

REFLECTIONS ON THE BUREAU OF ANIMAL POPULATION

By

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Caroline Pond who ‘read-in’ the entire oeuvre.**

If I have any right publicly like this to reflect on the Bureau of Animal Population, it is mostly because I was a research student at the Bureau doing my D.Phil., from 1949 to 1953, supervised by Dennis Chitty, then a Senior Research Officer of the BAP, and later moving to be Professor of Zoology at the University of British Columbia.

I will commence by telling you what the Bureau of Animal Population was, and who was its only Director. I will then give my account of the origin of the BAP, of the work it fostered, of the people who played crucial roles in its development and its survival, and finally I shall describe the circumstances which brought about its end, and remark upon what has followed on from it. What I will chiefly talk about are some of the people who were part of the Bureau, or instrumental in its development, in sustaining it, and bringing about its disappearance. I will only incidentally talk about the ecological research which was carried out by its members. I’m really going to talk about, for the most part, the people whom I knew at first hand and who affected me. It will be an eclectic account, in the sense (O.D., loosely interpreted) of “Selecting from each school of thought such doctrines as please me”.

From the way I look at the BAP, and more particularly my own involvement in it, there was a complex way of interacting people, but this may not distinguished it from the general run of other organisations, scientific or not. Compared with the

account given by Tom Halsall of the history of the Dyson Perrins laboratory, this is short, and pretty recent part of the *Recent History of the Science Area* (of which, for more than half its existence, from 1947 to 1967, it was not, from a geographical point of view, a part). I should add that an excellent account of the history of the Bureau has been written by my fellow Australian and contemporary at the Bureau, Peter Crowcroft, who did real Ecology while there (unlike my own research) (**Slide of title page of “Elton’s Ecologists”**). His “*Picture Post*” treatment of me, a double page spread, is flattering, quite out of proportion to my role at the BAP, and the caption of one photo contains a couple of amusing errors.

1. *What was the Bureau of Animal Population?*

The Bureau of Animal Population was the ecology research Institute created in 1932 by Charles Elton, subsequently Reader in Animal Ecology, subsequently Fellow of the Royal Society. It survived until the end of September 1967, when Charles retired (**Slide of CSE, rain forest, Central America, c. 1967-68**). So there is one central character in my story, Charles Elton. I am very much, in fact crucially, indebted to him: I doubt if I would now be in Oxford had it not been for Charles Elton, not because I ever did true ecology research, but because of the encouragement and support he gave me at several crucial stages in my life in Oxford. So, if nothing else, I want this talk to be a eulogy of Charles Elton.

The Bureau of Animal Population became, in 1947, one part of the Department of Zoological Field Studies, the other part being the Edward Grey Institute for Field Ornithology, whose first Director was David Lack (**Slide of David Lack**) famous for the “*Life of the Robin*”, and “*Darwin’s Finches*”, among many other publications. Both institutes were part of the Department of Zoology and Comparative Anatomy, as it was then called. The Linacre Professor of Zoology and Comparative Anatomy at the time the Bureau began was E.S. Goodrich (**Slide of Goodrich**), renowned for his studies on comparative anatomy and his meticulous, if time consuming, drawings on the blackboard, but not overimbued with enthusiasm for other aspects of biology, so that it is an extraordinary measure of their resilience, intelligence and no doubt shrewdness that John Baker, J.Z. Young, E.B. Ford and Peter Medawar emerged from what may have been a rather claustrophobic atmosphere in the Department in Goodrich’s time, but more especially is Charles Elton to be admired: Goodrich is reputed to have said to Charles, at an early stage in Charles’s career, “You know, Elton, that there can be no advances in zoology except through comparative anatomy”, and besides Goodrich’s failure to see the importance of ecology, Charles had to put up with the scepticism of some of those more nearly of his age and status.

Charles died on 1 May 1991, aged 91. His first publication was printed in the *Proceedings of the Zoological Society* in 1922, he had his first book published in 1927 when he was 27 – “*Animal Ecology*” which had an immediate and lasting effect on ecological ideas, he published a very large number of papers throughout the rest of his life, which together could have constituted a number of separate D.Sc.s, yet he was not concerned with taking out a higher degree, unlike almost all of his contemporaries in the Zoology Department, not because he was scornful of higher degrees, indeed he very actively encourage research students in their work for D.Phils.

There is absolutely no doubt that he profoundly influenced the ideas of ecology throughout the world, through his work at first on animal (more especially small rodent) population cycles and then later in his life the ideas about the structure of animal and plant communities. We can attribute the development of fundamental ideas which are central to aspects of present-day ecology, to Charles Elton, ideas which now are regarded as beyond question, relating to the control of animal population size (including the control of pests), the pyramid of (animal) numbers, food chains, the structure, ontogeny and phylogeny of ecological communities, and to conservation with which we are all now so much concerned. I think he can properly be regarded as one of the, if not *the*, founding figure of ecology for this century.

I first became aware of this, as it seemed to me then, curiously named Bureau of Animal Population when I was an undergraduate in this institution (***Slide of University of Western Australia***), which was, incidentally, in effect an extension of my home. In the neglected library there of the Department of Biology (other Departments were much more effectively run) there were, amongst the limited number of mostly fusty books, just two written by Oxford zoologists: (***Slides of title pages, Voles, Mice and Lemmings, by Charles Elton; Studies on the Structure and Function of Vertebrates, by E.S. Goodrich.***) Charles's book was published in 1942, and I must have seen it in the library in about 1945. It is surprising that someone in that department had had the imagination to order it, and that, is the turmoil of war, including the menace of U boats, a copy was to be seen so comparatively soon (this was 1943-46) on the shelf.

But it was not until I was going by cargo ship to Gambia in July 1948 as a member of the Oxford University Gambia Expedition that I read this very important and beautifully written book. By then I had already attended Charles's lectures on Ecology as part of the School of Zoology (repeating undergraduate life, as was the tradition with Rhodes Scholars of that epoch). Unlike the majority of my contemporaries (we were all 22 years or more, others being warriors of one sort or another returning from military service and the second world war) I enjoyed Charles's lectures enormously. They were delivered in a very low-key fashion, with Charles sitting on a laboratory stool behind the lecture theatre bench (this was in the old Department of Zoology and Comparative Anatomy, at the back of the University Museum, and now partly or wholly Atmospheric Physics). What gripped me was their authenticity, conveyed by his modest manner combined with an extraordinarily interesting, appropriate, display of 35 mm slides illustrating ecological problems and with many of which Charles had been directly involved. These included scenes from out-of-the-way places, such as Spitzbergen, appealing in his way to the journeys I had made during my first 22 years into the rough terrain in the almost exact opposite climate of the southern third of Western Australia. Charles's approach was, in a literal as well as metaphorical sense, global, or highly integrated, and I think that also appealed to me, coming from Australia where large or long or continental views and standpoints were a reality, and a very important part of the ethos. Charles did not have a high opinion of himself as a lecturer, though I only became aware of that decades after I had attended his undergraduate course.

I was to give a research talk in the Zoology Department here, and wanted to show a slide of Charles. I wrote asking his permission, remarking in my letter how the slides

in his lectures had had a particularly strong affect on me. He replied, allowing me to use a certain photo of himself (he was curiously sensitive about others using photos of him), and adding that he had used slides extensively in his lectures "...because I regarded myself to be such a poor lecturer". For me, he did not come across like that. If this crazy idea, supported or advocated by John Patten or William Waldegrave, reported in the "*Observer*" a couple of weeks ago, that 25% of a lecturer's salary should be dependent upon student assessment of the lecturer's ability to lecture, had been in place in 1947-1949, Charles, on a "beauty contest" type of judgement, might have been short of cash.

I first came into really close contact with Charles Elton in Hilary Term 1948, when I had been invited to be a member of the Oxford University Expedition to the Gambia (which took place from June/July to September 1948), where I would be required to investigate hippo damage to rice crops (I can claim to have dissected from a Hippo down to the field vole, about an 80,000 range in mass). Charles was the Senior Member of the Oxford University Exploration Club, for reasons that will emerge.

2. Why Study the History of Science, or for that Matter, History more Generally?

In preparing this talk I have asked myself this question and come up with the rather grand answer that we would like to know the political, social and economic circumstances which have influenced the development of science, or anything else. But I am incapable of analysing the history of the Bureau of Animal Population from this rather highfalutin viewpoint. More to the point is that perhaps studying the history of a science will tell us something about the way science progresses and scientists work, which I suppose would be a contribution to what is called the Philosophy of Science.

Are there any generalities about the nature of science and the life of scientists that can be gleaned from the history of the Bureau of Animal Population? If anything, the history of the Bureau of Animal Population, as I shall presented, illustrates chance rather than necessity (to borrow from Jacques Monod) at least in its origin and early development, and from within those haphazard circumstances, I will emphasise the decisive role of particular people, many of whom we shall see in slides.

3. The Origin of the Bureau of Animal Population?

How did the Bureau arise? Because Charles's brother, older than him by about 5 years, died before his time, at the age of 33, in 1927. That was decisive influence on Charles. He had been profoundly attached to Geoffrey Elton. In an unpublished talk to the members of the BAP on 18 April 1947 (when the BAP moved into new quarters, the St. Hugh's huts, see below) Charles explained: "He was a man of much genius, which he gave especially to educational research and experiment. He was also an extraordinarily good naturalist... He had trained and encouraged me continuously in the love of natural history since I was 9 years old, and I owe to him any capacity I have to be an ecologist. After his death, I decided to found an institute for studying population ecology, that would, through myself and those I should train to replace me perpetuate his influence as a field naturalist and teacher."

Though this idea of a memorial to his brother had been the crystallising factor, how was it that results focused, at the outset, on population ecology? This is made clear in another unpublished talk to the BAP on the occasion, 14 February 1962, of the 30th anniversary of its creation. Julian Huxley (brother of Aldous and both of them grandsons of Thomas Henry Huxley who, of course, among other contributions to biology, had been the chief protagonist for Charles Darwin), who was Charles Elton's tutor at New College in c. 1919-1922, invited Charles to join the 1921 Oxford University Expedition to Spitzbergen as Julian's assistant. Charles was an undergraduate, and Julian "let me do what I liked, and this was an ecological survey of animal life."

There is, for me, a pleasing, personal, link with Charles through his first, and my only, participation in an Oxford University expedition: in Hilary Term 1948, when I had been in Oxford for only about 5 months, I was, to my astonishment, asked by Francis Huxley, Julian's son (ex Royal Navy, war- and peace-time obligatory service, and in his final year reading Zoology) to be a member of the Oxford University Expedition to the Gambia. I was not Francis's assistant, nor could I do exactly what I liked, though in practice I had an entirely free hand within the problem allotted to me: I was expected to carry out a survey of the destructive effects of the Hippos on Gambian rice crops, and this I did. But just as Julian's invitation to Charles in 1921 had a profound effect on Charles's development as an ecologist and on his career, so Francis's invitation to me 27 years later had a crucial effect on my own career, chiefly because of the contact with Charles Elton that it brought me.

I think it is unlikely that the Bureau of Animal Population would have been set up, anyway with that particular orientation, had it not been for Julian Huxley's invitation to Charles in 1921, which led to other trips to Spitzbergen by him as a member of further Oxford University expedition, through which his interest in populations was aroused and focused, as I shall explain in a moment. And for me it is unlikely that I would have stayed those unintended extra 43 years here in Oxford had I not been invited by Francis Huxley to be part of an expedition to Gambia with the consequence of a close contact with Charles Elton than would have otherwise happened as an undergraduate, since, as the Senior Member (??) of the University Exploration Club, he quietly kept a close, committed and helpful, eye on its activities.

Charles went again to Spitzbergen in 1923 as a member of the Merton College Arctic Expedition, on which (as he said and written drily and with characteristic understatement "This time we tried to circumnavigate North-East Land, and were led to some very barren spots indeed. Indeed, on the whole of this island, about the size of Wales, I found only 9 species of dry land in vertebrates." We have to bear in mind that this was 1923, and these were Oxford undergraduates, or very recent graduates.

On the way back to Britain Charles spent his last £3 in a shop in Tromsø on a book by one Robert Collett about Norwegian mammals – "*Norges Pattedyr*", and in this he learnt (by translating parts of it, including records) about lemming migrations, and that they occur every 3 or 4 year somewhere in Norway. We can see in this rather unlikely find and purchase in a then remote Norwegian bookshop the further development of Charles's ideas about populations.

Charles was in charge of the scientific work of the 1924 Oxford University Arctic Expedition, again I think to Spitzbergen or else North-East Land, and he was at the base camp for the whole of the expedition carrying out a large, general, ecological survey. The expedition had a medical officer. It had recruited this young, recent, Adelaide medical graduate (*Slide of Howard Florey, 1924*), who had come to Oxford as a Rhodes Scholar in 1922, and in June 1924 had just done finals in Physiology. This is Howard Florey, later Nobel Prize winner for his work on penicillin, Professor of Experimental Pathology at the Sir William Dunn School in Oxford, President of the Royal Society, made Baron in 1965, Provost of Queen's College and who died in 1968. Charles spent two weeks at the base camp with "... Dr. H.W. Florey, and this led to a friendship that...had very important later results for the work of the Bureau", and indeed Lord Florey (*Slide of Florey later in life*) appeared to contribute to the unsuccessful defence of the Bureau in the last stages of its existence, besides at least two other very important successful contributions which he made in the early life of the Bureau.

That they were close friends became very apparent to me when, about 10 or 11 years ago, I met Charles in South Parks Road, and stop for a chat, as we often did both before and after this occasion. I had just finished reading Gwyn Macfarlane's splendid biography "*Howard Florey: the Making of a Great Scientist*" (given to me by Margaret Yekutieli, nee Cairns, see below). Florey, fellow Australian, fellow Rhodes Scholar, neighbour to us when we lived in a University house on the "Keble Triangle", I had met at dinner in Hilary term 1948 at the home of my contemporary Margaret Cairns whose Father, by then Sir Hugh, also fellow Australian, fellow Rhodes Scholar, and like Florey and (earlier) medical graduate from Adelaide, was Nuffield Professor of Surgery and also features later in my reflections. Frequently I would come out of our Parks Road gate in the morning going to the lab at the same time as Howard Florey, but there was never a glimmer of recognition or the faintest grunt of greeting. He was utterly granite-faced. But the Gwyn Macfarlane biography transformed Howard Florey for me, and I realised that behind the granite face there was a feeling, sensitive, perhaps over-sensitive, person. In South Parts Road I enthused to Charles about the biography. Charles's response was "He (Gwyn Macfarlane) went too far!!", and of course Charles was referring to the inner life of Howard Florey, insights into which had for me filled out the character of Howard Florey.

These expeditions to Spitzbergen had opened up the problem of regulation of population size, and small rodents illustrate basic aspects of this very well. Other ecological ideas were also generated during and as a consequence of those investigations of the simplified habitats of the Arctic, and indeed it was only in retirement that Charles felt competent to examine that most complex of habitats, tropical rain forest (the first slide).

Julian Huxley's influence had not ended with that invitation to Charles to join that 1921 expedition to Spitzbergen. It was through a suggestion of Julian's that Charles, while still an undergraduate, read, besides a book on population by Carr-Saunders, "*The Conservation of the Wild Life of Canada*" by Gordon Hewitt. This alerted Charles to the records of the fur returns of the Hudson Bay Company, those for snowshoe rabbits and lynx being particularly important, appearing to have a 10 year cycle of abundance. These writings on Norwegian and Canadian mammalian wild

life, and the regular fluctuations in their abundance, prompted Charles to study more completely, in the period 1925 to 1930, the contemporary and past fur returns of the Hudson Bay Company. He was able, from the Company's records, to go back as far as 1736, the longest known study of wild mammal population fluctuations and covering the vast area of the northern Canadian territories (his approach also inspired me to use Colonial Office reports of "ivory" returns (which included hippo teeth) to make estimates of hippo cullings in East Africa).

No doubt with the Canadian fur cycles and the lemming cycles in mind, it was in 1925, a year after return from his third Spitzbergen expedition, that Charles is said to his contemporary in the Department of Zoology and Comparative Anatomy, John Baker (*Slide of John Baker "mouzing", c. 1926*) "Shall we do some work on mice?" And John Baker replied "All right, I can supply a car" (a splendid big "Essex" roadster with a "dicky seat"). So was formed what they called the "*Mausgesellschaft*".

The car was not always used: here (*Slide of Charles c. 1925*) is Charles on a splendid motor bike, loaded with traps, heading off for Bagley Wood, where most of the work was done. Two further people added to the *Mausgesellschaft* – E.B. Ford (*Slide of Henry with Charles, Bagley*) and Dr. A.D. Gardner (*Slide of A.D. Gardner*). The intention was to study the population biology of field voles (*Slide*), bank voles, and wood mice (*Slide*). They divided up the work, John Baker investigation reproduction, Henry Ford the Protozoan parasites, Charles the multicellular parasites (e.g. helminths, worm parasites) and A.D. Gardner the Spirochaetes.

It was a very good example of co-operation, dividing up a problem to make it feasible, and then pulling it together, somewhat ahead of its time in this regard, and indicative of how Charles saw the nature of ecological research. All three of Charles's co-workers went on to be distinguished in one way or another and stayed in Oxford, John Baker changing from the study of breeding seasons to becoming a meticulous cytologist and made FRS, Henry Ford (he was Henry to his close associates in the Department) contributing substantially to the study of population genetics, especially in his study of mimicry in butterflies, and also made FRS., and A.D. Gardner later becoming Regius Professor of Medicine in Oxford.

In the several years over which the *Mausgesellschaft* existed, some 2000 wood mice and voles were examined, and out of it emerged important facts and ideas concerning the seasonal breeding and the parasites of the three species of rodent which they studied. Both John Baker's and Charles's work contributed decades later to my own work and those working with me: John Baker went on to do very original experimental studies on the effect of daylength or daylight on seasonal breeding, and much of my own research on that subject ("How do animals measure daylength"?) and that of many others, has been dependent on, and arises out of, John Baker's investigations (with Richard Ranson).

In 1986, my colleague and friend, Anne Keymer, and I got a grant from the NERC to investigate experimentally with laboratory stock and in wild populations, the influence of a helminth parasite on the fertility and other life table attributes of wood mice. Richard Gregory, our excellent research assistant we were lucky enough to

employ on that grant, thought that maybe there was no point in doing again what Charles had done, in the way of recording helminth parasites in wild populations of wood mice. Perhaps, he thought, we should re-examine Charles's data.

Richard got in touch with him, and Charles was extraordinary helpful. Of course (in his case) he had his original note books, with meticulous entries in them, and Richard was, indeed, able to re-work the data which Charles had scrupulously recorded. This made additional fieldwork unnecessary, Charles's note books certainly helped us, and I hope, or I think, it gave him pleasure, in his late 80s, to find that the data he had collected 60 years earlier could be so readily re-worked with a fruitful outcome.

It was after the Mausegellschaft was wound up, in about 1929, that Charles (as expressed by him) had the ambition "...to collect into one room all the publications concerned with lemmings": this could be regarded as the beginning of the idea of the Bureau of Animal Population.

I have already given you the most important reasons for Charles's ambition to create such an ecological research institute: a memorial to his brother, and the direct and indirect effects on him of his participation in expeditions to Spitzbergen. Now at the beginning of the 30s this ambition had to be translated into an establishment. A Conference, an organisation and a person decisively influenced the establishment, formally, of the Bureau.

The Matamek Conference took place on the Gulf of St. Lawrence in c. 1931, and involved the Hudson Bay Company, besides people named by Charles (unpublished 14/2/62). It was on Biological Cycles, and Charles was a scientific secretary. Of the conference Charles has written (unpublished 14/2/62) "It is the only conference I have ever known at which the Chairman in one morning and threw down two large river salmon that he had just caught, and at which not only professors and various biologists.... Were present, but also read Indians, game and fish wardens, poachers and the captain of the Québec ice-breaker (The last named would be a wonderful help in Oxford)". The New York Zoological Society,?? senior members of which participated in the Matamek Conference, gave Charles a grant (in about 1931) on which he was able to live for 2 years and (in his own words) "...without which the Bureau could not have started then". And this is the person (**Slide of Sir Douglas Veale**) to whom Charles expressed his great thanks, having "...a debt (to him)....that is immeasurable.

Without his pathfinding through the insane jungles of the University and Government Administration the Bureau could not have started or survived". Sir Douglas, as you can see, was the Registrar from 1930s in 1958. He was a very remarkable man, and deserves a lecture in his own right. He and Charles must have met and got on well together very soon after Sir Douglas arrived in Oxford (he had been an undergraduate here, reading....?), since he played this acknowledged crucial role in the setting up of the Bureau in 1932. He played an important role later on in the history of the Bureau and of ecological work more generally in Oxford, and there was an amusing unrecognised or unadmitted conflict of interest for him about 15 years later – or was it a *quid pro quo*? (That seems hardly likely in a person of such integrity).

Until 1936 Charles had no permanent position. Alas, in the exceedingly difficult times in which innumerable research workers now live, that might seem unsurprising, yet it is a mark of the difference between then and now that Charles has commented on this. However, in 1936 he jumped from having no permanent position to being made Reader in Animal Ecology, and also Senior Research Fellow at Corpus Christi College, of which I think Douglas Veale was a Fellow. I'm sure these improvements in Charles's position, the recognition by the University of the Bureau, and the coming of Douglas Veale are linked. What was the origin and nature of the interaction between Douglas Veale and Charles Elton? (Although Charles has said and written that he had no permanent position until 1936, I have thought he had, before that, been a University demonstrator: see University records?).

With the establishment of the Bureau in 1932, Charles began extensive field work with A.D. Middleton on field vole population cycles in Britain, with 9 census stations distributed from Oxford West and North to North Wales the Scottish Borders, West Scotland and Aberdeenshire. Of this work Charles wrote "Studying an animal population in the field is less comfortable and (less?) circumscribed than working on animals in the laboratory, though both can be very difficult....very hard physical work and long journeys by car....once a month 320 miles one day, did eight hours trace 'census' the second day, and got back home the third day": you have to remember that this was the early, mid and late 30s, and be aware of the primitive state of roads and cars compared with what we have and expect now.

Five people of great importance to the further development of the work of the Bureau joined it or became involved with its work in the mid or late 30s. In 1935 Marie Gibbs, at the age of about 27, came as a secretary (*Slide of Marie at her retirement 1967, together with Marjorie Nicholls, one time Bureau librarian*). Marie was the linchpin of the BAP, her contribution going far beyond straightforward secretarial responsibilities, not the least of which was her management of the accounts, and coping with the anxieties and angers of Charles.

Dr. A.Q. Wells, of the Dunn School of Pathology (*Slide of A.Q. Wells*) began work on the pathological aspects of voles. Once more Howard Florey played an essential part. Florey had moved on from Oxford in 1925, going to London, Cambridge, the Chair of Pathology at Sheffield, and returning to Oxford in 1935 as Professor of Experimental Pathology. Charles had written (unpublished): "Florey also gave us magnificent help in arranging that Dr. A.Q. Wells could come to his department, where we had built a small isolation laboratory...", and Dr. Wells went on to identify and isolate a tubercle bacillus from field voles. This was used, like the weak human strain BCG, in immunizing trials on people.

Howard Florey was also instrumental in bringing about the collaboration between the BAP and a person who went on to great distinction, and who also played a crucial role in my own career, whose son Sir Peter Leslie, I am most pleased to say, is here now: that was P.H. Leslie (*Slide of George Leslie, c. 1950*). Charles again, in an unpublished address, expressed his indebtedness to Howard Florey, who "....did us a very good turn, by putting me in touch with Leslie. P.H. (better known as 'George') Leslie was a trained pathologist who had been studying the whooping cough bacillus in the Sir William Dunn School of Pathology. Florey suggested that he might be interested in the epidemiological aspects of our work "But George in

addition went on to create mathematical models of population changes”..... which, wrote Charles, have done as much as anything else to enhance the intellectual standards of the BAP”. I think that’s something of an understatement.

In reply to an out-of-the-blue telephone call from me asking for a photograph, I had not only a photo of David Finney (of whom, more later, but he is now Emeritus Professor of ?? Statistical Mathematics, Edinburgh, and F.R.S.) but a very nice letter. He wrote “When I first came to Oxford in 1945, two of the first people I met were David Lack and George Leslie, both of whom became my firm friends. George soon introduced me to the important and congenial research environments of the BAP and the Lamb and Flag.... George was a great character, and he and Evelyn worked tremendously hospitable friends for a somewhat lonely bachelor (as David was then). He had all the makings of a truly great scientist; although of course he had no opportunity to go absolutely to the top in public esteem (this no doubt relates to George’s delicate health arising from an infection, tuberculosis, in his years as a clinical medical student), his work demanded and has received lasting recognition. I still remember discussing with him the matrices that are now known by his name.

Incidentally, you may be amused that only today while scanning medical literature I encountered a paper describing the use of mark-release-recapture techniques in the study of sexually transmitted diseases” (George had made very important theoretical and mechanical modelling studies of these techniques). And I can confirm the continued importance of his work as a result of chats with some of the more biomathematical members of my Department, some very senior, others undoubtedly on the way up. When I mentioned George, and explain that I mean P.H. Leslie, I invariably get a smile of recognition; “Oh you mean Leslie of Leslie’s matrices”. I first met George when I became a research student at the BAP in October 1949. He had, without any advance to formal training in mathematics, become a distinguished biomathematician, and was a Senior Research Officer at the BAP. This was a tenured post: the University had a number of them, but alas they have disappeared, to the detriment of all those departments which had had them.

It is delicate territory for me to attempt to conjure up the picture of a person in the presence of his son. I will dare, briefly. Imagine a tall man, an imposing figure, unobtrusively perfectly dressed in a comfortable fashion, with a most friendly look and a warm, quite deep, well modulated voice, and an urbane manner. He was immensely helpful and encouraging to me, and that will have been true for all the research students who worked at the BAP. He had a profound, lasting, influence on me, and I treasure the recollection of his warm, friendly manner. I spent many an evening, from about 5 to 6.30 at your home, Sir Peter, 9 Chadlington Road if I remember correctly, sitting with George in a front, left-as-you-approached-the-house, room, alongside him at his desk, with initially an entirely manual calculator, and later, miracle of miracles, and electrically operated one with, astonishing to us then, automatic systems. How George would have revelled in the computers to which we now have access. Yet the fundamentals of his work were thought, logic, pencil and paper. Those evenings during which he gently took me through his solutions to my difficult data, were invariably concluded with a glass of sherry.

He would not infrequently spend part of a summer afternoon watching cricket in the Parks, and wondered sometimes whether I had been or would come. Alas, to my

present regret, I never accompanied him: pressing work and family commitments seemed not to make it possible. I am quite sure that, while watching the cricket, George would be solving tricky biomathematical problems. He thought profoundly. There are three further things I want to say about him. His encouragement to non-mathematicians came of course because he solved problems for us, and explained the solutions to us, setting out arguments and calculations in immaculate longhand on squared paper (I have preserved a file to this day, labelled “George Leslie calculation”). But as important as the solutions, was his response to an initial enquiry. Faced with more or less extensive, messy, data, he would peruse them a little, and say “This looks extraordinary interesting. Just let me have it for a few days”. He never responded with some facile solution. And a few days later we might meet again, and again he would say “This really is very interesting” and he might give a little chuckle, as one would after tasting something delicious. Can you see how marvellously sympathetic and encouraging that response would be to a non-mathematician?

In spite of his imposing figure he had delicate health from that infection as a clinical student (which had obliged him to give up medicine – a benefit to biology, surely a great loss to medicine!). I was, of course, aware of his need to be careful. I was walking down the corridor in the BAP one day, past George who was leaning against a window sill at a window with a view onto a winter’s garden scene. As I passed, George gave a considerable groan. I was alarmed. I went with great haste to my supervisor, Dennis Chitty (of whom more in a moment). I told Dennis what I had witnessed. Dennis laughed. “Don’t worry, he said, George is thus struggling with an analytical problem”.

Finally it was my challenge to have as one of my D.Phil. examiners Peter Medawar (for reasons which need not bother us now) (the other was Niko Tinbergen). After Medawar’s attacking opening remarks, my determined response, and Niko’s offer of a cigarette, Peter Medawar said “So you have had help from George Leslie” “yes” – and that settled any questions about the biomathematical part of my thesis: if George had helped me, there was nothing that could be called into question, at least in that domain.

In the late 30s H.N. (Mick) Southern (*Slide of Mick*) joined the Bureau. He set out immediately to investigate rabbit behaviour and ecology, and that work has had as its motive the regulation of rabbit populations, which became a part of the Bureau’s war-time work on pest control. Mick was a dedicated and skilled field worker, and an extremely good naturalist, and these characteristics meant that he was very much in sympathy with Charles’s approach to ecological problems.

The personnel of the BAP was completed in the late 30s by Richard Ranson, who, by his skill at inducing field voles to breed in the laboratory, had made important contributions to some crucial studies by John Baker, and alas died before his time in 1945, and by the arrival from Canada of Dennis Chitty and his wife Helen (*Slide of Dennis, sewer inspection hole*). Dennis is seen here entering or leaving a sewer, I think outside the Kings Arms at the corner of the Broad, and that introduces us to the extensive work done by the whole Bureau during WW 2, to which I have already referred in connection with Mick Southern, aimed at investigating the ecology of rodent pests in order to find more effective methods of control.

But before Dennis became embroiled in this war work, which began within a week of the start of that war (see CSE, unpublished, 14/2/62), he had carried out two years of very demanding field work on field vole population fluctuations in the grassland recently planted with seedling conifers on Forestry Commission land round Lake Vyrnwy, Montgomeryshire: Lake Vyrnwy is a reservoir supplying Liverpool. The analysis of this field work had to be postponed until the end of the war. It led to Dennis formulating what became a quite general theory about the regulation of animal population size, the testing of which has kept ecologists busy ever since, without the problem of vole and lemming cycles being solved. His theory also kept me pretty busy between 1949 and 1953, during which I was examining, under laboratory, or semi-laboratory, conditions some of the implications of Dennis's theory (Dennis had considerable difficulty initially in publishing his results and theory, because he had broken rank with the general run of ?British ecologists and put forward a **theory** which could be **tested!** Peter Medawar, very much in tune with the Popperian analysis of science, played a crucial role in getting the work published in the *Philosophical Transactions of the Royal Society*).

Dennis was my D.Phil supervisor, and I am certainly profoundly indebted to him. I will talk again about Dennis and his work in a moment, but let me say a few words about the rodent pest control work. Charles very much saw this, quite correctly so, as a crucial part of the war effort: rodents, especially rats and mice and rabbits, could contribute substantially to the war time food shortages. The country was totally ill-prepared for the sort of study and action which was needed. Charles has written (14/2/62) "... in 1939 the Government had only one man, in the MAF, engaged in organising rodent control, and he was on sick leave." At the end of the war there was a well-trained organisation covering both town and country, and a research unit at the MAFF...; which took over our developed functions for permanent peace-time work". Charles was amused by the places in which they were obliged to work – quite apart from the sewers of Oxford and London, they worked in rubbish dumps, the Bodleian, a hen house, a grocer's shop in the Covered Market in Oxford, food depots, corn ricks and downland farms. He wrote "Police once nearly arrested Middleton for spooning cyanide powder into rabbit holes on a railway embankment, under the impression that he was trying to blow up a bridge".

The work extended overseas to Palestine (as it was) and the Sudan (***Slide of John Perry and Sharon Watson at the southern-most point of a journey to the Sudan***). This war-time work, published in ?3 massive volumes by the OUP, has implications for pest control well beyond the shore line of Britain, one representation of which is seen here (***Slide of Sharon Watson with an oversized New Zealand rabbit***).

4. Established and Flourishing Bureau: After 1945

After the end of WW 2 the Bureau comprised at least the following people: Charles Elton, the Director, George Leslie, Mick Southern and Dennis Chitty, as Research Officers, Marie Gibbs as the Secretary, and Marjorie Nicholls as Librarian. Others who had participated in the war effort had, in at least one case, died (Richard Ranson), or gone on to other jobs (John Perry). But one person returned. He had been an assistant in the Mausgesellschaft days, and had gone on to London University.

This was Denys Kempson, D.K. to everyone (*Slide of DK, perhaps at his retirement party*). He was a supremely gifted technician, and in a way analogous to George Leslie's role, helped decisively a very large number of research workers who came to the Bureau. Marie Gibbs, the Secretary, had an equivalent significance in a different part of the life and work of the Bureau. DK was also a marvellous photographer of National exhibition calibre.

He and Dennis Chitty invented the wrongly named Longworth trap (*Specimen of a trap*): wrongly named because, quite apart from the invention, including the trials, of the trap, Dennis and Denys had made the first 200 in the tiny workshop which, after 1945 the BAP had. Just as no one thought of patenting the penicillin process, being too much concerned with the war, so in the post-war period there was still no thought of patenting the design of these traps, whose manufacture was taken over by the Longworth Instrument Company of Abingdon. We are now alerted, or even obliged, to consider patents for the sake of University funding, and that's quite proper. Had there been an awareness of this matter in 1945 there might well have been generated large enough sums to endow studentships in population ecology (cf the Cephalosporin Trust).

The Bureau, in and after 1945, needed more space. It was obtained in an interesting way, involving 2 people, with whom I later had a very special working (literally) relationship, namely Douglas Veale, whom we have already seen, and Sir Hugh Cairns (*Slide of Hugh Cairns, c. 1944*), fellow Australian Rhodes Scholar, and by 1945 the first Nuffield Professor of Surgery. He was a world famous neurosurgeon, and had been very much involved with the establishment of the Clinical Medical School in Oxford, no doubt helped by his close friend Douglas Veale (The Cairns house in Charlbury Road became a second home for me).

Hugh Cairns had established during the war a most important Head Injury hospital based on St. Hugh's College, in the garden of which a one storey annex was built (*Slide of St. Hugh's garden front with the connecting annex*). After the end of the war this annex was no longer needed as a hospital, and negotiation between Charles, Douglas Veale and no doubt St. Hugh's College resulted in the "St. Hugh's huts" becoming the home from the beginning of 1947 until 1952 of the Bureau, the Edward Grey Institute for Field Ornithology (David Lack, already seen, the Director), and for the lecturer in the Design and Analysis of Experiment, David Finney, to whom I have already referred when recalling George Leslie (*Slide of David Finney, Prague 1992*).

The BAP, and no doubt the EGI and David Finney, moved into their new quarters early in 1947, and in an opening address on 18 April 1947, Charles gave handsome thanks to the efforts of the then new (1946?) Linacre Professor of Zoology, Sir Alister Hardy FRS, (*Slide of Alister Hardy, 1967, Marie Gibbs' retirement*): "To our Professor we owe to a great extent the circumstances that we are here at this moment, either as an institute at all, or in this building, so grave have been the obstacles in changing over from wartime to peacetime arrangements and so formidable the difficulties of housing".

There is a slight contrast of this in Charles' approach to me in 1952, when the Bureau had once more moved, this time to what had been the Botany Building, now

the Bursary of Magdalen College – that fine building in front of the Botanic Gardens: “You know our Professor, he said to me, well he wants to move people from the main department here. I want you to fill up your room (for we had the luxury of our own rooms as D.Phil students) with as much equipment and other things as possible”. So I did, and that included a subsidiary field vole colony some members of which, unintended by me, spent some of their free time in the room. This had the consequence of illustrating the discriminating gnawing activity of rodents; escaped animals gnawed the red binding of the substantial book on “*Stress*” by Hans Selye (I was working, amongst other things, on aggression stress in field voles), which had been kindly loaned to me by Dr. A.H.T. Robb-Smith, Reader in Morbid Pathology. The liberated voles by-passed the immediately adjacent green-bound book by Julian Huxley, “*Evolution: the New Synthesis*”.

It had been in 1943 that the fennels had given the University Wytham Wood (***Slide of the Singing Way***), and that soon became as important to ecologist in Oxford as, by rough analogy, the Bodleian is for the Humanities (***Slide of Duke Humphrey library***). In some curious way, unknown to me, Douglas Veale and Hugh Cairns were given “wooding right” in Wytham for several years, certainly from 1948 to 1950. They were in need of healthy, out-door young people to help them, so (through my, by then, social connection with the Cairns family) I spent a number of Saturdays and Sundays in Wytham Wood helping them to gather, cut up, and load onto a hired Pickford lorry logs for the Veale and Cairns family winter fires. I am unique amongst the present members of the University, and amongst my contemporaries of those days, in having been on the other end of a cross-saw with, on the one hand the then Registrar, and on the other the then Professor of Surgery (perhaps the saw was an appropriate symbolic instrument in both cases, cutting through bureaucracy, Veale and tissues, Cairns). There was a certain ambiguity to my position in these wooding trips to Wytham, because certainly later Charles wanted all fallen timber to stay and rot, for ecological reasons.

The acquisition of Wytham Wood had marvellous benefits for ecological and ornithological research in Oxford. It is surely unique in the world for the thoroughness with which its plants and animals have been studied. Mick Southern, and research students such as Rick Miller, from USA (***Slide of Mick, with Rick and also Winnie Phillips***), and Peter Crowcroft (***Slide of Peter heading into Great Wood***) carried out their own important ecological studies on wood mouse populations and on shrews, and at the same time helped Mick with his very important, long-term, investigation of predator-prey relations, as illustrated by owl predation on wood mice, bank voles and field voles.

And another of my direct contemporaries Gill Godfrey (***Slide of Gill with Geiger counter sweep, on Rough Common***), with great ingenuity, invented a Geiger counter sweep by which she could locate and follow isotope-labelled field vole in the field. Gill had friends in the Clarendon laboratory who also had links with Harwell, then very much a high security establishment: this is 1949, the years of the Bomb. Her ingenuity, linked with her impulsiveness, got her without difficulties straight into Harwell without being bothered by the security net, where she picked up some small bits of radioactive cobalt which soon after were on rings on the legs of field voles in Wytham Wood. She had not consulted Charles. When he heard what she had done, he was, understandably, furious. But the work was completed.

Charles, by now, was prepared to let others, like Mick Southern, Dennis Chitty, and their co-workers carry on the investigation of small mammal populations, and increasingly turned his attention to large-scale issues of whole ecological communities or systems. Thus arose the massive Wytham Survey, recording on cards every ecological incident recognised in Wytham. Kitty Paviour-Smith from New Zealand (later she married Mick Southern), after finishing her D.Phil. (***Slide of Kitty up a birch tree***), worked in a very committed way with Charles on this Wytham Survey, the usefulness of which was a cause for discussion and some unfortunate disagreement between Charles and Dennis, who had a very different, “hypothetico-deductive”, approach to ecological problem.

I was immensely lucky to become, in October 1949, one of Dennis’s research students (Gill Godfrey was another). He was consistently encouraging, enthusiastic, critical, committed to an experimental approach to ecology, in our case the understanding of the mechanism of vole and lemming population cycles. He gave me complete freedom of action, though we discussed frequently the work I was about to undertake. He never imposed himself on me but was always available for discussion. He was an exemplary supervisor, who set me a standard for supervision which I hope I have succeeded to some extent in following.

His intense, even passionate, analysis of ecological problems was (and is) always link to, or became, a synthesis, within which were testable hypotheses which he was prepared to reject if that is how the evidence from experiments fell out. In his experimental approach he believe very strongly in the pilot experiment, to see what the technical hitches might be and also to find out whether an experiment on a large scale would be worthwhile. His Popperian approach to science did set him apart from other ecologists, certainly in Britain and that included his BAP colleagues, with the undoubted exception of George Leslie. But he had disciples, of which I was and am one, and there are others in North America, influenced by him on visits to the Bureau or later when Dennis so successfully was Professor in the Zoology Department, University of British Columbia: there he was recognised as an outstanding teacher, and some of us had been able to recognise his ability when we had heard him give papers at scientific meetings during the Bureau days. In those days he began exploring problems of the history and philosophy of science, which he carried out much further in courses he ran in British Columbia.

This attitude of going beyond his immediate scientific interests I found very stimulating, and it gave rise to quite a lot of discussion between us then, and it has, recently, continued in correspondence. Two further qualities come to my mind. He actively sought out people both in the main Zoology Department, and elsewhere in the University who might have insights into scientific (or philosophical) problems which could help in the advancement of his scientific (or philosophical) questions. He did not isolate himself from the rest of knowledge! He also had and has a strong interest in the arts, and translated this into action by attending art classes in Oxford, and creating at that time some very powerful portraits, having at least one exhibition (jointly with Audrey Blackman) at what is now Queen Elizabeth House.

My gratitude for all the stimulation he provided, which includes his friendship, now maintained largely by letters to and from British Columbia, is unbounded. Scientifically, my position as a research student was ideal. Dennis had formulated a

theory about the regulation of vole, and other, population cycles, and there were certain simple, but fundamental, inferences from the theory which needed first to be tested under laboratory, or laboratory-like, conditions. One proposition, which now seems obvious, was that voles have aggressive interactions which seriously deranged physiological processes: Stress, as we would now immediately regard it. In October 1949 we hadn't a notion of how to investigate this, but in Hilary term 1950 I was fundamentally helped, indirectly, by Howard Florey. He was then trying to decide whether or not to go back to Australia to be part of the newly formed John Curtin School of Medical Research (??), being set up in Canberra.

In beginning to plan this move, a graduate in veterinary medicine in Canberra who was helping Howard Florey with plans for proposed animal accommodation there, came to Britain to look at facilities here. That person was, and is, Wesley Whitten (who has since made fundamental contributions to the understanding of pheromonal influences on mammalian reproduction, and of the best culture systems for mammalian blastocysts). When in Oxford he came to look at Dennis's (and my) vole breeding colony. I told him about our proposed work, but that we did not know how to proceed. He said: "Hans Selye (Professor of Experimental Medicine, Montréal) is giving a lecture in Oxford in a few days time. Go and listen to him". I did. Selye was a brilliant lecturer. From that I learned about his theory of the "General Adaptation Syndrome and the Diseases of Stress" (see above, the gnawed book on "*Stress*"), and that enabled me to carry out experiments which demonstrated the now not so surprising fact that the aggressive encounters which do occur between field voles (and between other animals) do bring about important arrangements of physiological systems. This is the penultimate impact, as far as I am concerned, of Howard Florey on the BAP.

Exactly contemporaneous with me starting at the BAP, was a junior technician, pretty-well straight from school, Ken Marsland, seen here (*Slide of Ken on Farmoor*) a few years later, and a few more years later where we see three generations of head technicians of the Zoology Department (*Slide of Ken, Leonard Small, Percy Trotman*), Ken now being the Laboratory Superintendent in the Zoology Department. He and I often remark on the excellent training we received from Denys Kempson. It is some interest, I think, that Ken's father, Tommy, was a pillar of the technical staff of the Physiology Department, where, many decades ago, at the start of his career, he worked with Sir Charles Sherrington, Nobel Prize winner and creator of fundamental ideas in neurophysiology.

In those days in the St. Hugh's huts, admirably suited to, and adaptable for, the research of both the Bureau and the EG I, there were very frequent helpful interactions between the research workers there and others from the adjacent EGI. This was partly through occasional seminars, but also essentially because of the atmosphere Charles created at afternoon tea.

It had been my intention to go back to Australia after doing a year's research with Dennis (following on the 2 years I spent re-reading Zoology), to work in the newly formed Wild Life Survey. The one request made by me to Francis Radcliffe, the founding director of the Survey, was this: "What ever else you do in that year, and I'm not much concerned about that, don't miss going to tea", because it was at tea Charles would give his thoughts, George would sometimes have stayed on until the

afternoon, and others would, in an amiable way, discuss a whole range of ecological problems. Tea, with cakes, was an essential part of BAP life. Not infrequently during the day David Finney (see above) would come in to look at the latest issue of journals laid out in the excellent library (where we had tea), and to discuss biomathematical problems of an ecological sort, with George, Dennis and others. It was a marvellous atmosphere, friendly, and stimulating, created by Charles, and that small, intimate, working group was exactly how he thought science should be arranged, without ignoring links with others (as David Lack's and David Finney's ready access to the BAP illustrated but the BAP was some distance away from the main Department, and for those who had not done the undergraduate course in Oxford, this was an important disadvantage).

In 1952, I think because the then new Forestry and Botany buildings had been completed in South Parks Road, the Bureau and the EGI moved into the Old Botany Building, the present Bursary Building of Magdalen College in front of the Botanic Gardens, and by then I was very much involved with my Departmental Demonstratorship in Animal Physiology in the Department of Agricultural Science, so I will now turn to the concluding days of the Bureau, in which, to a limited extent I was involved.

Alister Hardy resigned the chair in 1961 (?), 2 years early, in order to let his successor start the work which Alister had begun, of planning a new Zoology building. His successor was John Pringle (*Slide of Alister, John, and Dick Southwood, 1979 or after, three generations of Linacre Professors, with Darwin's watchful eye*). In planning the new building John Pringle considered it was essential to bring into it the two outlying stations – the EGI and the Bureau. Charles thought this would destroy the unique character of the Bureau. He and John Pringle did not get on together – I will hazard that they were too alike. Charles fought a rear-guard action to save the independent nature of the Bureau, to save its very existence, after his retirement in 1967. Before he retired, and before the decision taken by Council in November 1966 to “..... terminate the Bureau as an institute and cease its name,...” Charles organised a symposium at the BAP to display its work, I think in the hope of persuading the University not to take this decision. All former members of the BAP were invited to attend. I recall the significant presence of, by then **Lord** Florey, President of the Royal Society, Provost of Queens, Nobel Prizewinner, etc etc alongside John Pringle, in the front row. But a lifetime's friendship, however it was manifest at that time, did not prevent the merging of the outlying institutes with the main Department, and I think it cannot be doubted that this was the right decision.

Charles's successor as Reader in Ecology was John Phillipson (*Slide of John*), Fellow of Linacre, and his successor, yet to be appointed, will, I am glad to say, also be a Fellow of Linacre.

It was, obviously, a very profound loss to Charles that the Bureau ceased with his retirement – a second death of his brother Geoffrey. Poignantly he said on 14/2/62, the 30th anniversary of the formation of the Bureau “After another 30 years, I may not be taking much interest in things, as I should, if I lived, then be 92! (He died on 1/5/91, aged 91). But even then I would like to know that the BAP was still going strong as an institute, and that its research had advanced so far as I could hardly

understand anything that they were doing” (*Slide of the St. Hugh’s huts being knocked down: though not the final site of the Bureau, their destruction symbolic*).

Charles had decades of happy married life with E.J. Scovell, Joy, and joy she was to him, a most distinguished poet, and I will conclude with a poem by her inspired by, and about, Charles, the naturalist:

A Naturalist (by E.J. Scovell)

The stones and dust seem flowers in the lane’s warm shade,
He in the dust-white coat went down through the breached
Low wall by the road onto a flowering glade
Where the small briars his hand, the cow-parsnip reached
His shoulder, with flower-heads, the level umbrels spread
On their thick fluted pillars, head beyond head.

Spacing the parsnip flowers and passenger rose,
The grass like air stood everywhere in channels.
There he thigh-deep, a patient man in flannels,
With his glass-green net still, and in repose
His heavy thoughtful head, seemed rooted in the brome,
Stock of that natural garden, never so at home.