Gideon Louw

# Bioenergetics and Eusociality

Born in Johannesburg, South Africa in 1930 and matriculated at St. Johns College. Received B.Sc. degree from Stellenbosch University in 1952; M.Sc. conferred at Pretoria University in 1957 and Ph.D. at Cornell in 1960. Most of my academic career was spent as Professor and Head of the Zoology Department at the University of Cape Town. From 1989-91 I filled a contract appointment as Executive Director of the Foundation for Research Development, which is the major funding agency for university research in South Africa. Acted as Visiting Professor and Visiting Scholar at various universities, including Arizona, Cambridge and Zurich. Some 90 scientific articles have been published as well as two books: *Ecology of Desert Organisms* (with M. K. Seely, Longmans, London 1982), and *Physiological Animal Ecology* (Longmans, London 1993). — Address: Zoology Department, University of Cape Town, Rondebosch 7700, Cape Town, South Africa.

The invitation to spend an academic year at the Wissenschaftskolleg came at a very opportune time in my career, namely after a three-year contract period as a senior administrator and before returning to active academic life. I have therefore used part of this valuable period to prepare myself for a major new research project on social insects, beginning in 1994. Considerable time has been devoted to a systematic study of both the recent and classical literature in this field, with particular reference to the Formicidae. My studies were greatly facilitated by the recent encyclopaedic review by Hölldobler and Wilson (1990) and my personal collection of reprints. The above studies proceeded on a broad front involving, at first, an overview of the major diagnostic criteria used in the taxonomy of the Formicidae. Specimens were collected in the Berlin area to test the use of important keys and to gain at least an appreciation of the immense complexity of the systematics of circa 9000 species of Formicidae.

The next challenge was to review the literature on the evolution of eusociality among the insects. Eusociality has evolved about twelve times among the Hymenoptera and once in the protoblattoid line that led to the evolution of the termites. In spite of many imaginative explanations for the development of this fascinating and highly successful life-style, including Hamilton's haplodiploidy theory and the hypothesis of parental manipulation, I could not find a truly satisfying explanation of how the evolution of eusociality occurred. In fact, it would seem that this problem has now become a central issue in evolutionary theory, as it does not easily fit into either classical or neo-Darwinian conceptual thinking. Modern molecular and mathematical approaches may be more successful in contributing to a more acceptable solution in the near future. However, for the present at least, it is comparatively easy to answer "why" eusociality evolved but the "how" question remains for the most part a challenging and important mystery.

The remainder of my period of study was centred on the biology of the Formicidae. These studies included the life cycles of colonies, communication, castes, social homeostasis, foraging and symbioses with other organisms. This review left me with two major impressions. First, there is an immense literature on these subjects, which is of a highly variable quality. Much of it requires confirmation by new, well-controlled experiments. Secondly, one of the sub-disciplines which has not received sufficient attention is the nutrition of colonies. This is particularly true for the comparative analyses of net energetic yields of different colonies and different castes within colonies. This problem lies at the heart of the advantages associated with the flexible eusocial life-style. I intend to research certain aspects of this sub-discipline in 1994.

To date all my writing has been directed at my professional colleagues, but for several years I have had the ambition to write for a much wider audience of lay persons. I have therefore devoted a considerable amount of my time at the Kolleg to writing a series of ten essays on the general theme of "Animals at Work". They are essentially about the universal dependence of animals on energy and the fascinating ways in which energy is used, saved and wasted by animals as disparate as mosquitoes and elephants. In each essay an attempt was made to reach a generalised theoretical conclusion of some heuristic value. The following is a brief synopsis of the different essays.

1. This introductory essay concentrated on the most unusual physical properties of the water molecule and how life has evolved around these unusual characteristics. The importance of water for transporting energy from cell to cell and among organisms has been emphasised by tracing the journey of a water molecule from a vineyard in France, through Napoleon, to the Antarctic and eventually via whales and a salmon in a Scottish river to a tea cup in Britain.
2. This essay describes how efficiently fish use energy for a variety of purposes. The way in which schooling reduces the cost of locomotion has

been explained and how fast swimmers, such as marlin, `waste' energy in their specialised eye muscles to keep their optic nerves warm, thereby enhancing their visual acuity for hunting their prey. Other examples include the way in which oxygen-starved fish of the cyprinid family ferment sugar into alcohol to produce energy in the absence of oxygen without, unfortunately, affecting their sobriety.

3. Any explanation of energy exchange among organisms requires an understanding of the fuels that animals consume to provide energy for countless biochemical reactions. This essay is entitled `Fuels for Beating Entropy' and provides a general description of the major nutrients, their function and the efficiency with which they are used by animals. The tremendous variation that animals exhibit in their modes of feeding has been emphasised and contrasted with the very similar metabolic fates of the nutrients in all animal cells. Perhaps a reflection of our common cellular ancestry in the primordial soup.
4. This essay is devoted to a discussion of the bioenergetics of flight with emphasis on the special problems of small birds, such as humming-birds and small flying insects like honeybees and bumblebees. Many other examples, e. g. moths flying in a snow storm at 0 ° C and dung beetles with thoracic temperatures of 40 ° C, have been used to explain the physical and physiological phenomena involved. The interesting question of why there are no flying birds smaller than two grams and no flying insects larger than thirty grams has been analysed at some length.
5. In this essay the crucial importance of cellulose digestion in providing energy in many ecosystems has been explained. This then immediately raises the question why so few animals have evolved the enzyme cellulose to digest the huge amounts of cellulose produced in nature. Instead, many use symbiotic micro-organisms within their specialised digestive tracts to break down the cellulose. The miraculous chemistry of symbiotic digestion transforms crude, dry plant material into such refined products as meat, milk and wood and these processes have been explained. The physiological discussions have been interspersed with a zoological travelogue through the African bushveld.
6. Much energy is expended in keeping animals warm. In fact, warm-blooded animals require some 13 —17 times more energy than similarly sized cold-blooded species in order to survive in the wild. This essay analyses how energy is husbanded and `wasted' by a variety of animals such as polar bears, Saharan ants, musk oxen, Antarctic penguins, giant monitor lizards and many others to maintain their preferred body temperatures, as well as the evolutionary and ecological implications of these phenomena.

7. Sexual reproduction requires a great deal of energy in terms of male combat for mates, courtship behaviour, the growth and maintenance of secondary sexual characteristics and often involves serious injury and exposure to predation. The physiological basis of various patterns of sexual reproduction has been described, including the surrender of the maternal endocrine system to foetal control in mammals during pregnancy. In conclusion, the profound question of how and why sexual reproduction evolved has been examined, but without arriving at any clear conclusion.
8. The ability to orientate and navigate can often be of critical survival value for both humans and animals in their quest for obtaining sufficient energy from the environment. The remarkable abilities of birds and insects to navigate have been examined in this essay by explaining the relative importance of the sun, stars, polarised light, geomagnetism and odours as possible navigational cues.
9. This essay is entitled `Desert Sands' and is essentially a scientific travelogue through the Namib Desert, during which the reader is introduced to some of the more important desert animals, like ostriches, oryx, darkling beetles, ground squirrels, sand-diving lizards and many others. Emphasis has been placed on how the animals are physiologically adapted for survival in the desert, which we anthropomorphically regard as `harsh'.
10. The final essay attempts in broad terms to describe how energy usage by humans has developed and expanded exponentially from the Stone Age to the late twentieth century, and is entitled `From Silicone Tools to Silicone Chips'. The key importance of fire, nomadism and eventually primitive agriculture has naturally been emphasised. Quantitative examples of energy usage during the era of cathedral building and space travel are reported. The social life of humans and eusocial animals is compared as a basis for speculating on how modern technology may soon drastically change the social life-styles of humans in the cause of stability.

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