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A century of research and teaching in animal behaviour and welfare in the Graham Kerr Building

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John Graham Kerr knew well that how animals behave has important consequences for many aspects their biology. In his book *Evolution* (Kerr, 1926) he describes how both the foraging strategies of visually-hunting predators and the protective habitat selection and immobility of their prey are critical for the effectiveness of animal camouflage. He also gives an account of the importance of nest building in the evolution of sociality in insects. An interest in animal behaviour was therefore represented within the Graham Kerr Building (GKB) from the start. The ensuing century has seen many important developments in behavioural biology, both reflected in and promoted by the research carried out in the building. An early example of such a development was the emergence in the 1960s of ethology as a recognised discipline for the biological study of behaviour. Ethology is characterised by focusing on spontaneous natural actions and by addressing all four of the questions that Niko Tinbergen famously identified as essential for understanding behaviour: What is it for? How does it develop in an individual animal? How did it evolve over the history of the species? How does it work? (Bateson & Laland, 2013).

A key role in the history of behavioural studies in the GKB was played by Samuel (Tony) Barnett (1915-2003), a graduate in Zoology from Oxford University, promoted to Chair of Zoology at Glasgow before moving to the Australian National University in 1973. His main research interest was the behaviour of rats, summarised in his most famous book (Barnett, 1963), based on his work on wild and laboratory rats in nature and in captivity. Barnett's approach was unusual for a zoologist of the time in combining elements from ethology and comparative psychology, reflected in his clear recognition that the simple distinction between instinctive and learned behaviour drawn by many ethologists was misleading. Barnett was also unusual in discussing emotions in rats (albeit firmly placed in inverted commas) and their underlying physiological bases. One of his graduate students, David Fraser, moved from Glasgow to Edinburgh while still writing up his PhD thesis on social and exploratory behaviour of laboratory rats and mice. In Edinburgh he started a highly distinguished career in animal welfare (taking him to the University of British Columbia, Vancouver) with some of the earliest research on the welfare of intensively reared pigs. Barnett's expertise in rat behaviour had been put to practical use during World War 2, when he advised the British Government on the possibility of an epidemic of bubonic plague. In a sense, this looked forward to the strong epidemiological theme developed later by researchers in the GKB.

Another important and influential zoologist, Mike Hansell, was recruited in 1968 by David Newth, then Regius Professor, to strengthen research and teaching in animal behaviour in Glasgow. He came from the University of Khartoum, having gained his doctorate at Oxford, on case building in caddis flies. In Glasgow, Hansell continued his broadly-based studies of animal architecture, with a special interest in nest building by insects and birds. In this context, Hansell established the National Nest Reference Collection of the Hunterian Museum. His research addresses all of Tinbergen's four questions, from the development of case building in caddis larvae, to the evolution of nest building in social insects and the functions served by bird nests. An important aspect of Hansell's work on the causes of behaviour is his demonstration that impressively complex structures can be generated by relatively simple actions. His internationally recognised academic research has always been accompanied by a commitment to public engagement, through popular books, for example *Built by Animals* (Hansell, 2007) and exhibitions such as *The Animal Construction Company*, devised in 1999 with collaborators in the Hunterian Museum as part of Glasgow's year as City of Architecture and Design. Hansell, a highly effective and popular teacher, was responsible for consolidating animal behaviour as a recognisable discipline within the zoology curriculum taught in the GKB.

From the late 1970s onwards, further important developments took place in how zoologists studied behaviour, including an increasingly interdisciplinary approach, with behaviour being seen as not so much an isolated trait, but as contributing to, among other things, ecological adaptations, physiological processes and life history patterns. This broader approach was facilitated by revolutionary advances in molecular biology and computing science. An additional trend was towards increasingly putting knowledge about behaviour to practical uses. Again, such developments were both reflected in and promoted by research carried out in the GKB.

Felicity Huntingford moved from Oxford to Glasgow in 1974 to join the zoologists working in the GKB, also appointed by David Newth. Her research focuses on the behaviour of fishes, particularly on the marked individual differences they show when challenged by a rival or a predator. She developed and broadened this theme through collaborations with colleagues from other disciplines, including physiologists, molecular

biologists, life-history biologists, theoretical ecologists, fisheries scientists and veterinarians. Aggression and anti-predator behaviour are both areas that raise ethical questions when studied in captive animals and Huntingford was involved in drafting the first statement on the ethics of animal behaviour research (Huntingford, 1984), developed to promote good ethical practice in articles submitted to the journal *Animal Behaviour*. These guidelines were adopted by the Fisheries Society of the British Isles and, consequently, Huntingford was asked to prepare a briefing paper on fish welfare for the Society, subsequently published as a review (Huntingford *et al*., 2007). Her interest in fish welfare reflects a general shift towards using knowledge about natural behaviour to promote sustainable and welfare-friendly aquaculture. This trend has now moved into the treatment of complex invertebrates such as decapod crustaceans, as studied by another GKB researcher, Douglas Neil (Albalat *et al*., 2022)

Many more researchers based in the GKB than we have space to mention have worked on topics that involve animal behaviour. Particularly eminent among these are the current Regius Professor of Zoology, Pat Monaghan (also appointed by David Newth), whose work on reproductive behaviour, life history patterns and conservation in birds is described in a separate article, and Neil Metcalfe, who investigates the behaviour of fishes, among other animals, in relation to their ecology, life history patterns and conservation, also covered separately.

The welfare strand in research and teaching in the GKB has been strengthened and expanded by later recruitments and recently (in 2022) by the establishment of the School of Biodiversity, One Health and Veterinary Medicine. This brings together staff and students from across the University and includes the research theme of Physiology, Ageing and Welfare, the aim of which is to improve the health and wellbeing of domestic and wild animals. Among these later recruits, Ruedi Nager came to the GKB in 1996, having gained his PhD in Switzerland (Basel) and working as a postdoctoral researcher in the Netherlands (Groningen) and France (Montpellier). Nager's research focuses on how organisms (mainly birds) cope with the environment in which they live. This has included experimental studies of the effects of stress on reproductive strategies in laboratory-reared zebra finches, which led him naturally to an interest in monitoring and protecting the welfare of his own study animals. In this Nager was greatly helped by Graham Law, responsible as Named Animal Care and Welfare Officer for the welfare of all captive animals kept in the GKB. Law used his considerable intellectual and technical skills and his vision for enriched living spaces to improve the welfare of the animals in his care. The combined expertise of Nager, Law and Michael Wilkinson (the named Veterinary Surgeon) led to their being commissioned to develop guidelines on the welfare of captive zebra finches for the Universities Federation for Animal Welfare first in 2010 and updated in 2024 (Nager *et al*., 2024).

This aspect of Nager's work has involved close collaboration with Dorothy McKeegan, who studied for a BSc in Zoology in the GKB in 1994, before moving to Edinburgh. Here she gained an MSc and PhD in behavioural, physiological and ethical aspects of animal welfare and subsequently worked at the Roslin Institute. McKeegan came back to Glasgow in 2005 to a lectureship at the Veterinary School, initially part-funded by the British Veterinary Association Animal Welfare Foundation to promote teaching of animal welfare science and ethical issues to veterinary students. Her research integrates behavioural, physiological and neurophysiological techniques to improve the welfare of captive animals; her findings have influenced U.K. legislation on beak trimming in laying hens and EU regulations on Low Atmospheric Pressure Stunning in poultry. McKeegan is also interested in developing novel methods for assessing welfare and affective state, one of which has brought her together with Nager and Dominic McCafferty, an ecologist who has been associated with the University of Glasgow since 1999, both in the GKB and at SCENE. McCafferty's research focuses on thermal adaptation, behavioural thermoregulation and microclimate selection in mammals and birds. Drawing on common interests and complementary expertise, Nager, McKeegan and McCafferty collaborate to explore (among other things), the use of a novel, non-invasive technique based on thermal imaging to monitor stress and welfare in captive hens, captive rats and wild blue tits (Fig. 1).

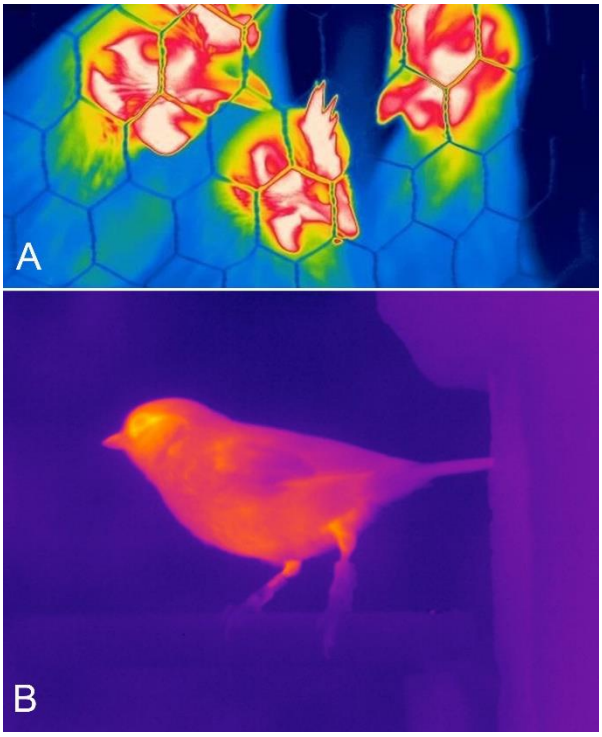

Fig. 1. Thermal images of (A) hens and (B) a blue tit. The images are false colour images translating surface temperature into colours ranging from white and yellow (highest temperatures) to blue (lowest temperature). Both images show clearly the warmest body regions of each bird and these are the regions that cool when an individual is exposed to a stressor. (Photos: (A) Kathrine Herborn and (B) Paul Jerem)

This strong research theme in animal welfare is well represented in the programme of teaching and training run from the GKB. Both McKeegan and Nager make important contributions to Home Office Personal Licence Training courses, based on their expertise in the ethics of using animals and in handling birds, respectively. Research projects about animal welfare have been offered to many students in the taught MRes programme, and since 2011 through the dedicated MSc in Animal Welfare Science, Ethics and Law, currently training 15-20 students per year, from diverse backgrounds and many different countries.

In summary, animal behaviour has been a key component of research and teaching since the opening of the GKB and through the ensuing century. This has seen successive researchers and teachers addressing fundamental and applied questions, working with a wide variety of animals, in the laboratory and at field locations across the U.K. and overseas. The contexts in which behaviour has been studied and the tools for doing this have changed greatly, but at core the fundamental questions are the same and we probably all spoke and still speak the same zoological language. Barnett would have been intrigued to see his hunch on the possible physiological bases underlying "emotions" in rats come in full circle with the help of modern imaging technology and Graham Kerr would certainly have had much to discuss with Hansell about his work on the evolution of nest building in social insects. In contributing to animal welfare, conservation and disease control, animal behaviour research based in or linked to the GKB continues to help Glasgow University to fulfil its responsibility to contribute to matters of public concern.

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