

Book Reviews

Mammoths, Mastodonts & Elephants Biology, Behaviour, and the Fossil Record

Gary Haynes

Cambridge University Press 1991

413 pp

Price: £16.95 (paperback)

In a decade of fieldwork and research, much of it taking place in Zimbabwe's Hwange National Park, Gary Haynes came to realise that most of the alleged facts about proboscideans are fabrications whose foundations are exceptionally shaky. Using a combination of an incredibly diligent literature search, and his own meticulously recorded fieldwork, Haynes has attempted to 'reconstruct' the behaviour of extinct mammoths and mastodonts based on what can be observed of modern elephants and the concept that a living species is a good parallel to an extinct one. He has succeeded admirably, and has produced a work of scholarship to be savoured not only by palaeontologists, but by all who are interested in the anatomy, behaviour and ecology of Africa's megafauna.

The short introductory chapter on the classification of fossil and living proboscideans leads into a well-researched chapter on the physical appearance of mammoths, mastodonts and modern elephants. In this, and the next chapters on social structure, habitat use, and mass mortalities, Haynes starts to introduce his own observations from Hwange. For example, there are some very interesting and hitherto unpublished data from 8468 elephants culled in Hwange from 1983 to 1985, and some fascinating accounts of die-offs of elephants and the subsequent weathering and breakdown of their skeletons. Some of the mortality observations have been published before, but most of them in archaeological or palaeontological journals likely to be overlooked by African wildlife biologists.

In attempting to 'reconstruct' the behaviour and ecology of extinct proboscideans, Haynes has selected specific biological parameters to explore theoretically by relating them to living analogues. There is obviously a great deal of merit in this approach, and Haynes has generally argued his case convincingly. Although modern and extinct proboscideans are different genera, they are clearly related with common phylogenetic origins. The amazing degree of similarity between the Asiatic and African elephants (*Elephas* and *Loxodonta*) supports his argument by showing how these two genera have so much in common in terms of anatomy, physiology and behaviour.

At the end of the Pleistocene, most of the proboscidean taxa then living became extinct, a phenomenon which continues to intrigue biologists and palaeontologists, and which has given rise to much speculation. The question: 'Were they killed off, or did they die off?' is addressed by Haynes with particular authority, and the book is worth reading for that chapter alone.

In any well-researched publication of this nature, authors tend to pack in too much detail, and this is one criticism I

have of this book. There are too many long and unnecessary tables, which could have benefited from a good editor. The quality of the black and white photographs also leaves a lot to be desired — most could have been left out altogether. But these are minor issues. In writing *Mammoths, Mastodonts and Elephants*, Gary Haynes is to be congratulated in bringing some exciting new dimensions into the zoology of African mammals, extinct and living.

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A Fieldguide to the Amphibians and Reptiles of Madagascar (Second Edition)

Frank Glaw & Miguel Vences

M. Vences & F. Glaw Verlags GbR, Köln, December 1994

480 pages

Price: DM88,00

On a recent trip to Madagascar I saw a copy of the first edition of the book under this title, and was disappointed to discover that it was out of print at the time. A letter to the authors revealed that a second edition was on the way, and here it is (my copy is paperback, though it may also come in hardcover). This edition is not merely a revision of the first edition, but a greatly expanded volume which includes the mammals and freshwater fishes. The title as it stands is therefore rather inadequate, and I think does the authors a disservice. Nor does the book cover merely the identification of these four vertebrate taxa (amphibians, reptiles, mammals and fishes), but the Introduction includes two maps of Madagascar, showing the nature reserves and some important localities respectively, as well as fairly detailed accounts of the climate, flora, invertebrates, birds, conservation in Madagascar, and a historical overview of herpetological research in Madagascar. Indeed, the 35 pages of the Introduction, along with its numerous black-and-white photographs, is a succinct natural history of the island.

The 185-page section on the 179 species of amphibians starts with some clear diagrams showing how frogs and tadpoles are measured, the mouthparts of a typical tadpole, definitions of colour patterns of frogs, types of forelimbs and hindlimbs, positions of femoral glands, shapes of pupils, vocal sacs, and skeletal features. A series of halftone photographs illustrates the eggs, tadpoles and adults of a number of species. Identification keys are provided for clutches of eggs, tadpoles, and genera, subgenera and species groups of adults. Each species text is laid out in standard format, giving description, a distribution map, a little about biology and a brief section on similar species. Some black-and-white photographs illustrate many adult frogs, while several pages of line drawings show features of tadpoles. Two 'determination tables' to the genus *Mantidactylus* and a key to the species of *Mantella* add to the usefulness of this carefully thought-out section. In addition, 164 superb coloured photos illustrate most of the species of frogs as adults. Some of these are truly

beautiful animals, especially the gaudily coloured species of *Mantella* and *Heterixalus*.

The texts for the reptiles are somewhat similar, though less expansive, and not divided with subheadings. Coloured photos illustrate one species of crocodile, 60 chameleons, six iguanids, 54 geckos, 14 gerrhosaurids, 13 skinks, 36 snakes, 15 tortoises, three typhlopids, 61 mammals and 15 freshwater fishes. This is truly an amazing compendium of biological pictures for a region so relatively poorly known. Keys are provided to the tortoises of Madagascar, the sea turtles, the genera and species of all the lizard families (some of these keys are very extensive) and all the snakes. The text is interspersed with distribution maps for most species, as well as fine drawings of scale patterns.

Treatment of the mammals is less formal and detailed than for the lower vertebrates, but there are distribution maps of most species and a key to Malagasy bats. The freshwater fishes are also somewhat briefly dealt with, but a key to the Malagasy families of fishes is provided, with helpful diagrams. Further keys identify the species of cichlids, cyprinodontids, the genus *Rheocles* (Bedotiidae) and eleotrids. The book ends with seven appendixes: 1. Formal descriptions of four new frog subgenera; 2. Taxonomic changes for amphibians and reptiles; 3. Summaries in English, German and French; 4. Checklist of amphibian and reptile species and subspecies; 5. Sonagrams and oscillograms of frog vocalizations; 6. References; 7. Gazetteer and index of all genera and species covered in the book.

This book contains an astounding wealth of information and is indispensable to any visitor to Madagascar. The text is clear, though it contains a host of obvious 'Germanisms', in spite of the authors' brave attempts to have them weeded out by Carl Cornish of Leicester. These will not put off the interested reader, however, and indeed add to the charm of the language. The authors are to be congratulated on their dedication to a mammoth task, and on their achievement of a major biological milestone in the literature on Malagasy fauna.

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The Physiology of Reproduction

Second edition 1993

Editors in Chief: E. Knobil & J.D. Neill

Associate Editors: G.S. Greenwald, C.L. Markert and D.W. Pfaff

A two volume set, 3302 pages

Raven Press, New York

Price: US \$454

This impressive tome on reproduction is not for light reading — it runs to 3302 pages and contains 61 chapters authored by more than 100 experts. These two volumes provide an up-to-date and extremely comprehensive treatise on mammalian reproduction. It is a treasure trove of information and each chapter ends with a very extensive bibliography — sometimes exceeding 1000 references.

We obviously were not able to read the two volumes from cover to cover and concentrated on areas of particular interest to us.

The first volume begins with eight chapters grouped under the general heading of *The gametes, fertilization and early embryogenesis*; this is followed by nine chapters on *The female reproductive system* and seven on *The male reproductive system*.

The last ten chapters in the first volume are dedicated to the role of the hypothalamus and pituitary in reproduction. The chapters complement each other extremely well. We found this section of the book particularly fascinating because great advances have occurred in this field over the last decade. Despite these advances, the book also highlights the many areas in which there is still a dearth of knowledge. The initial chapters provide a comprehensive coverage of the anatomy of the pituitary and hypothalamus and also an extremely useful overview of the mechanisms and the neuromediators involved in the regulation and release of the gonadotrophins and prolactin. The later chapters are more for the specialist and concentrate on such areas as the chemistry of GnRH and its synthesis, the regulation of gonadotrophin gene expression, and the molecular mechanism of GnRH action in the pituitary. The section ends with a summary of current knowledge of the chemistry of inhibin and activin and of their actions on the gonadotrophins, especially FSH.

The second volume is less human orientated and is also perhaps easier reading for the non-specialist. It begins with five chapters on *Reproduction behaviour and its control* — chapters in this section of particular interest to us were on the physiology of male sexual behaviour, the cellular and molecular mechanisms of female reproductive behaviours, the role of hormones in communication of vertebrate aggression and reproduction, and finally, pheromones and mammalian reproduction. The remaining 21 chapters in the book are grouped under the main heading *Reproductive processes and their control* and cover (amongst other things) puberty, rhythms in reproduction, seasonal regulation of reproduction in mammals, neuroendocrine control of the ovarian cycles, the recognition of pregnancy, the placenta as an endocrine organ, parturition, lactation and reproductive aging.

Because of the multiple authorship of the book there are obviously omissions and some duplication of information. We were surprised that the marsupials had very scant coverage and that the most atypical of all mammals, the monotremes, were ignored completely. These, however, are minor criticisms of what will be an invaluable and very comprehensive reference book on mammalian reproduction. It is too detailed and costly for the private library of most zoologists, but those active in reproductive research should certainly seriously consider buying it or ordering it for the university library.

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The Economics of Non-Human Societies

Gordon Tullock

Pallas Press, March 1994 Tuscon, Arizona
87 pages

The transfer of ideas between disparate disciplines serves the vital role of providing fresh insight into both old and new problems. This, in essence, is what Gordon Tullock has attempted to achieve in this short book — an economist's interpretation of how non-human societies are organized.

The danger in this commendable endeavour to bridge the gap between biology and economics lies primarily in the broad generalizations that are drawn by the author from the wealth of published information concerning non-human societies. Thus to the student of animal social systems this book will do little more than provide brief overviews of more rigorous published scientific works (e.g. Hölldobler & Wilson 1990) However, biologists in general who have been forced to become progressively more specialized as their fields rapidly expand, may benefit from this short synthesis, which requires little prior knowledge of the concepts and terminology associated with the study of non-human societies.

Although Tullock's book is not specifically aimed at the biologist, it contains condensed information on a range of animal societies ranging from slime moulds and sponges to bees and mole-rats. In addition, it provides a well thought-out account to facilitate the non-biologists' understanding of evolutionary theory and reproduction in non-human societies, and also how natural selection may lead to the evolution of both cooperative and non-cooperative behaviours.

Tullock's main objective is to emphasize the remarkable degree of coordination and the efficiency of non-human societies. He provides reasons why this requires an explanation not based on anything we see in human societies. To provide the reader with an understanding of how a complex society functions, Tullock focuses his attention on the ants, providing the uninitiated with an informative account of how their lives are organized. A more general account is afforded to the bees and termites, followed by a brief account of the life history patterns of mole-rats, sponges and slime moulds. Throughout his discussion of these non-human societies Tullock develops a theory on how cooperation works within these societies and how the individuals make decisions within the social environments of the nest. The question posed to the reader is: how is cooperation achieved in nature? Tullock maintains this question is seldom if ever asked by biologists, and is one for which they have no answer. In providing an answer to this question the author purports to fill a niche that has been left open by biologists.

Tullock's answer is encapsulated in the term 'environmental coordination' which may be summarized as follows: each entity, whatever it is, carries out its own pattern of behaviour and that changes the environment, possibly only to a tiny extent, for other entities. Each of these entities then 'decides' what it should do in terms of the new environment. The decision that the entity makes is based on a preference function, which is that task or behaviour that each entity prefers to do.

The student of non-human societies will be familiar with

these ideas, but not the terminology, for they have long been exposed to the writings of the likes of Wilson (1971), Oster & Wilson (1978) and Hölldobler & Wilson (1990). The very problems that Tullock claims remain unattended have been dealt with in detail and the answers provided go a great deal further than Tullock's in improving our understanding of the economics of non-human societies (or in the biologists' words, the ergonomics of social homeostasis and flexibility in social organisms).

There are many parts of the book where the biologist must exercise considerable patience with the use of incorrect terminology (the naked mole-rat is simply referred to by its generic name 'the mole-rat' of which there are several different species!), but it is Tullock's claim to be among the first to address the aforementioned problem, and similarly to have arrived at a conclusion that fills a previously vacant niche in our knowledge, which shows that the author has not read sufficiently around his subject.

As early as 1937 the acclaimed natural scientist Eugène Marais published his observations and theories relating to the termite (*Die Siel van die Mier*). Ten years of close observation led him to the conclusion that the termite mound functions as a superorganism and that cooperation is achieved through the inherent actions of individual termites responding to changes in their immediate environment exacted by external factors in addition to the efforts of their fellow workers. Subsequent to Marais, numerous biologists and in more recent years mathematicians have addressed this problem in considerable detail and have in my opinion provided a more factual and reasoned account of how cooperation is organized within animal societies.

In the author's own words 'this book I hope will attract both biologists and students of human societies. I hope it will also be of help to them, but I would be very surprised if that help was really major'. I would have to agree.

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Bird Atlas of Botswana

Huw Penry

University of Natal Press, Pietermaritzburg
319 pages
Price: R89,95 (paperback)

This is the first semi-quantitative description of the distribution and abundance of birds in Botswana. It is the culmination

of a 10-year project (1980–1990) during which Botswana's birds were mapped on a 30° × 30° grid. This is a coarser resolution than has been used in other southern African atlases, each grid square being approximately 2500 km². However, when one considers logistical problems such as the small number of resident observers and the difficulties in gaining access to remote areas, it is without doubt a sterling effort.

The opening chapters of the book provide an introduction to the project, explaining in detail its aims, methodology and limitations. There are useful sections covering factors affecting bird distribution in Botswana and there are particularly welcome descriptions and colour photographs of the main vegetation types. The bulk of the book, however, is devoted to distribution maps and accompanying succinct texts describing the status and habitat preferences of each species. Inset within each species map is a map showing its Afrotropical distribution and a histogram of the number of records per month which provides a crude index of the seasonality of occurrence.

A section at the end provides a brief text for rare (< 10 records) and probable species. Gazetteers of place names, rivers and fossil valleys are also provided.

The maps are easily assimilated, the text is clear and easy to read and the consistent layout of four maps/species accounts per double page spread makes the book easy to use.

The author points out that 'standard works containing extrapolations of (bird) distribution for Botswana in a Southern African context have been misleading ...'. This is certainly true, but this new book will go a long way in ironing out such errors in future and, as such, it makes an important contribution on a geographical scale much larger than Botswana. Anyone with an interest in bird distribution patterns in either Botswana or southern Africa should seriously consider adding this book to their library: it is an important ornithological contribution from what was, until now, an ornithologically rather poorly known country.

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Colobine Monkeys: their Ecology, Behaviour and Evolution

A.Glyn Davies and John F. Oates

Cambridge University Press, Cambridge UK (1994)

Pages xiii + 415

Price: R250

In the preface to *Colobine Monkeys* Davies and Oates express the hope that this book will be a useful reference work and will fill a gap in the primatological literature. Of this they can be sure. Indeed, this long overdue and useful text will be of interest not only to primatologists but also evolutionary ecologists, physical anthropologists and tropical biologists. In a series of 12 review chapters, in many instances written or co-

authored by the editors, *Colobine Monkeys* provides a highly readable synthesis of the paleobiogeography, taxonomy and diversity, dietary morphology and gut physiology, behaviour, ecology, socioecology and population biology of this group.

What are the colobines (Oates: Chapter 1)? Together with the Cercopithecinae, the Colobinae make up the 'Old World monkeys' or Cercopithecidae. They comprise 31 extant species of African and Asian distribution. They can be separated from the cercopithecines on the basis of a variety of differences in cranial and post-cranial morphology (they derive their name from the very reduced or absent thumbs of the African species — Greek *kolobus*, mutilated). However, the most diagnostic trait of the colobines, and the one that has the most profound influence on their ecology, is their stomach morphology (Chivers: Chapter 7). Along with ruminant artiodactyls (although colobines themselves do not ruminate), sloths and kangaroos, colobines have much larger stomachs than expected on the basis of body size. Given the unique nature of the colobine digestive system, it is not surprising that a major part of this book is concerned with detailed reviews of dentition, gastrointestinal anatomy, digestive physiology, and food selection and plant chemistry.

Although the conventional view is that the enlarged and multi-chambered stomach allows colobines to digest plant fibres, the evidence presented in this book raises doubts about the essentially folivorous nature of these monkeys. There is no doubt that folivory is important to colobines, or that bacterial microflora in the forestomach do assist in the digestion of cellulose. Indeed, there is an increase in stomach size in relation to the amount of foliage in the diet — from the leaf-monkeys (*Presbytis*) of South-east Asia, through the langur monkeys (*Trachypithecus*) and the unusual-looking proboscis monkey (*Nasalis larvatus*) from the same region, to the colobus monkeys of east, central and western Africa. However, several extant populations of colobines have been found to have diets dominated by seeds, especially immature seeds (Chapters 4 & 6), and some of the anatomical peculiarities may be more closely tied to processing these seeds. For instance, Lucas and Teaford (Chapter 6) have shown that colobine dentition, particularly molar structure, is more useful for processing seeds than foliage. Waterman and Kool (Chapter 9) extend the argument discussed by Chivers (Chapter 7) that foregut fermentation was primarily an adaptation for detoxifying plant secondary compounds such as found in seeds. In explaining how an ancestral frugivorous mammal might start consuming large amounts of leaves, Chivers suggests that solving the problems of digesting seeds preadapted colobines for a greater degree of folivory than other primates. This process would, at least, have made young leaves accessible. Later increases in body size would have allowed for a larger gut and longer retention times, which in turn, led to an increased ability to digest mature leaves (Chivers: Chapter 7).

The chief benefit of a foregut fermenting system may be flexibility (Kay & Davies: Chapter 8); it allows a mix of fruits, seeds and foliage to be eaten, with the highly digestible components (fruits) passing rapidly through while the less digestible fibre is retained in the sacciform part. These ideas run somewhat contrary to previous arguments of the superior advantages of hindgut fermentation systems, and the notion that folivorous colobines are in an evolutionary dead-end and

can only become better at being folivores.

Paleontological evidence, although somewhat speculative, suggests that these dietary specializations were present in the earliest members of the subfamily (Delson: Chapter 2). Of local interest is late Pleistocene material from Taung which indicates the presence of colobines, of comparable size to living taxa, in association with *Cercopithecus cf. aethiops* and *Papio hamadryas cf. ursinus*. One of the more intriguing problems of colobine distribution is their complete absence from the southern African sub-region today.

There is no doubt that their unique digestive system has opened niches closed to other mammals, and colobines are often the most abundant arboreal mammals in the forest and woodland habitats of the Old World tropics. The diversity of colobines is well covered (Oates, Davies & Delson: Chapter 3) and supported with high quality maps and photographs. Two detailed chapters cover the natural history of African (Oates: Chapter 4) and Asian (Bennett & Davies: Chapter 5) colobines. Although the former chapter summarizes data under section titles for each species (social organization, diet, feeding sites, activity patterns, range size and defence, and reproduction), this format is not followed in the latter chapter. This can be frustrating if one wants to make quick comparisons between Asian colobine species, although tables collating some of the relevant data are provided for some species. I suppose with many more Asian species a change in format was necessary.

Population ecology and the factors limiting population growth are reviewed by Davies (Chapter 10). Once again the far-reaching consequences of diet and digestion strategy are emphasized. For instance, the relationship between mature-leaf digestibility and colobine biomass across the Old World tropics, and between legume abundance and biomass across South-east Asia, indicate that colobine populations are commonly limited by food availability. Problems associated with measuring food availability (some universal method is required) confound detailed comparisons and site-based field tests of these findings.

Leading on from these essentially descriptive chapters, Newton and Dunbar (Chapter 11) provide a socioecological framework, based on a comparative approach, for explanations of the evolution of colobine social systems. One of the more interesting and challenging chapters, it provides an insight into the future of colobine field research. The chapter examines reproduction strategies, social behaviour among and between the sexes, the benefit of and constraints on group living, and the determinants of group size and structure.

While the coverage of the book is extensive, some aspects of colobine behavioural ecology are poorly represented. The editors explain the absence of any data on foraging theory by claiming that ranging behaviour in relation to food availability and distribution is poorly known from the colobines. Nevertheless, some data could have been drawn from the literature to suggest trends for a few species. In addition, more detail on intra-group feeding competition would be useful.

Colobines are known to have very low levels of overt intra-group aggression. This may be because colobine foods occur in large, relatively dense patches, permitting the monkeys to feed together without competition. However, at least three chapters in this book demonstrate the highly selective nature

of colobine leaf-eating, and the distinctly patchy distribution of high quality foliage. Furthermore, seed predation is common among many colobines, and must constrain feeding behaviour as much as frugivory does in arboreal cercopithecines, which live in highly competitive social groups. Why do we not see similar levels of competition in colobines? But these are relatively minor concerns given the overwhelming wealth of information in the book. Well written and referenced, *Colobine Monkeys* is destined to become essential reading (at least for those who can afford it) for those who are serious about primatology or tropical ecology.

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Water Relations of Terrestrial Arthropods

N.F. Hadley

Academic Press, 1994

356 pages

Price: US \$79.95

This book is a sequel to Eric Edney's classic text, *Water Balance in Land Arthropods*, published by Springer in 1977. Neil Hadley has kept a similar logical sequence of topics, dealing first with water content and osmoregulation, then cuticular, respiratory, and excretory water losses, the various avenues of water uptake (drinking, feeding, metabolism and vapour absorption), and the water relations of eggs. He concludes with chapters on salt and water balance, and on aspects of thermoregulation most relevant to water relations. An effort has been made to include all life history stages, and there is a strong focus on the non-insect arthropods. The writing style is concise and readable.

Much of the progress since 1977 has depended on technical advances, and there is an appropriate emphasis on methodology throughout this book, with useful diagrams and explanations of the experimental set-ups developed to measure cuticular and respiratory water losses, often concurrently with gas exchange. Neil Hadley is active in research on these matters, and provides a lucid synthesis of the current state of the field. Especially interesting are the controversies about the hormonal control of cuticular permeability, and about the significance of discontinuous respiration for the water economy of arthropods. The account of evaporative cooling in desert cicadas is also fascinating.

Chapter 5, on excretion and osmoregulation, seems less up to date than other sections of the book. For example, this chapter lacks any reference to the recently discovered proton pump in Malpighian tubules, to the microperfusion technique which has been applied to insect tubules since 1984, and to the recently characterized insect diuretic peptides.

My favourite chapter is the penultimate one, on balancing salts and water. While previous chapters cover the individual avenues of water gain and loss, this one provides a whole animal approach, classifying terrestrial arthropods into five gen-

eral 'adaptive types' in terms of their water relations. The five categories chosen are: behavioural avoidance, such as burrowing or nocturnality, with many examples living in deserts; enhanced water conservation, with minimization of all avenues of water loss (control over excretory water loss being the most important for overall water conservation); dehydration tolerance (which in my opinion does not warrant treatment as a separate type); high fluid turnover, as in insects feeding on sap, nectar or blood, or generating excess metabolic water during flight; and water sorption dependence, occurring only in arthropods and apparently over a much wider range of taxa and habitats than previously thought (e.g. in the intertidal iso-

pod *Ligia oceanica*!). The mechanisms of active uptake of atmospheric water have received much attention since 1977. There are still very few arthropods, however, for which we have accurate measures of all avenues of water influx and efflux.

In conclusion, this is a worthy successor to Edney's book. Hadley's book should be a standard text for many years to come.

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