the Northern Insect Survey and learn of their tremendous accomplishments in Arctic Canada. Apart from Antony Downes himself, they included Phil Corbet (Gold Medal, 1974), Don Oliver, Frank McAlpine and several others. Contact with these people was going to stand me in good stead for the rest of my academic career in Artic entomology.

The third and perhaps largest door to open for me in my academic life was in 1966 when I applied for and was offered a position as Assistant Professor in Biology at the brand new University of Victoria, B.C. This appointment was what allowed me to set up my own laboratory, my own



Figure 1. Lauritz Somme, Bill Block, Richard Ring, Roger Worland and Preben Ottesen (left to right) at South Georgia, Antarctica in 1988 to study the cold hardiness of arthropods.

research initiatives and, therefore, my long-term Arctic research programme.

Places

Arctic Canada. What a fantastic place in which to work, unlike any other major biome in the Nearctic zone. As one of my colleagues (John England, Northern Chair in Geology/Glaciology) said recently at the sixth Northern Students Conference held at the University of Alberta, one shouldn't think of the Canadian polar desert, but, rather, the Canadian polar dessert! Yes, indeed! The Arctic tundra is one of the largest biomes in Canada, and occupies almost 25% of our land surface area, yet is one of the least understood, at least from a biological perspective. Although I have traveled extensively in the Arctic, the two regions where I have done most of my research are: (1) the low Western Arctic in the region of Inuvik, Tuktoyaktuk and the adjacent Peninsula (69°N; 133°W), and (2) the high Eastern Arctic on Ellesmere Island at Alexandra Fiord (79°N; 76°W). Both are fantastic places in which to work and have unique biological, geological and historical attributes. The low Western Arctic is dominated by surface water, arctic shrubs like willows, alder and dwarf birch, a variety of grasses and sedges and a great diversity of flowering herbs. The climate is moderate compared to the North-Eastern Arctic. It is a fascinating area in which to work as a biologist, since not only is it a transition zone between the northern limits of the boreal forest and the southern limits of the tundra biome, but also a West-East transition zone due to the dominating presence of the mighty MacKenzie River and its delta. On the west we have Beringia and the Cordilleran Region and on the east are the Interior Plains and Canadian Shield, each with its distinct faunal elements.

The high Eastern Arctic, on the other hand, has a much more extreme climate and is dominated by snow and ice. The vegetation is depauperate, as are the animal consumers, but nevertheless it remains of great interest to entomologists, especially at arctic oases such as Alexandra Fiord (Fig. 2), which represents a terrestrial arctic oasis that is generally characterized by elevated summer temperatures and higher moisture levels compared to the surrounding "arctic desert". The lowland's physiography is largely responsible for the amelioration of the weather patterns. Snow cover on the surrounding scree slopes and glaciers tends to reflect solar radiation into the lowland increasing its temperature, while the surrounding edges act as a wind foil. Water collected from glacial tongues, which spill out from the Ellesmere ice cap, drains through the gently sloping lowland and irrigates it through a network of small channels before flowing into the Fiord. The mean July temperature is 5.1°C compared to an average of 4.4°C for the

Figure 2. Sampling insects and plants at Fiord, Alexandra Ellesmere Island. Nunavut as part of the International Tundra Experiment (ITEX). The ITEX is a scientific network of experiments focusing on the impact of climate change on selected plant species in tundra and alpine vegetation.





Figure 3. Lee Humble with a pingo in the background near Tuktoyaktuk NWT sampling for insects, while the mosiquitoes sample him.

surrounding regions. The plant and insect communities are consequently much richer in the Fiord lowland than in adjacent areas. This high relative abundance of organisms found in Alexandra Fiord lends itself to the study of insect life cycles, adaptations to extreme conditions and responses of arctic insects (and other organisms) to global climate change.

Projects

My research programme has been, in essence, a study of the ecophysiology of insect adaptations to northern climates and northern habitats dominated by long, cold winters and short growing seasons often combined with low levels of precipitation. So it is the combination of cold hardiness, diapause and desiccation resistance that has occupied my research interests for a long time now. Some of the major contributions from my laboratory have been (1) identification of a multi-component cryoprotective system in successful overwintering insects, including a combination of glycerol, trehalose and sorbitol; (2) the discovery of the lowest supercooling point (-61°C) ever recorded for an insect, Pytho americanus, in the Western Canadian Arctic (Ring 1982); (3) the close relationship between cold hardiness and desiccation resistance that exists in overwintering insects; the role of increased levels of trehalose in the haemolymph of these insects has also been implicated in increased resistance and/or tolerance of dehydration (Ring and Danks 1994); and (4) identification of various anomalies that exist among arctic insects, such as being freezing tolerant, yet having very low supercooling points and, in some species, having double supercooling points. Several other anomalies await elucidation, such as the winter survival of arctic coccinellid beetles which lack any known cryoprotectants. My very first PhD student, Lee Humble (Fig. 3), made an important attempt to tease apart the co-evolutionary problems of cold versus desiccation tolerance. In arctic sawflies, he demonstrated that their abilities to survive low winter temperature and desiccation stress are co-adapted - that is, they are overlapping adaptations (Ring and Danks 1994). My second PhD student to work in the arctic, Dean Morewood, studied the life history strategies and temperature versus development relationships of the high arctic woolly bear caterpillars (Gynaephora spp.) and their parasitoids at Alexandra Fiord. Other contributions made by my laboratory regarding adaptations to extreme conditions are those by Neville Winchester on arctic trichopteran larvae of the Tuktoyakuk Peninsula and by Adrian DeBruyn on the overwintering behaviour and habitats of two species of diving beetles (Hydroporus spp.) in ponds at Alexandra Fiord. As a result of these studies, the University of Victoria was chosen as the venue for two international symposia on insect cold hardiness (1985 and 2000), as hosts for the Society for Cryobiology meetings (1980), and for organizing a session at the International Congress of Entomology in Vancouver (1988). Although most of my studies have been on arctic insects, several similar studies on adaptations have been carried out on insects from southern Vancouver Island.

Passion

Almost one third of you in the audience today are graduate or undergraduate students, so at some time in your lives you have been inspired by your supervisors, or mentors, or peers to enter the field of research in entomology and to attend meetings like this. I suspect you would not be here today if you did not already have the passion! After all, this is where you are most likely to meet like minds and be constantly reminded of the passion that has brought you to this point.

It would be remiss of me not to acknowledge the many people who have helped fuel this passion in me. I thank the many students (too numerous to mention by name) at all academic levels who have been a great inspiration in my life, and without whose questions, challenges and support I would not be here today. There are a few people in particular I wish to acknowledge, all of whom have been involved in the study of insect adaptations to Canadian Arctic habitats and envi-



Figure 4. This lecture is dedicated to the memory of Antony Downes (left) (1914-2003), one of Canada's greatest and most respected Arctic entomologists, photo taken at the Biological Survey of Canada meetings in Ottawa in 2001. ronments. Among my very first graduate students are Lee Humble and Neville Winchester, who have become eminent entomologists in their own right, yet still remain close friends and colleagues; Olga Kukal who introduced me to Alexandra Fiord and, with her partner Tom Allen, further introduced me to the fascinating world of *Gynaephora groenlandica*, one of the most cold-tolerant insects ever studied; other colleagues such as Peter Kevan and Joe Shorthouse who were studying insects in the high eastern arctic long before I was; and, finally, I acknowledge the close parallel career paths, the research collaboration and the friendship that has developed over the years with Hugh Danks (Gold Medal, 2003).

As I prepare for retirement from the daily teaching and research activities at a university, I do so with a sense of optimism and celebrate this combination of people, place, project and passion that I am certain is in each one of you here today. I hope that this will fuel you for the rest of your lives and that it will result in personal fulfillment as well as important contributions to this rich heritage we call Canadian Entomology.

I wish you well in your future careers.

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