Only in Africa The Ecology of Human Evolution

That humans originated in Africa is well-known. However, this is widely regarded as a chance outcome, dependent simply on where our common ancestor shared the land with where the great apes lived. This volume builds on from the 'Out of Africa' theory, and takes the view that it is only in Africa that the evolutionary transitions from a forest-inhabiting frugivore to savanna-dwelling meat-eater could have occurred. This book argues that the ecological circumstances that shaped these transitions are exclusive to Africa. It describes distinctive features of the ecology of Africa, with emphasis on savanna grasslands, and relates them to the evolutionary transitions linking early ape-men to modern humans. It shows how physical features of the continent, especially those derived from plate tectonics, set the foundations. This volume adequately conveys that we are here because of the distinctive features of the ecology of Africa.

Norman Owen-Smith headed the Centre for African Ecology at the University of the Witwatersrand before his retirement as Emeritus Professor there. He is an A-rated scientist and Fellow of the Royal Society of South Africa. He received Gold Medals from the Zoological Society of Southern Africa and the South African Association for the Advancement of Science, Wildlife Excellence Award from the Southern African Wildlife Management Association, Honorary Life Membership in the Ecological Society of America, and was awarded a Harry Oppenheimer Fellowship in 2005. He has written or edited six books, including *Megaherbivores: The Influence of Very Large Body Size on Ecology* (Cambridge University Press, 1988) and *Adaptive Herbivore Ecology: From Resources to Populations in Variable Environments* (Cambridge University Press, 2002).

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This book is dedicated to my extended family: my much-loved wife Margie, daughters Trishya and Lynne, and all of my former students.

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Foreword

Picking through a pile of elephant dung with a twig, quizzically chewing a leaf from a newly identified plant, interrupting a conversation to clap binoculars to his eyes and scrutinise something moving in the distance … that is the characteristic behaviour of Norman Owen-Smith in his preferred habitat, African savanna. His keen curiosity about nature is combined with an incisively analytical mind and seemingly inexhaustible capacity for integrating his observations and ideas into the published literature. Driven by his enthusiasm for science, it was inevitable that Norman would achieve the international recognition that he has today as a leader in the field of animal ecology. Now, this book exemplifies his meticulous style of investigation, analysis and inference. It is a personal synthesis of Norman's observations, notes and photographs collected during a rich career involving extensive travels across Africa. Generously integrated with information and ideas from the literature, the book not only reviews African savanna ecology and human evolution, but also articulates an important message for humanity. The message – that it is *only in Africa* that humans could have evolved – is as provocative as it is compelling from the line of reasoning laid out with characteristic rigour in this book.

It all stems from a sequence of unconnected events and circumstances, like an asteroid slamming into a planet. That happens all the time, somewhere in the universe, but when a particularly big one slammed into Earth about 66 million years ago the implications for the biosphere were profound. Non-flying dinosaurs – and many other groups of organisms – quickly died out, opening a game-changing evolutionary opportunity for our mongoose-sized mammalian ancestors. Over the next 60 million years, while the mammals radiated into a diversity of taxa over a widening range of body sizes and trophic niches, plate tectonics moved the continents around and broke them up. Different assemblages developed on different continents that had different shapes and positions on the Earth's crust. By the time the common ancestor of humans and chimpanzees evolved, it occupied a species range in the middle of the big and geologically complex continent we call Africa, positioned squarely over the equator. That was crucial, because climatic cycles caused by the eccentric Earth-around-Sun orbit drove advances and retreats of the equatorial forest, taking 100,000 years per cycle. When the forest advanced, it covered mountains, plains and valleys; when it retreated, it left refugia of montane forest in a matrix of savanna. That forest–savanna ecotone, advancing and retreating at a rate suiting the speciation of large mammals, was the 'species pump' that drove the dramatic radiation of wildlife (as we now view it) in

African savannas. And among those radiating species there just happened to be a bipedal savanna-adapted large primate making its evolutionary appearance in just the right place and at just the right time. It coexisted with perennial supplies of big carcasses to scavenge from, diverse plant communities to gather from, and dry grass and wood to fuel lightning fires that could be weaponised and harnessed, sparking a complex social system.

Such is the sequence of events and circumstances that allowed the highly branched tree of human evolution to take root, and *could only have*, in African savannas, as Norman Owen-Smith explains here. Paradoxically, the biodiversity of African savannas – particularly the megafauna that sustained our ancestral scavengers – is now being shredded by the very species it spawned. This important book, by outlining the unique significance of African savannas for humanity, should leave readers with added resolve to conserve our ancestral habitat.

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Preface

That humans originated in Africa is generally accepted, but this is considered to be a chance outcome, dependent simply on where our common ancestor with the great apes lived. The story that I will develop in the pages of this book is that it is *only in Africa* that the evolutionary transitions from a forest-inhabiting frugivorous ape to savanna-dwelling meat-eater could have occurred. Distinctive features of the ecology of Africa shaped these transitions. They are only partly recognised in the literature on human origins and inadequately covered in textbooks of ecology.

The concept for this book emanated from my awareness that the evolutionary origin of the animals that I studied – Africa's large mammalian herbivores – was coupled in time with the divergence of our earliest human predecessors from the ancestor that they shared with the great apes. Prior to 12 million years ago, during the Miocene epoch, Africa was thronged by a variety of strange beasts, most of them very large and many elephant- or rhino-like, browsing in quite dense woodlands. Monkeys and apes were around in profusion, but adapted especially for a lifestyle in the tree-tops. Following a vague hiatus in the fossil record, the fauna that took shape some 5 million years ago at the start of the Pliocene was radically different. A diverse assemblage of medium-sized ungulates (hoofed mammals) had evolved, many of them adapted for grazing grass rather than browsing tree leaves. The animal that I studied for my doctoral degree, the white rhinoceros (*Ceratotherium simum*), had emerged and other very large herbivores also showed signs of switching towards grass-based diets. Moreover, some of the apes showed adaptations for upright locomotion to traverse widening spaces between the trees, reinforcing evidence of the spread of savanna grasslands. How had environmental conditions changed to foster the contemporaneous evolutions of grasslands, grazers and bipedal apes? I recall while out in the gloom of an African night, brightened by moonlight and a starry milky way, watching a white rhino bull munching grass in the shadows, and noting that one star was moving – a satellite recently placed in orbit. I tried to comprehend the enormous sweep in time covering the transition from the world that generated this primeval-looking animal to the object circuiting the Earth that had been created by the human descendants of certain apes.

The connections were not covered in standard ecology texts because grasses and grazers were not as prominent outside of Africa where the authors lived. Indeed, Africa's savannas were interpreted as formations disturbed by humans from their 'natural' wooded state, through clearing and the promotion of fires. But humans of various forms had inhabited Africa for millions of years and

recurrent fires were a necessary outcome of the accumulation of seasonally dry grass, however ignited. Now, towards the end of my career, there is time to look back and identify the connections that made Africa's ecology different in several ways from that of other continents. Hence this book is basically a compendium of savanna ecology, within which the evolution of the lineage leading to modern humans – to us – is embedded.

Recognition of Africa's distinct features crystallised from the bold claim by geologists that plate tectonics – movements of the continents – were ultimately responsible for the origins of humankind.[1] The ecology of its plants and animals was connected somehow to the physical features of landforms, geology, climate and soils that took shape following the splitting of the supercontinent called Gondwana in the early Jurassic period as far back as 180 Ma. I needed to expand my comprehension by reading into the literature of these other fields of science. The linkages that I recognised are explained in the chapters of this book.

My experiences have made me unusually well-grounded in Africa for this synthesis. During my doctoral research, I walked almost daily following white rhinos while they went about their lives for 3.5 years. Their world was my world – the undulating landforms, soils and plants and how they changed with wet and dry seasons. I shared the dung-heap established by the neighbouring white rhino bull situated conveniently close to the caravan where I lived, parked under a spreading thorn tree. I became fascinated by the patterns formed by plants, particularly the shifts in grass species within a few metres. Having been grounded in this diversity, while furthering my studies in the USA I found it hard to accept that uniform vegetation formations could have existed over vast areas of North America as climax states of closed forest or treeless grassland. Names given to soil types did not capture the links I had discerned between soils, vegetation and where I was most likely to find white rhinos. During my subsequent academic career, my academic horizons became widened to encompass other parts of southern Africa, coupled with visits to parts of the continent further north. Nevertheless, this book inevitably expresses a southern perspective on Africa's ecology.

The book begins with a set of chapters identifying the physical features distinguishing Africa from other continents, forming Part I. They establish that Africa is unusually high-lying, relatively dry, subject to widespread volcanism, has widely varying river flows and lake levels and soils that are unusually fertile for the tropics. Part II covers the ecology of the vegetation, establishing the mechanisms contributing to the predominance of grasses. Part III covers the large mammalian herbivores that are central to the story and have been the focus of most of my academic research along with my students. They establish how the diversity and abundance of medium–large

grazers in particular is founded on features of the grasses, leading into the wider roles of these herbivores in ecosystem dynamics. The chapters forming Part IV place the evolutionary origins and subsequent adaptive transitions of the hominin lineage within Africa's ecological contexts. Finally, I contemplate what the role of Africa's unique biological heritage might be in the future. The broad sweep covered by this book does not allow me scope for delving into detail on any one topic. Hence, at the end of each chapter, I suggest a few publications for further reading in greater depth. The text is supported by a profusion of colour illustrations, largely gleaned from my own travels. Ecology expressed in words can be boring. The images are intended to relate the words to the world beyond.

My focus is specifically on the ecology of Africa's savannas. The ecology of its forests is beautifully covered by Vande Weghe[2] with numerous colour illustrations. That of its southern deserts is treated by Lovegrove and Siegfried.[3] The comparisons I draw with other continents remain superficial, merely noting the features that seem distinctive of Africa. For an ecological perspective on all forms of open ecosystems worldwide, encompassing savannas, grasslands and shrublands, I refer you to Bond.[4]

Many people contributed to my intellectual advancement and hence to this book, in various ways. Rudi Bigalke opened the opportunity for me to study white rhinos under the auspices of the Natal Parks Board, before I became a biologist. John Emlen provided academic guidance into behavioural ecology at the University of Wisconsin, where I arrived to switch fields from chemistry to zoology. Salmon Joubert invited me to study kudus, believed to be centrally involved in spreading anthrax in Kruger Park. John Skinner supported my postdoctoral fellowship through the Mammal Research Institute of the University of Pretoria. Brian Huntley drew me into the South African Savanna Ecosystem programme undertaken in the Nylsvley Nature Reserve and the opportunity provided to move ecology into the computer era, traipsing behind tame kudus. Brian Walker hosted me in the Centre for Resource Ecology at the University of the Witwatersrand and challenged me about how to link behavioural ecology to ecosystem management. Tony Starfield led me into computer modelling, a perspective that has permeated my scientific approach. Wayne Getz expanded this orientation into the metaphysiology of biomass dynamics, linking behavioural responses to their outcomes for population and community processes. Joseph Ogutu inducted me into the statistics of handling big data through model selection while he was a postdoc in my group. Martin Haupt offered me two GPS collars for testing on disappearing sable antelope and opened the field of movement ecology, which stopped me from retiring when I should have. Barend Erasmus, Robyn Hetem, Francesca Parrini and Melinda Boyers joined me in one last team study tagging animals

in the vast Kalahari region of Botswana, which has kept me working on abundant data long into retirement. To my PhD students, I acknowledge how you have widened my knowledge: Susan Cooper, Johan du Toit, Ignas Heitkonig, Peter O'Reagain, Laurence Watson, Mark Vandewalle, Jonas Chafota, Angela Gaylard, Adrian Shrader, Randal Arsenault, Michelle Henley, Kirsten Neke, Joanne Shaw, Valerio Macandza, Joe Chirima and Gabi Teren; plus also the postdocs, belatedly supported by my university: Andrew Kennedy, Joseph Ogutu, Steve Henley, Sander Oom, James Cain, Sophie Grange, Jason Marshal, Yoganand Kandasamy, Jodie Martin, Lochran Traill, Sze Wing Yiu and Melinda Boyers. Marco Anson contributed the original artwork illustrating Chapter 17. Very special thanks go to my life partner, Margie Loffell and our two girls, Trishya and Lynne, who put up with having all of our family holidays diverted to where my students were based in some game reserve.

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Africa is my home continent and I hope that I have adequately conveyed the special features of its ecology to you in the pages that follow. All photographs were taken by the author unless otherwise acknowledged.

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Abbreviations

BCE	Before the Current Era (replacing BC)
CAM	crassulacean acid metabolism
CE	Common Era (replacing AD)
CEC	cation exchange capacity
CV	coefficient of variation
ENSO	El Niño–Southern Oscillation
ESA	Earlier Stone Age
GR	Game Reserve
ITCZ	Intertropical Convergence Zone
ka	thousand years ago
kyr	thousand years
LGM	Last Glacial Maximum, ~20,000 years ago
LSA	Later Stone Age
Ma	million years ago
MAR	mean annual rainfall
MSA	Middle Stone Age
mtDNA	mitochondrial DNA
NP	National Park
NR	National Reserve
SNP	single nucleotide polymorphism
TEB	total exchangeable bases